IMPACTS OF MAN-MADE STRUCTURES ON MARINE BIODIVERSITY AND SPECIES STATUS - NATIVE & NON-NATIVE SPECIES

BY

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Abstract

Coastal environments are exposed to anthropogenic activities such as frequent marine traffic and restructuring, i.e., addition, removal or replacing with man-made structures. Although maritime shipping and coastal infrastructures provide socio-economic benefits, they both cause varied perturbations to marine ecosystems. The ports and marinas receiving a high frequency of international vessels, act as 'hot-spots' for marine invasions. The disturbed and modified habitats found in harbours and ports provide opportunities for non-native species to settle due to their competitive traits. Once established, the non-native species may spread to neighbouring habitats, thereby modifying the adjacent natural environment, its biodiversity, ecosystem structure and functioning.

Up to 70% of coastlines around the world have now been modified and is expected to rise in future. New bioinvasions are still being reported even with various biosecurity and management approaches across the globe. It is essential to understand the potential factors influencing the bioinvasions to have effective biosecurity measures and management plans. The overall aim of this thesis is to determine the influence of man-made structures on the marine biodiversity and presumptive fitness of native and non-native species on these structures. This thesis investigates ports and harbours as man-made environments, their impacts on marine biodiversity and the species status – native, non-native and cryptogenic, and the factors facilitating the spread of non-native species.

Chapter 2 focussed on two large national-scale baseline port surveys; a) Australian Port Survey (APS), and b) New Zealand Port Survey (NZPS). The two datasets were analysed to determine the community structure and species status, i.e., native, non-native and cryptogenic as a function of the surveyed ports, port type (major vs minor ports) (based on the volume of vessels) and latitudinal groups. A) APS: The results for community composition indicated significant effects as a function of surveyed ports, port type and latitudinal group. The community composition was relatively more abundant at major ports than at minor ports. The factor, the latitudinal group indicated significant results, and a distinct separation in community composition was observed between low (15, 20^{o}S) and high (35, 40^{o}S) latitudes. The species status showed a significant and positive relationship between native vs non-native, indicating with an increase in the number of native species there was an increase in the number of non-native species. The species status indicated significant results for the factors; surveyed ports, port type and latitudinal group. The native species were abundant throughout the study.

However, the non-native species were relatively abundant at major ports compared to minor ports. Regarding the latitudinal groups, the abundance of non-native species was observed to increase at higher latitudes (latitudinal gradients). B) NZPS: The community composition and species status showed significance among the 27 surveyed ports; however, no significant results were observed for the factor port type (major vs minor). The community composition significantly varied as a function of latitudinal groups, with species at higher latitudes (45^{o}S) being better discriminator explaining the differences. Latitudinal groups, however, highlighted sub-groupings of ports with similar community composition (e.g. Bluff and Dunedin; Nelson, Wellington and Picton; Lyttelton and Timaru; Whangarei, Tauranga and Taranaki; Auckland, Gulf Harbour Marina and Opua Marina). The ports in question are within close proximity of each other (distance). This suggests the possibility of natural dispersal of species between ports on top of the human-mediated dispersal. The responses in Australia were very different from those in New Zealand, which suggests that the responses are regional or country-specific and not global.

Chapter 3 describes fieldwork using settlement tile arrays to examine the effects of man-made built structures and natural rocky reefs on marine biological community composition and successional patterns over two years. The work also tests the preference of native and non-native species in terms of habitat type (natural reef vs man-made habitat) and substratum type (PVC vs slate tile). The results showed a rapid increase in species settlement on bare tiles as the available bare space was 30% just after 3 months of submersion. The community composition significantly differed as a function of the interaction of factors, habitat × substratum × sample interval. However, differences between the habitat types and substratum types, respectively, were explained by the difference in abundance of the same suite of species. The species were abundant at marina sites compared to reef sites; however, in terms of substrata, the species were abundant on slate (natural) tiles than on PVC tiles.

The succession patterns of species over time (8 sample intervals) showed a similar trend on both the habitat type and substratum type, with differences in the average abundances of each species. The differences in abundances highlight the influence of species dispersal patterns, recruitment patterns and post-settlement processes of species between habitat type and substratum type, respectively. Subsequently, the species status indicated significance as a function of habitat type, substratum type and sample intervals. The cryptogenic species were abundant throughout the study. The cryptogenic species, however, decreased in abundance over time, with an increase in abundance of native and non-native species. Subsequently, the

non-native species significantly varied between habitat type, with relatively higher abundance at marina (man-made) sites compared to reef (natural) sites. However, the non-native species did not show significant variation as a function of substratum type (PVC vs slate). The results are discussed in the context of the recruitment of species on a new barren substrate, and the preference of habitat type and substratum type by native, non-native and cryptogenic species.

In Chapter 4, the reproduction output (gonadosomatic index, GSI) of the Southern hemisphere, native (SH*Mg*) and Northern hemisphere, non-native (NH*Mg*) lineages of the blue mussel, *Mytilus galloprovincialis* were measured. The GSI and shell length of NH*Mg* and SH*Mg* were compared between habitat type; reef (natural) vs marina (man-made) sites. This study aimed to identify reproductive patterns (i.e., timing and magnitude of spawning events) and differences in performance (presumptive fitness) of the native and non-native blue mussel lineages at the natural and man-made habitats. The results for shell length indicated significance for habitat type and no significance as a function of lineage. The mussels were relatively bigger mussels at marina sites compared to reef sites; however, the differences were trivial. The GSI values as a function of habitat type, lineage and sampling time showed a significant difference between habitat type, with high GSI values at reef sites than at marina sites. However, this indicates that the blue mussels at marina sites had comparatively higher spawning activity than at reef sites. The temporal variation of GSI of NH*Mg* and SH*Mg* showed a similar reproductive trend (i.e., spawning and gametogenesis) at both habitats. However, significant spawning activity was observed in July and November when compared between reef and marina habitats. The results are discussed in the context of management implications and strategies regarding the establishment and success of non-native *M. galloprovincialis* lineage and whether their eradication is necessary or even possible.

The findings of this research are summarised and discussed in relation to our understanding of biological community composition and diversity on man-made habitats and the subsequent invasion in the neighbouring natural habitats. This study, from an eco-engineering perspective, highlights the importance of complex habitats and surfaces, and not just material type. However, from a biosecurity and management approach, even though Australia and New Zealand have one of the strong international biosecurity country-specific legislation; the continuous arrival of non-native species in these countries indicates that such marine legislation is not sufficiently compelling on its own. This study highlights the interaction of non-native species at proximity ports, and it provides recommendations towards regional-scale management measures concentrating on intra-coastal transfer of invaders

through domestic maritime traffic or natural dispersal. The life-history traits, recruitment timing and post-settlement processes, plays an essential role in determining long term patterns. Lastly, this research indicated that native and non-native species with ecologically similar responses lead to limited management options to some extent. Therefore, from a manager's perspective, the eradication of non-native species may not be necessary if it does not cause any negative impacts to the biodiversity or the environment.

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Table of contents

List of Tables

List of Figures

CHAPTER 1

GENERAL INTRODUCTION

1.1. Modification of marine ecosystems

Marine ecosystems provide a large number of ecological benefits, including complex habitats for marine biodiversity and socio-economic benefits, including tourism, fisheries, mariculture and trade (Costanza et al. 1997, 2014). More than 40% of the world's population lives along the coastline leading to exploitation of marine resources and altering the coastline by building coastal infrastructures (Dafforn et al. 2015a; Dafforn et al. 2015b). With an increase in the human population, an increase in demand for food and energy production is evident. More than 90% of global trade is dependent on marine shipping routes, resulting in the building of numerous shipping ports and berths on the coasts (Kaluza et al. 2010; Cope et al. 2015). Additionally, natural phenomena such as storms, flooding, erosion, and sea-level rise due to climate change have led to the building of coastal defence structures such as seawalls, groynes and breakwaters (Naylor et al. 2012; Hinkel et al. 2014). Subsequently, the profound changes to the coastlines due to the dominance of man-made structures are called 'ocean sprawl' (Duarte et al. 2013; Firth et al. 2016). This proliferation of 'ocean sprawl' has already modified up to 70% of coastlines around the world and a rise in this percentage can be expected in the future (Bulleri & Airoldi 2005; Dafforn et al. 2015b).

Studies focussing on changes to the biological species assemblage following the changes in habitats have been fundamental in ecology studies. Early studies concentrated on how the man-made structures modify coastal marine communities (Connell & Glasby 1999; Bacchiocchi & Airoldi 2003; Chapman & Bulleri 2003; Moschella et al. 2005). These studies further developed to examine if man-made structures can be surrogates for the natural rocky reefs (Bulleri & Chapman 2010; Perkol-Finkel et al. 2012; Carvalho et al. 2013; Pastro et al. 2017). The results clearly show the alteration of the local habitats as well as local community (Browne & Chapman 2011; Perkol-Finkel et al. 2012; Firth et al. 2013; Serrano et al. 2013). Furthermore, man-made habitats are often shown to support different marine communities compared to natural rocky reefs (Moschella et al. 2005; Perkol-Finkel et al. 2006; Clynick et al. 2007; Lam et al. 2009; Bulleri & Chapman 2010; Airoldi & Bulleri 2011; Chapman &

Underwood 2011; Bulleri & Chapman 2015; Lai et al. 2018). For example, relatively low numbers of individuals (with associated low species diversity), high abundances of early colonisers, opportunistic and non-native species colonised man-made structures.(e.g. Glasby et al. 2007; Vaselli et al. 2008; Dafforn et al. 2009; Bulleri & Chapman 2010; Airoldi & Bulleri 2011; Chapman & Underwood 2011; Firth et al. 2011, 2015; Dafforn et al. 2012; Floerl et al. 2012; Mineur et al. 2012; Bracewell et al. 2013; Airoldi et al. 2015; Pastro et al. 2017). The realisation of facilitation of non-natives due to proliferation of man-made coastal structures has only been relatively recent (Thompson et al. 2002; Airoldi et al. 2005; Chapman & Underwood 2011; Kueffer & Kaiser-Bunbury 2014; Firth et al. 2016; Bishop et al. 2017; Dafforn et al. 2017).

Commercial shipping ports, harbours, seawalls and other man-made structures play an important role in providing suitable habitats 'hot-spots' and act as 'stepping stones' for the introduction of species (Apte et al. 2000; Moschella et al. 2005; Clark & Johnston 2009; Bulleri & Chapman 2010; Dumont et al. 2011; Firth et al. 2013, 2015; Rivero et al. 2013; Firth et al. 2016; Johnston et al. 2017). For example, hard coastal structures along the North Adriatic, Italy (Bacchiocchi & Airoldi 2003; Airoldi et al. 2005) and along the coast of the Yangtze River, China (Ma et al. 2014; Huang et al. 2015) create corridors for species expansion. The high supply of introductions (propagule pressure) at port areas due to receiving marine traffic (e.g. biofouling and ballast water discharge) results in a high probability of successful establishment of non-native species in port areas (Lockwood et al. 2005; Clark & Johnston 2009; Johnston et al. 2009; Lo et al. 2012).

Marine trade around the world is thought to have transported thousands of species through accidental introductions such as ballast water tanks and attachment on ship hulls (Gollasch et al. 2002; Hewitt et al. 2009). Attachment and detachment of species on the hulls of vessels and exchange of large volumes of ballast water holding numerous planktonic species, larvae and egg masses are major marine pathways for marine introductions (Hewitt and Martin 2001; Campbell et al. 2007; Hewitt et al. 2009; Lo et al. 2012). The marine vessels form connectivity pathways linking all the major shipping ports and harbours, thereby exchanging marine species from their native habitat to a new environment (Apte et al. 2000; Wyatt et al. 2005; Clark & Johnston 2009; Clarke et al. 2011; Hopkins et al. 2011a; O'Brien et al. 2017). Marine transport facilitates a steppingstone model for the spread of species by overcoming biogeographical barriers and by providing direct introductions (Adams et al. 2014). Regional domestic marine traffic and recreational boating may then act as a secondary source of non-

native species dispersal within a country (e.g. Forrest et al. 2009; Clarke & Johnston 2011; Hänfling et al. 2011). For example, the non-native tunicate, *Didemnum vexillum*, was first introduced in New Zealand in 2001 and has spread over various harbours and ports on marine vessel hulls and ballast water (Coutts & Forrest 2007).

1.2. Man-made habitat characteristics and impacts

Development of coastal man-made structures has led to the displacement of natural habitats resulting in habitat loss and fragmentation, thereby altering physical, chemical and biological environments (Dugan et al. 2012; Firth et al. 2016; Todd et al. 2019). Man-made structures differ in terms of physical aspects to adjacent natural reefs, factors including structure materials (e.g. wood, plastic, cement) (Andersson et al. 2009; Burt et al. 2009; Chapman & Blockley 2009; Spagnolo et al. 2014; Tan et al. 2015; Cacabelos et al. 2016; Johnston et al. 2017; Albano & Obenat 2019), vertical orientation (e.g. seawalls, breakwaters) (Andersson et al. 2009; Perkol-Finkel et al. 2012; Albano & Obenat 2019; O'Shaughnessy et al. 2019), surface complexity (e.g. smooth flat surfaces) (Perkol-Finkel et al. 2012; Ferrario et al. 2016), movement (e.g. floating pontoons) (Holloway & Connell 2002) and age (newly built structures) (Perkol-Finkel et al. 2006; Burt et al. 2011; Dong et al. 2016). There is growing evidence of non-native species taking advantage of these built structures, which is not the case for local species (Bulleri & Airoldi 2005; Glasby et al. 2007; Tyrrell & Byers 2007; Vaselli et al. 2008; Ruiz et al. 2009; Dafforn et al. 2012; Mineur et al. 2012; Duarte et al. 2013; Airoldi et al. 2015; Ferrario et al. 2016).

Man-made structures may form physical barriers obstructing ecological connectivity (e.g. larval dispersal and movement of mobile species), nutrient flow, altering genetic and trophic connectivity (Moschella et al. 2005; Airoldi et al. 2010; Duarte et al. 2013; Adams et al. 2014; Firth et al. 2016; Moss 2017). Loss of connectivity between species results in biotic homogenisation, thereby altering ecosystem functioning and ecosystem services (Perkol-Finkel et al. 2011; Macdonald & King 2018; Mayer-Pinto et al. 2018a; Mayer-Pinto et al. 2018b). For instance, species with low dispersal potential may fail to overcome physical barriers and settle at short distances, however, with time the genetic diversity decreases resulting in a reduced gene pool (Fauvelot et al. 2009; Sammarco et al. 2012). This limitation of the spread of species to regional scales may lead to changes in the biogeographic ranges of species (Schiel 2011). Construction of offshore structures provides a steppingstone for the spread of species across biogeographical boundaries (Adams et al. 2014). Therefore, it is

essential to evaluate the ecological impacts of man-made structures on the local marine ecosystem at local, regional and national scales (Airoldi, et al. 2005; Ma et al. 2014).

Movement of marine vessels in marinas and the building of new structures along the coast cause physio-chemical disturbances and may affect both the marine biodiversity and the invasibility of communities (Clark & Johnston 2011; Ceccherelli et al. 2014). Physical disturbances can cause sedimentation, displacement of the intertidal community, and provide bare substrata (Guerra-García et al. 2004; Oricchio et al. 2016; Pastro et al. 2017). Studies have shown a subsequent increase in occupancy of bare substratum by non-native species and opportunistic species (Sousa 1979; Paine & Levin 1981; Sousa 1985; Airoldi et al. 2000; Erlandsson et al. 2006). For example, physical removal of seagrass due to anchoring and dredging led to the fragmentation of seagrass habitat, which promoted the spread of the non-native green alga (Ceccherelli et al. 2014). Several manipulative experiments, for example, applying disturbance (e.g. dredging) to reduce the already existing local species cover resulted in the habitat to be susceptible to invasions (Valentine & Johnson, 2003; Airoldi & Bulleri 2011; Clark & Johnston 2011; Bulleri et al. 2016).

The modification of environments may result in changes to biological interactions, distribution of species and ecosystem functioning, at both natural and man-made environments (Bulleri & Chapman 2010; Boström et al. 2011; Knights et al. 2012; Johnston et al. 2017). For instance, limited resource availability can alter prey-predation interactions (Kimbro et al. 2009). Therefore, species-specific interactions and life-history traits of species determine the negative and positive connectivity between lower and higher trophic levels and genetic transfer between species (Boudouresque & Verlaque 2012; van de Koppel et al. 2015; Firth et al. 2017). Ocean sprawl and alteration of natural habitats may cause changes to the energy allocation of species for reproduction, growth or survival (Mayer-Pinto et al. 2018). At disturbed habitats and low resource availability, the species tend to allocate/ exert more energy towards survival and feeding instead of reproduction and growth (reviewed in Bishop et al. 2017). For instance, seawalls exhibit relatively reduced reproductive output of limits with fewer and small egg masses compared to adjacent natural rocky reefs (Moreira et al. 2006). However, it is still not evident if there is a difference observed in the energy exertion by native and invasive species on man-made or disturbed habitats.

1.3. Bioinvasions

Biological invasion, i.e. bioinvasions, in a broad sense, means the movement of local species from their native habitat to a new environment (Olenin et al. 2017). Bioinvasions are ubiquitous and universally accepted as one of the significant threats to marine biodiversity and the global economy (Ojaveer et al. 2015; Gestoso et al. 2017; Olenin et al. 2017; Simpson et al. 2017). Apart from human-mediated spread of species through maritime transport, the species show natural range expansion due to changing global climate (Occhipinti-Ambrogi 2007). With changing climates, the species have been showing anti-equatorial shift, i.e., moving from highly diverse, warm equatorial regions to slightly cooler, less diverse temperate regions (higher latitudes) 'Latitude diversity groups hypothesis' (Darwin 1860; Sax 2001). Biological stresses are important in natural selection and evolution of species (Lockwood et al. 2005). The colder environmental temperatures in the temperate regions may hinder the natural selection processes. However, this is not the case in terms of tropical regions (Currie et al. 2004). The introduction of species in higher latitudes can lead to competition among species (introduced and local species) for habitat and food, change predator-prey interactions or cause co-existence (Shea & Chesson 2002; Jeschke et al. 2012; Marraffini & Geller 2015; Papacostas et al. 2017).

There are many terminological ambiguities around the definition of non-native species. Throughout the invasion process, the species are called 'introduced species', once established they are called exotic, non-native, non-indigenous or alien species. However, when the species causes negative impacts in the marine habitats they are termed 'invasive' or 'unwanted species' but when the species is introduced without causing any adverse effects in the habitat are 'naturalised' species (Lockwood et al. 2005). There have been emerging studies related to 'invasion biology', non-native species and their impacts on the native assemblages and permanent destruction of marine ecosystems where they are introduced (Johnston et al. 2015). Knowledge about mitigation and management approaches towards marine invasions, and human impacts have also been growing in recent years (Moschella et al. 2005; Pyšek & Richardson 2010; Airoldi & Bulleri 2011; Airoldi et al. 2015; Dafforn et al. 2015; Dafforn 2017).

1.3.1. Invasion ecology

Invasion ecology is the study of establishment, spread and ecological impact of species translocated from their natural geographical boundaries (Lockwood et al. 2007). Specific individuals within a species or group of species which are successful colonisers and immigrants that expand their native range are called invasive species. However, not all invasive species

can survive in new environments. The invasive species tend to disrupt the already existing species community therein to affect the species interaction and further poses a threat to the marine ecosystems (Shea & Chesson 2002). Consequently, studies related to biological invasions, also called as 'invasion ecology' has gained much attention to investigating the ecology and evolution of populations and their interactions to maintain the natural ecosystems (Ricciardi 2007).

Elton (1958) first identified biological invasions as an ecological threat, since then ecologists around the world have made efforts to understand the patterns of non-native species, their establishment – successful or failed, spread and impacts on natural ecosystems once established. Considerable progress has been made in understanding the species traits such as life history, genetic and other biological characteristics promoting invasion (Ehrlich 1984; Sakai et al., 2001; Callaway & Ridenour 2004; Snyder & Evans 2006). Recently much work has been focussed on developing methods to predict and even quantify the impacts of non-native species (Hewitt et al. 2009; Ruiz et al. 2011). Invasion ecology thus far could guide managers and policymakers to identify the risks of invaders and undertake appropriate management plans.

To understand and to reduce the impact of invasive species on ecosystem functioning, it is crucial to identify the key mechanisms which contribute to the invasion success of a species. Most of the invasion conceptual framework theories are dependent on factors such as a) human-mediated activities move species overcoming environmental, physical or biological barriers (Campbell & Hewitt 1999; Carlton & Rutz 2005; Hewitt et al. 2009; Ruiz et al. 2011), b) despite the increase in invasive species into novel environments , invasion success is low and variable (Williamson 1996; Sala et al. 2000), c) the number and quality of offspring released into a novel environment i.e. 'invasion pressure' or the 'propagule pressure' is important for the establishment and success of non-native species (Lockwood et al. 2009), d) the traits of non-native species determine the rate of spread and invasion success (competitive abilities, ecological and evolutionary species history), e) biotic interaction hypotheses- 'biotic acceptance' by native species to establishment and coexistence of non-native species, 'competitive release hypothesis' where non-native species are released from competition with the native competitors or no competitors for food and space (Sorte et al. 2010), 'biotic homogenisation' of replacement of native species by non-native species (McKinney & Lockwood 1999), 'biotic resistance' by native species to the establishment of non-native species (diversity-invasibility hypothesis) (Elton 1958), 'invasional meltdown' is where the non-native

facilitates establishment and spread of other non-native species (Simberloff & Von Holle 1999; Simberloff 2006).

1.3.2. Invasion stages

The typical biological invasion process includes steps such as introduction, establishment, spread and impact (Hulme 2006). The non-native species are introduced through human mediation (e.g. shipping) or natural processes (e.g. rafting) from their native environment to a new environment. The invasion through human mediation helps the non-native species to overcome biogeographical barriers (Gribben et al. 2013; Adams et al. 2014). However, once introduced to a new environment, the non-native species must overcome environmental barriers (e.g. temperature, salinity) to the successful establishment (reviewed by Olenin et al. 2017). The probability of the species' successful establishment in a new environment is influenced by the species' life-history traits and the environmental conditions of the receiving habitat (Glasby et al. 2007; Petes et al. 2008; Piola et al. 2009; van de Koppel et al. 2015; Fava et al. 2016; Firth et al. 2017; Purroy et al. 2019). There is evidence of non-native species being relatively competitive and adaptable to harsh and disturbed environments. These competitive and adaptable traits of non-native species help them overcome biological (e.g. predation) and environmental stressors (e.g. turbidity) (Leppäkoski et al. 2002; Bownes & McQuaid 2010; Marraffini & Geller 2015).

Propagule pressure plays an important role in the successful establishment of non-native species, i.e. potential for introduction (Johnston et al. 2009). The 'propagule pressure' includes not only the number of arriving individuals in an area (propagule supply) but also the rate at which they arrive (propagule frequency) (Lockwood et al. 2005). For instance, ports and marinas are areas that are susceptible to invasions due to marine traffic bringing with it increased propagule pressure (e.g. biofouling and ballast water exchange) (Lockwood et al. 2005; Clark & Johnston 2009; Lo et al. 2012). It is often presumed that of the vast number of introductions, only a few introductions are successful (Leppäkoski et al. 2002). However, it is difficult to determine the number of successful introductions and more challenging to quantify the number of failed introductions due to the lag phase, i.e. the time between introduction and spread/ expansion of the non-native species (Mack et al. 2000). This lag phase might last for years or decades due to differences in environmental conditions, genetic factors and habitat heterogeneity (Melbourne & Hastings 2009; Zaiko et al. 2016). For instance, where introductions are relatively frequent, the invasive species may show overall positive effects after establishment, i.e. 'equilibrium state' (Clark & Johnston 2011).

Once a non-native species has established, it may spread at regional levels to new environments (Forrest et al. 2009), i.e. the expansion phase. The spread of the species may be due to domestic, commercial ships or recreational boats and spread may also be via larval dispersal which is highly dependent on larva dispersal potential (Forrest et al. 2009; Fava et al. 2016). Species with a low larval dispersal rate will settle at semi-enclosed ports and harbours and can only spread to regional distances through human mediation (Johnston et al. 2011). Following the successful introduction, establishment and spread of the non-native species, there may be possibilities for negative and positive impacts on the marine ecosystem and economic services (Hänfling et al. 2011; Oliver et al. 2015). For example, a recent meta-analysis reported that 35% of non-native species have a positive impact on other species (Katsanevakis et al. 2014). Many non-native species may facilitate other non-native species which may be harmful, and that can impact the native environment, native species and the economy (Simberloff & Von Holle 1999; Leppäkoski et al. 2002; Hänfling et al. 2011; Simberloff et al. 2013; Oliver et al. 2015).

1.3.3. Non-native species - characteristics and impacts

Most of the non-native species have r-selected life-history traits, where the species have high fecundity, small-sized, have early maturity, competitive, phenotypic plasticity and can live in a novel low-quality environments (Glasby et al. 2007; Petes et al. 2008; Piola et al. 2009; Fava et al. 2016; Purroy et al. 2019). Few experimental studies comparing the native and non-natives and their response to pollution (e.g. metal pollution, turbidity) indicated high tolerance to pollutants and increased non-native species dominance with increased pollution (Piola & Johnston 2008; Crooks et al. 2011; Johnston & Keough 2011). These traits help the non-native species to rapidly colonise the available substratum even in disturbed coastal habitats and thereby contribute to invasion success (Marraffini & Geller 2015). However, the success of their introduction is dependent on the abundances and competitive abilities of native species. For example, there is evidence of relatively less occupancy of native species on man-made structures, i.e. absence of competitors or predators of non-native species, thereby resulting in successful invasion 'enemy release hypothesis' (Shea & Chesson 2002; Bulleri & Airoldi 2005; Glasby et al. 2007; Tyrrell & Byers 2007; Vaselli et al. 2008; Ruiz et al. 2009; Dafforn et al. 2012; Jeschke et al. 2012; Mineur et al. 2012; Duarte et al. 2013; Airoldi et al. 2015; Ferrario et al. 2016; Papacostas et al. 2017).

Studies have suggested that man-made habitats have a negative impact on the adjacent natural habitats especially in terms of modifications to water flow, sedimentation, nutrient

transport, light availability and turbidity (Dugan et al. 2012; Dafforn et al. 2015a; Heery et al. 2018) and native community structure (Byers 2000; Ojaveer et al. 2002; Rodriguez 2006; Browne & Chapman 2014; Airoldi et al. 2015; Tan et al. 2015; Ferrario et al. 2017). Competition for resources and food utilisation between native and non-native species can lead to 'competitive exclusion' of native species as non-native species have high levels of phenotypic plasticity (Griffen et al. 2011). However, with time, displacement/replacement of native species impairs 'biotic resistance' by reducing species diversity, species interactions and alter trophic level (top-down or bottom-up trophic cascades) at natural habitats (reviewed by Johnston et al. 2011; Bulleri et al. 2016; Johnston et al. 2017; Skein et al. 2020). 'Biotic resistance' resulting from an increased number of native species and/or individuals, competition between native and non-native species and/or predation pressure by native species on non-native species may contribute to invasion failure (reviewed by Johnston et al. 2017; Skein et al. 2020). Recent management approaches consider monitoring the performance of the key species at different trophic levels, reduction of key species and alterations in species interactions may aid as predictors of possible invasions as the native species may not support biotic resistance (Bulleri et al. 2016; Skein et al. 2020).

Multiple introductions, i.e., increased propagule pressure, may result in changes to the evolutionary and adaptation processes at genetic levels (Roman & Darling 2007; Hänfling 2007; Hänfling et al. 2011). The multiple introductions influence hybridisation between native and non-native species (Hänfling 2007; Chan & Briski 2017). The increased exchange of alleles makes the non-native more adaptable whereas there are some instances where the hybrid individuals perform better than the parent lineages (Williams & Grosholz 2008; Hänfling et al. 2011; Franscisco et al. 2018). Hybridisation further raises concerns of genotypic displacement of native species by non-native species (reviewed by Geller et al. 2010; Johnston et al. 2011; Saarman & Pogson 2015; Bulleri et al. 2016; Johnston et al. 2017; Skein et al. 2020). Molecular genetic studies have been used for many years to identify the origin, pathways of introductions and interactions of closely related native and non-native species (Daguin & Borsa 2000; Goldstien et al. 2013; Westfall & Gardner 2013; Tay et al. 2015; Gardner et al. 2016; Oyarzún et al. 2016; Larraín et al. 2018). However, the question remains whether the rate of native species displacement increases or decreases with the interbreeding of native and non-native genotypes.

1.4. Management and Mitigation

With changing global climate and the vastness of marine systems, it is difficult to detect, investigate, manage marine bioinvasions, and predict future impacts on the marine environment and economy (Firth et al. 2016). Growing evidence of adverse effects of marine urbanisation and bioinvasions has raised the need for ecologically-driven planning and long-term mitigation and management approaches (Airoldi et al. 2005; Airoldi & Beck 2007; Bulleri & Chapman 2010; Airoldi & Bulleri 2011; Browne & Chapman 2011; Perkol-Finkel et al. 2012; Firth et al. 2014).

1.4.1. Marine port management approaches

The most critical approach in the management of non-native species is to prevent introductions (Hulme 2006). Pre-border, at-border and post-border management measures have been undertaken in different countries around the globe (e.g. Australia and New Zealand). These measures help to reduce successful introductions, establishment and spread of non-native species in the recipient environment (Hewitt & Campbell 2007; Forrest at al. 2009; Hopkins et al. 2011b; Ojaveer et al. 2015). Effective preventive measures are mainly conducted on the human-mediated vectors that may involve ballast water treatments and hull maintenance 'anti-fouling' to avoid propagule pressure (Secord 2003; Hewitt and Campbell 2007; Coutts et al. 2010a, 2010b; Tamelander et al. 2010; Hopkins et al. 2011b. For example, the New Zealand Government developed a preventive management action, Craft Risk Management standard to minimise the arrival and spread of non-native biofouling species through marine vectors (MPI 2014). Such management approaches to limit their spread has been undertaken by many countries and have shown gradual effectiveness (GloBallast 2014 and GloFouling 2017).

The International Marine Organisation's (IMO) International Convention for the Control and Management of Ships' Ballast Water and Sediments" implemented ballast water management plans and recorded the per tank basis onboard mid-ocean ballast water exchange as the intermediate solution (IMO 2017). IMO created the GloBallast and GloFouling programmes that provide training, technical support and help with ballast water management and antifouling methods. However, no international regulations have been established to prevent the regional spread of non-native species through domestic marine trade or recreational boating (Forrest et al. 2009; Sinner et al. 2013; Inglis et al. 2014). There have been management ideas to establish contingency de-ballasting zones to discharge the ballast water safely (Hobday et al. 2002); however, establishing suitable areas for the same is still a struggle. Goldsmit et al.

(2019), examined two alternative de-ballasting zones in eastern Canada through these zones were formed without any scientific ecological assessments. The authors described the locations to be the primary route for marine traffic in the eastern Canadian Arctic, thereby risking the establishment of non-native species at coastal areas (Goldsmit et al. 2019).

New introductions of non-native species are still likely as some introductions go undetected and establish before they are reported (Ruiz et al. 1999; Hewitt et al. 2004; Floerl et al. 2009). It is important to have surveillance or risk-assessment to detect non-native species early on to enable fast and more effective eradication response (Hewitt & Campbell 2007; Gardner et al. 2016; Zaiko et al. 2016). For example, successful eradication of the invasive black striped mussel in Darwin Harbour occurred within 6-7 months of its detection (Willan et al. 2000). However, such successful detection and eradication of non-native species are infrequent (Hopkins et al. 2011a). For instance, eradication programmes of the fouling pest, *Didemnum vexillum*, failed miserably in New Zealand due to its widespread - first recorded in 2001 in Whangamata, North Island after its establishment but quickly spread to the South Island on barges, recreational vessels and moorings (Coutts & Forrest 2007). The attempt to eradicate *D. vexillum* from New Zealand cost NZ$2.2 million (Biosecurity New Zealand 2010). Therefore, cost-effective and timely eradication approaches are necessary for positive ecological and economic impacts. Even though a species has been eradicated, it may be required to have a continuous survey and monitoring of high-risk pests to enable quick detection of re-introductions (Hewitt et al. 2004, de Rivera et al. 2005; Campbell et al. 2007; Brockerhoff et al. 2010; Tobin et al. 2014). Local fishers, local boat owners and commercial vessel operators should be made aware of high-risk marine pest species through educational or awareness programmes (Pollard & Pethebridge 2002).

1.4.2. Marine ecosystem monitoring

In the light of increasing pressures on the marine ecosystem globally, the impacts on the ecological and environmental conditions and the conservation and management of marine biodiversity is a complex issue. Monitoring is a crucial component in marine management; it provides a more consistent spatial and temporal analysis of different chemical, physical and biological parameters in a marine system. These programmes offer integrated knowledge of the current functioning of the ecological systems and the disturbances caused by human impacts. Appropriate evaluations of data can determine the effectiveness of the surveys and monitoring programmes, report key gaps and weaknesses for future monitoring (Miller et al. 2019). The monitoring reports provide scientific advice to the stakeholders and managers to

take adequate conservation planning and successful management measures (Hewitt et al. 2004; Hewitt & Campbell 2007; Ojaveer et al. 2018).

Monitoring programmes' key role is to provide an understanding of community structure (species abundance, species diversity, spatial distribution, species status), the health of the habitat, environmental conditions and socio-economic characteristics and impacts. Different monitoring techniques provide the different type and quality of information. Standardised protocols and consistent survey designs will help achieve the purpose of the surveys (Hewitt & Martin 2001). Baseline assessment of an area provides information about the overall species diversity for temporal and spatial variations in species composition. Species diversity is one of the indicators of the functioning of trophic levels in marine ecosystems. Species diversity affects the top-down (prey-predators) and bottom-up (space and nutrients) interactions which are fundamental in the functioning of marine ecosystems (Paine 1966). Species diversity can be quantified by species richness, species abundances, species composition and species interactions. These assessments provide an opportunity to understand the changes in ecosystems and species diversity due to human impacts. Long-term surveys detect effects of environmental variables on species diversity, composition, abundances and spread of non-native species (Branch et al. 2008; Goldstien et al. 2013). Species-specific surveys focus on a particular species or taxa and its ecosystem functioning; in contrast, high-risk pest surveys concentrate on detection and quantification of high-risk invasive species to form effective management and eradication plans (Hewitt et al. 2004, de Rivera et al. 2005; Campbell et al. 2007; Brockerhoff et al. 2010; Tobin et al. 2014).

Monitoring surveys act as tools to detect invaders and implement rapid management and eradication strategies (Hewitt & Campbell 2007). Early detection is critical for effective control and eradication. Several countries in recent years have adopted national scale surveys to identify the already entered non-native species as well as new arrivals (Simberloff 2003; Olenin et al. 2014; Ojaveer et al. 2016). Monitoring surveys provide a baseline for native and non-native biodiversity, which will further inform about the impacts of invasions on the biodiversity. For instance, nationwide based Australian port surveys with standardised CRIMP protocols and designs aimed to examine the marine biological invasions in Australian waters (Hewitt & Martin 1999, 2001). In addition, the New Zealand government implemented marine biosecurity monitoring strategies focussed on nationwide baseline surveys, New Zealand Port Biological Baseline Survey Marine (NZPS). Development of NZPS led to form monitoring surveys for target species, i.e. High-Risk Site Surveillance Programmes (Woods et al. 2015).

The high dispersal rate of marine species has implications for the geographic distribution and genetic connectivity among marine populations. Therefore, the dispersal potential of various species can be tested using genome divergence patterns. Development of molecular techniques for genetic analyses helps analyse the genetic connectivity among populations (Palumbi 2000). However, the use of molecular tools in invasion ecology have been adopted in recent years (Holland 2000; Ruiz & Fofnoff 2000). The molecular techniques (PCR tools and genetic markers) examine the genetic structure of native and non-native species and their geographic distribution (Ruiz & Fofnoff 2000; Holland et al. 2004; Goldstein et al. 2011). Several molecular studies now are focussing on early detection of non-native species and provide optimal identification of non-native species especially congeners which are morphologically similar to their native species (Darling & Blum 2007; Pochon et al. 2013). Several countries, including the USA, Canada, New Zealand, and Australia have already adopted molecular techniques to survey non-native species and aid management decisions (Geller et al. 2020; Ruis et al. 2015; Zaiko et al. 2015, 2018). For successful monitoring and management plans, it is crucial to have a robust taxonomic foundation. Current limited taxonomic knowledge and decline in taxonomic specialists are a big concern to have effective monitoring and management programmes. Misidentification of introduced species may lead to cryptic invasions, and most of the non-native species remain unnoticed. Molecular analyses, together with large-scale surveys, form the basis of rapid and effective monitoring programmes, however, are costly and time-consuming.

1.4.3. Mitigation approach - Eco-engineering

Human-mediated vectors are mostly responsible for initial transport of non-native species from their native ranges, whilst anthropogenic urbanised habitats facilitate invasion success, establishment and further spread (Mineur et al. 2012; Airoldi et al. 2015; Johnston et al. 2015; Ferrario et al. 2017). Recent management attention has focussed on re-designing and engineering coastal structures to have multifunctional uses, i.e. benefit ecosystems and economic services via 'eco-engineering' or 'green engineering' (Chapman & Underwood 2011; Dafforn et al. 2015; Morris et al. 2019). Marine urbanisation and bioinvasions are ubiquitous and are predicted to increase in the coming years. Studies adopting eco-engineered coastal structures have revealed enhanced habitats and enhancing the biodiversity of different functioning species groups (Morris et al. 2017, 2019; Strain et al. 2018). Hence, there is a strong argument to focus on the design of the structures not just to enhance assemblages but to target specific species or taxa (Correia et al. 2013). For example, increased micro-habitats on

seawalls reduced fish predation on native mussel species (Strain et al. 2018b) and reduced shading improved native species growth (Dafforn et al. 2012). Studies have shown increased colonisation of benthic encrusting species such as algae, barnacles, mussels and oysters to promote a 'bioprotective effort', i.e. contributing to the structure's stability and longevity. For instance, to increase protection against extreme environmental conditions, e.g. fluctuating temperature or wave action (Coombes et al. 2013; Coombes et al. 2015). Another factor to consider whilst re-assessing man-made structures and the ecological processes that occur on them is to preserve the natural marine biodiversity (Perkol-Finkel et al. 2012; Dafforn et al. 2015). An increase in native biodiversity will facilitate enhanced biotic resistance and may help to reduce or avoid invasions, i.e. 'bio-control' (reviewed by Johnston et al. 2017; Skein et al. 2020).

Increased complexity on the surfaces of coastal man-made structures such as the addition of rockpools, crevices, and cracks provides refuges for organisms, thereby increasing biodiversity and modifying community structure (Moreira et al. 2007; Chapman & Blockley 2009; Loke et al. 2014; Loke & Todd 2016; Morris et al. 2019). Addition of overhangs or flowerpots increased species assemblage by 65% out of which 25 species were not previously observed (Browne & Chapman 2011). Engineering of cost-effective hybrid structures such as revetments, tetra-pods, and geo-tubes can provide substrata where natural habitats have declined (Moschella et al. 2005; Chapman & Underwood 2011; Browne & Chapman 2014; Firth et al. 2014; Loke et al. 2014). For example, the endangered seahorse, *Hippocampus whitei* inhabits specially designed eco-engineered artificial habitats' Seahorse Hotels' in Port Stephens, New South Wales, Australia due to significant decline in natural habitats (Simpson et al. 2019). The field of eco-engineering requires stakeholders, engineers and scientists to work together and produce new strategies for the design and deployment of coastal structures that will reduce the opportunities for non-native species (Dafforn et al. 2009; O'Shaughnessy et al. 2019).

To summarise, it is well established that marine built systems have a negative impact on marine biodiversity and facilitate non-native species (Bulleri & Chapman 2010; Airoldi & Bulleri 2011; Chapman & Underwood 2011; Clark & Johnston 2011; Firth et al. 2011, 2015; Dafforn et al. 2012; Airoldi et al. 2015; Firth et al. 2016; Dafforn et al. 2017; Bishop et al. 2017; Pastro et al. 2017). High introduction rates of non-native species at port areas through marine traffic have resulted in the spread of non-native species from port to port, and also to natural (i.e., not modified by human activities) areas. International and domestic shipping plays

a vital role in transporting non-native species at regional to national scales (Hewitt, 2002; Lockwood et al. 2005; Clark & Johnston 2009; Johnston et al. 2009; Ruiz et al. 2011; Lo et al. 2012). For example, the economies of Australia and New Zealand are dependent on international maritime trade (Piola & McDonald 2012). With their unique coastlines and given the high levels of endemism amongst Australia and New Zealand's marine biota, many preventive marine biosecurity and management strategies have been developed and implemented by both countries to control marine invasion risks (Hewitt & Campbell 2007; DoE 2015; DAWR 2017, 2019; MPI 2018). However, there is no infallible solution to the invasion problem.

The first major step before attempting to control the introduction and spread of non-native species is to determine the current distribution and abundance of non-native species (Hewitt & Campbell 2007; Coutts & Forrest 2007; Kaiser & Burnett 2010; Simberloff et al. 2013). Surveys at heavily disturbed and modified port areas help keep a record of the native species present and to detect non-native species so that further action (e.g., eradication or containment) may be carried out. It is necessary to understand better how such non-native species may respond to challenges raised by the ongoing development of the built environment at local, regional and national scales. Baseline monitoring surveys are critical to answer such questions, which will help planners and managers better understand how built structures in heavily developed areas such as ports influence native biodiversity, contribute to bioinvasions and modify the health of the marine environment. Increased maritime traffic with the proliferation of construction of marine harbours, ports, seawalls, and breakwaters along the coasts raise the risk of bioinvasions and its subsequent spread (Floerl et al. 2009; Seebens et al. 2013). Bioinvasions can lead to devastating and unforeseen impacts on new environments. The effect of marine built systems on marine biodiversity and determining the influence on native and invasive species is increasingly important. In this thesis, I will investigate the ports and harbours as man-made environments, their impacts on the marine biodiversity with regard to the species status – native, non-native and cryptogenic – and the factors facilitating the spread of non-native species.

1.5. Thesis aim and objectives

The general aim of this thesis is to determine the influence of man-made structures on ecosystem structure and function in natural and man-made habitats with regard to native and non-native species. Whilst there has been quite a bit of this sort of work done around the world, there has been very little done in New Zealand. This study focusses on marine biology and invasion ecology but extends into biosecurity and conservation. The potential impact of this thesis will be as a contribution to new knowledge about the marine built environment, thereby supporting management decisions to improve marine coastal environmental health and eco-engineering of modified habitats.

The following objectives were developed to provide a more specific indication of the purpose of this research:

1) To assess community composition with regard to species status - native, non-native and cryptogenic species in Australian ports and New Zealand ports, and how this varies between ports as a function port type (major vs minor ports) and latitudinal groups.
2) To evaluate the effect of natural and man-made substrata (PVC vs slate tiles) and habitat type (marina vs reef) on the ecological successional patterns (temporal variation of species) and presence of native, non-native and cryptogenic species.
3) To assess if/how natural and man-made habitats influence energy allocation to reproductive output and reproduction patterns by two closely related congeneric blue mussels, native (SH*Mg*) and non-native (NH*Mg*) lineages.

1.6. Chapter outline and hypothesis testing

Chapter 1 is a general literature review, to help set the scene, and to make clear the state of knowledge. As such, there is no hypothesis testing in this chapter.

Chapter 2 focusses on two large nationwide datasets to observe and interpret patterns of distribution of species status - native, non-native and cryptogenic species. Also, to understand the potential impacts on the marine biodiversity as a correspondence between ports, port types (major vs minor ports), latitudinal and longitudinal groups. The analyses were performed on presence/absence data for community composition and frequency data for species status (i.e. tally of the presence of species as per their status-native, non-native and cryptogenic). The data was analysed to observe patterns of species composition and species status as a function of ports, port type and latitudinal groups. The results obtained in this chapter will help highlight the patterns of distribution of species status and help understand the impacts on the marine biodiversity as a correspondence between ports, port types (major vs minor ports), and latitudinal and longitudinal groups. The patterns observed in this study among ports, port types and latitudinal groups will help managers to take cost-effective measures to analyse the impacts of the target (i.e. high occurring/contributing) non-native species and their spread with respect to the above-stated factors.

A. Australian port survey – a national port survey program commissioned by the Australian Association of Port and Marine Authorities (AAPMA) and carried out by the CSIRO Centre for Research on Introduced Marine Pests (CRIMP) in 1995. This program aimed to report the occurrences of non-native species in Australian ports. Identification of non-native species at the national level will help understand the spread of the non-native species from port-to-port at a local, regional and national scale.

I hypothesised that;

H_1: Occurrences of non-native and cryptogenic species will be relatively greater at major commercial ports than at minor ports because of increased international marine traffic at the major ports.

H_2: Frequencies of non-native and cryptogenic species increases with an increase in latitude (15-40°S) as there is evidence of high invasibility at temperate climates compared to tropical climates.

B. New Zealand Port Biological Baseline Survey (NZPS), New Zealand Government initiated a nationwide biological baseline survey in 2000 at 13 international shipping ports and 3 marinas in New Zealand. The principle aim of this survey was to record the native, non-native and cryptogenic species in New Zealand port areas and to identify new invasions.

I hypothesised that;

H_1: Occurrences of non-native and cryptogenic species will be relatively greater at major commercial ports than at minor ports because of increased international marine traffic at the major ports.

H_2: Frequencies of non-native and cryptogenic species increases with an increase in latitude (35-45°S) because there is evidence of high invasibility at temperate climates compared to tropical climates.

Chapter 3 aimed to compare the ecological successional patterns (temporal variation of species), community composition and species status (native, non-native, cryptogenic) in both natural and man-made habitats (marinas vs reefs) using natural and man-made substrata, i.e., settlement tiles (PVC vs slate). This study was carried out in Wellington Harbour at 3 marinas (man-made habitat) and 3 neighbouring rocky reef sites (natural habitat). The data of this experimental study compares the differences in community structure and status of the species, at the natural and man-made habitats/substrata. Results highlight the settlement preferences of native, non-native and cryptogenic species for habitat and substratum types, and differences in community structure on natural and man-made substrata/habitats.

I hypothesised that;

H_1: Community composition at man-made habitat (marina) is less diverse than at adjacent natural habitat (rocky reef).

H_2: Community composition on the man-made substratum (PVC) is less diverse than that on the natural substratum (slate).

H_3: Non-native species are more abundant at the man-made habitat and on man-made substratum relative to natural habitat and substratum.

Chapter 4 aimed to compare the reproductive timing and output of the closely related native and non-native blue mussels, *Mytilus galloprovincialis* (invasive North hemisphere lineage; native Southern hemisphere lineage) by analysing the gonadosomatic index (GSI) of mussels

to determine the energy expenditure and changes in reproductive patterns at natural (reef) and man-made habitats (marinas). I also measured mussel shell length (size), Molecular assays were employed to distinguish the native and non-native species, and estimates of GSI helped determine the timing of gametogenesis and spawning events, as well as the energy invested into reproduction, for the two lineages. This study was carried out for a year to examine an entire reproduction cycle. Fieldwork was conducted at 3 marina sites (man-made) and 3 neighbouring rocky reef sites (natural) in Wellington Harbour, which is a semi-enclosed harbour receiving high volumes of commercial shipping traffic and highly developed coastline. The output of this chapter will help understand the impact of man-made structures on the performance of native and non-native species and if these structures facilitate the non-native species.

I hypothesised that;

H_1: Mussels on natural habitat will have a greater reproductive output (GSI) than those on man-made habitat

H_2: NH*Mg* will have greater reproductive output on man-made habitat than on natural habitats.

H_3: SH*Mg* will have greater reproductive output than NH*Mg* on natural habitats.

Finally, **Chapter 5** summarises the thesis findings and the analyses carried out for this study whilst answering the research objectives. I further explain the significance of my findings, the contribution my work makes to biosecurity science and management decision making, and I present specific recommendations to improve the changing habitat which impact the marine biodiversity. I conclude by addressing the limitations of this study and by reviewing future research that may build on my research.

CHAPTER 2

PORT AREAS AS INTRODUCTION FOCI FOR NON-NATIVE SPECIES

2.1. Background

2.1.1. Marine shipping and port pressures

The 21st century is known as the era of globalisation (Ehrenfeld 2003). Global interactions facilitating marine trade has transported thousands of species from their native regions around the world has immensely increased, and a future rise is expected (UNCTAD 2014), this raises the risk for a high volume of marine introductions. Transport of marine organisms associated with ships' hull and ballast water is the primary source of vessel-based introduction of non-native species (Hewitt & Campbell 2007; Hewitt et al. 2009; Seebens et al. 2016; Ziako et al. 2016; O'Brien et al. 2017). Inglis et al. (2016) reported that more than 65% of 187 non-native species in New Zealand arrived as biofouling on international vessels.

Furthermore, regional domestic trade, cargo vessels or pleasure crafts 'intra-coastal shipping' transfer the non-native species from major shipping port areas to minor port/marinas (Forrest et al. 2009; Clarke & Johnston 2011; Hänfling et al. 2011). The ports are classified into major and minor ports as per the annual cargo volumes. Major commercial ports manage at least 1 million tonnes whilst minor ports operate annual cargo volume of fewer than 1 million tonnes (Department for Transport Statistics United Kingdom 2016). There is evidence of relatively higher densities of non-native species at major commercial ports (e.g. San Francisco and Los Angeles) (Foss et al. 2007). With major ports being the focal point of entry for international vessels, it is also a focal point of transfer of non-native species to minor ports and marinas (Floerl et al. 2009; Firth et al. 2016; Olenin et al. 2016; Johnston et al. 2017).

The disturbed environment and modified substrata that harbours provide might be less attractive for native species; however, it provides opportunities for the non-native species to settle on 'unoccupied spaces' and proliferate (Johnston & Keough 2002; Dafforn et al. 2015; Olenin et al. 2016). The high supply of introductions, i.e. propagule pressure at port areas due to receiving marine traffic results in a high probability of successful establishment of non-native species in port areas (Lockwood et al. 2005; Johnston et al. 2009; Clark & Johnston 2011; Lo et al. 2012; Seebens et al. 2016; O'Brien et al. 2017).

Another aspect to consider the successful invasion is the suitability of environmental conditions of the receiving habitat (Lockwood et al. 2005; Petes et al. 2008; Piola et al. 2009; van de Koppel et al. 2015; Fava et al. 2016; Firth et al. 2017; Purroy et al. 2019). There is evidence of anti-equatorial and latitudinal shifts in species' distributions due to changing global climate (Herbert et al. 2007; Keith et al. 2011; Poloczanska et al. 2016). For example, Occhipinti-Ambrogi (2007) highlighted the range expansion of non-native species due to increasing water temperatures. It is evident from early studies that the tropics have a greater level of species diversity than temperate or polar climates 'Latitudinal diversity groups' (Darwin 1860). Diverse species interactions may reduce invasion success into species-rich compared to species-poor areas (e.g., Sax 2001; Freestone et al. 2013). However, this is not the case in higher latitudes, where studies have indicated relatively lower species diversity (Sax 2001). Thus, marine shipping carrying trade from lower to higher latitudinal regions may pose more risk of bioinvasion at high latitudes (Hewitt, 2002; Ruiz et al. 2011). However, the success of invaders also depends on their life-history traits and species interactions (Shea & Chesson 2002; Jeschke et al. 2012; Marraffini & Geller 2015; Papacostas et al. 2017).

2.1.2. Biosecurity strategies

Management of spread of non-native species is problematic due to the complex marine ecosystems (Rilov & Crooks 2009). Once the non-native species have established, it is challenging to eradicate the invader (Kaiser & Burnett 2010). Early detection and timely eradication measures prove as a successful management approach (Ricciardi et al. 2017). Numerous international, national and regional agreements and regulations have been adopted by many countries to minimise the spread of non-native species (Lehtiniemi et al. 2015). Australia and New Zealand, for example, have established among the world's strongest biosecurity and management measures, i.e. a comprehensive pre-border, at-border and post-border management responses (Hewitt & Campbell 2007; Ojaveer et al. 2015). Australia and New Zealand Environment and Conservation Council (ANZECC), reported introduced non-native species as one of the key threats to the biodiversity. The International Maritime Organisation (IMO), introduced many policies and management guidelines to avoid the introduction of non-native species through ballast waters and biofouling on shipping vessels (IMO 2017).

Ballast water loaded in other countries are not allowed to discharge waters in national territorial waters without permissions and permissions are granted to those vessels which have evidence of the mid-ocean ballast exchange and should follow guidelines to manage ballast

water under the Biosecurity Act. New Zealand is one of the few countries in the world to have specific topics of legal legislation for biosecurity control “an act to restate and reform the law relating to the exclusion, eradication, and effective management of pests and unwanted organisms” known as the ‘Biosecurity Act 1993’. Regarding Australia, ‘Biosecurity Act 2015, replaced the Quarantine Act 1908 and aims to strengthen and manage the existing framework for biosecurity risks "managing diseases and pests that may cause harm to human, animal or plant health or the environment" in Australia. Therefore, to eradicate the biofouling issue, frequent hull maintenance and cleaning are required, and vessels with evidence of biofouling maintenance and record books are allowed into national-territorial regions (Ministry of Primary Industries 2018; Australian Government Department of Agriculture and Water Resources 2019). Recreational vessels posing risks on intra-coastal species transfer are required to follow Craft Risk Management Standard (CRMS) and IMO guidelines (i.e. Biofouling Management Plan and BioFouling Record Book) (MPI 2014; IMO 2015).

The NZ’s Ministry of Fisheries and Australian National System for the Prevention and Management of Marine Pest Incursions are a government-controlled institution which deals with rapid detection and management of non-native species with this many regional councils also hold responsibilities regarding introduction management (Wotton & Hewitt 2004).

2.1.3. Monitoring strategies

To have effective biosecurity measures, it is crucial to have accurate identification of species, i.e., native, or non-native species. For example, the invasive northern Pacific seastar, *Asterias amurensis,* was misidentified as a native species for nearly 10 years (Wotton & Hewitt 2004). Some introductions go unnoticed leading to cryptic invasions. Therefore, to apprehend these challenges, there is a need for extensive surveillance and monitoring for non-native species (Hewitt & Campbell 2007; Kaiser & Burnett 2010; Zaiko et al. 2016; Ricciardi et al. 2017). Early detection of the invasive species (non-native species which have adverse impacts on the environment) enables the managers to take effective eradication response (Hewitt & Campbell 2007; Gardner et al. 2016; Zaiko et al. 2016). However, managers are often faced with technical and financial constraints to undertake extensive monitoring surveys (Hewitt & Martin 2001; Campbell et al. 2007). To overcome this problem, prioritising harbours to monitor non-native species can be of great importance (Peters et al. 2017). As stated earlier, harbours as port areas (vessel berths) are ‘hotspots’ for bio-invaders and can serve as the perfect invasion study areas.

The last decade has seen an immense increase in harbour surveys all around the world to record non-native species (Pollard & Pethebridge 2002; Campbell et al. 2007; Russel et al. 2008; Inglis et al. 2016; Woods et al. 2018). Harbour surveys attempt to establish an optimal sampling design to increase the species detection ability to form baseline records of the presence of species and help monitor the spread of non-native species (Campbell et al. 2007). The baseline surveys can feed into risk assessments as a tool to monitor the introductions, whether it be species, pathway or vectors. The assessment of baseline surveys has given rise to many cost-effective nationwide surveillance programs targeting high-risk pest species whereas only a few focussed on the underlying factors influencing the introductions of non-native species (Campbell et al. 2007; Woods et al. 2018). The first step at risk assessment is species-specific assessments to identify the potential of the introduced species to cause harm to the environment or economy (Andersen et al. 2004; Pyšek & Richardson 2010; Hayes et al. 2019). The species attributes such functional traits (e.g. grazers, predators) and native biodiversity may help understand the invasion success (Hayes et al. 2019). However, this is a difficult task to practice due to complex species interactions (Simberloff 2006) and are rarely explored in monitoring surveys.

The above-stated text gave an overview of human-mediated bioinvasions, and the strategies developed to manage their spread. Baseline port surveys provide a comprehensive record of the presence of non-native species on a site-by-site basis. However, the evaluated reports of port surveys have only highlighted the high-risk pest species and the need for further surveillance and eradication response (Inglis et al. 2006, 2008 MPI Technical Reports). Rarely do they consider the factors promoting invasions, whether it be the suitability of habitats or native biodiversity. For this reason, I have used Australian Port Survey (APS) and New Zealand Port Biological Baseline Survey (NZPS) as base datasets to identify the factors promoting the spread of non-native species at local, regional and national scale across the port areas. The two-port surveys (APS and NZPS) have covered numerous ports; major commercial and minor shipping ports and ports expanding across latitudinal groups. This study provides separate comparative analyses on presence/ absence data across all surveyed ports in APS and NZPS. The frequencies of species status, i.e., native, non-native and cryptogenic species will be indicated as a function of the port type (major vs minor ports) and latitudinal groups.

2.1.4. Port Surveys

A. Australian Port Survey

In 1995, the Australian Association of Port and Marine Authorities (AAPMA) and the CSIRO Centre for Research on Introduced Marine Pests (CRIMP) commenced a national port survey program to collect a baseline dataset of the introduced species in Australian ports and the threat they pose. This program went on for 10 years and was conducted at 39 Australian ports to form a baseline dataset of the introduced species across Australia including Tasmania. The ports were selected based on commercial shipping facilities, non-commercial facilities and adjacent areas outside ports.

The baseline survey aimed to define the distribution of non-natives in Australia (Hewitt & Martin 1999, 2001). The results of the APS were further entered into a National Port Survey Database (Hayes et al. 2019). The survey was designed by Hewitt & Martin, 1996, 2001 to cover most of the habitats within each port with replicated sampling. Even though this survey was designed to detect non-native species, information of native and cryptogenic species within ports was also provided. This protocol was later adopted by various other countries such as GloBallast programme undertaken countries South Africa, Brazil, China, India, Iran, Ukraine and some to form baseline surveys at a larger scale; Australia, New Zealand, USA, Scotland, Ireland, Guam and Chile (see Campbell et al. 2007). A complete list of the survey methods adopted to form 'CRIMP protocols' is given in section C (Table 2.1). The species were identified and categorised as native, (resident species), non-native (non-resident/ invaded invasive species) and cryptogenic (species whose status is unclear) by various specialised taxonomic experts and scientists in Australia.

The Australian Port Survey dataset the Australian dataset was provided to me by my co-supervisors Prof Chad Hewitt and Prof Marnie Campbell. However, due to some inadequacies in the dataset with regards to presence/ absence data in each port. The ports with less than 5 species listed in the dataset were eliminated. Analyses were carried out on 27 ports out of the 39 ports for my study. Individuals with only genus name and missing species name were excluded to keep the dataset consistent which resulted in 70% deletion of unknown cryptogenic species.

B. New Zealand Port Biological Baseline Survey (NZPS)

In 2000, the New Zealand Government, encouraged by the International Maritime Organisation (IMO), funded a comprehensive five-year (2000-2005) biological baseline survey programme

called the 'New Zealand Port Biological Baseline Surveys (NZPS)' to identify non-native species in port areas. National Institute of Water and Atmospheric Research Ltd (NIWA) was commissioned to carry out the baseline surveys (and the resurveys) at commercial shipping ports (13) and marinas (2) in New Zealand (Table 2.2.2). The principal aim of the NZPS was to form an inventory of native, introduced and cryptogenic species present in New Zealand ports. In 2010, the Ministry of Primary Industries (MPI) and NIWA made the port survey dataset available to the general public. Moreover, this baseline survey provided a preliminary inventory of native and non-native species in New Zealand ports. The NZPS datasets were acquired from the Biosecurity New Zealand Technical Papers available at https://www.marinebiosecurity.org.nz/ (Inglis et al. 2006, 2008).

The sampling methods used were based on the CSIRO Centre for Research on Introduced Marine Pests (CRIMP) protocols developed by Hewitt & Martin (1996, 2001) for Australian port surveys. The list of surveys methods is given in section C (Table 2.1). MAF Biosecurity New Zealand funded NIWA and Marine Invasive Taxonomic Service (MITS) to provide with species-level identification of collected species and management of the specimens. Each identified sample was further categorised as native species, non-indigenous species (NIS), cryptogenic species 1 (previously recorded as cryptogenic in New Zealand), cryptogenic species 2 (recently reported in New Zealand), and species indeterminate (not identified to species level). However, in this study, cryptogenic 1, cryptogenic 2 and species intermediate were grouped as cryptogenic species.

C. Overview of the sampling 'CRIMP protocols'

The 'CRIMP protocols' (Hewitt & Martin, 1996, 2001) were first designed for Australian Port Surveys which was which were later adopted by more than 15 countries including New Zealand (Campbell et al. 2007). The surveys were designed to determine distribution and abundance of target species, baseline assessment of native, introduced and cryptogenic species. The surveys concentrated on specific sites at port areas (e.g. harbours) and adjacent harbour areas that are most likely to be invaded. Samplings were carried out by consistent qualitative and quantitative methods in marina areas, on wharf piles by scraping method (0.10 m^2 quadrats were fixed at -0.5 m, -3 m and -7 m below the surface). Visual surveys by divers, sediment corers and cyst identification, beam trawl/benthic sledge, traps, plankton and drop nets at various habitats as explained in Table 2.1.1. (see Hewitt & Martin, 1996, 2001 for detailed methodology).

However, for this study, samples from 'Quadrat scrapping' were analysed to be consistent with the theme of the thesis, which is dealing with the impacts of man-made hard substrata.

Table 2.1.1. Sampling methods for port surveys as per CRIMP protocols (Hewitt & Martin 2001).

Sampling Technique	Taxa	Sampled habitats				
		Soft substrate	Hard substrate	Seagrass/ algal bed	Plankton/ nekton	Beach wrack
Small core	dinoflagellate cysts	X				
Large core	benthic infauna	X		X		
20 µm plankton net	dinoflagellates				X	
100 µm drop net	zoo/phytoplankton				X	
Traps	crab/shrimp	X	X	X	X	
Qualitative visual survey	macro biota	X	X	X		X
Quadrat scraping	**sedentary/encrusting**		**X**			
Video/ photo transect	sedentary/encrusting	X	X	X		
Beam trawl/benthic sledge	mobile epifauna	X		X		
Poison station	fish	X	X	X	X	
Beach seine	fish/mobile epifauna	X		X	X	

2.1.5. Limitations of large surveys

Large datasets are formed by passive surveillance strategies, i.e. quantifying single occurrences of species; however, depending on the environmental conditions and experimental strategy, the species can settle selectively. Detection, identification of small or initial stages of an organism and can lead to cryptic invasions. It is also important to consider similar sampling methods at each sampling areas to have a fair interpretation of the study.

Current surveillance programmes are conducted with preliminary taxonomic identification based on morphology instead of molecular techniques, very few taxonomic experts, time-consuming and costly (Bishop & Hutchings 2011). Such inadequacies in surveillance and monitoring programmes can hinder the processes of well-developed biosecurity and management approaches to restrict invasions (Peters et al. 2017). Lastly, carrying out large-scale surveys and monitoring studies are a costly affair. For instance, New Zealand's species-specific survey for detection of 7 high-risk species (green alga *Caulerpa taxifolia*, northern Pacific seastar *Asterias amurensis*, Mediterranean fan worm *Sabella*

spallanzanii, European green crab *Carcinus maenas*, Chinese mitten crab *Eriocheir sinensis*, Asian clam *Potamocorbula amurensis* and clubbed sea squirt *Styela clavannually*) cost annually approximately NZ $2 million (Arthur et al. 2015).

This study aimed to examine the community composition and spatial patterns of species with regard to species status – native, non-native and cryptogenic as a function of the surveyed port, port type, and latitudinal groups. These variables act as predictor factors to describe the spread patterns of non-native species among Australia and New Zealand ports, respectively. I hypothesised that; 1) occurrences of non-native and cryptogenic species will be relatively greater at major commercial ports than at minor ports due to high levels of international marine vessels berth at commercial ports may carry invaders, and 2) frequencies of non-native and cryptogenic species increases with an increase in latitude because there is evidence of high invasibility at temperate climates compared to tropical climates.

2.2. Methods

2.2.1. Data analysis

A. Australian Port Survey (APS)

A total of 39 ports across Australia were surveyed for the Australian port baseline survey (Figure 2.2.1) with 4 major and 23 minor shipping ports. The ports used for analyses in this study are listed in Table 2.2.1. Australian latitudinal scale ranges from 43.0 to 12.46°S, and longitudinal scale ranges from 13.66 to 153.61°E. The dataset was assessed to observe and interpret patterns of distribution of species status - native, non-native and cryptogenic. And, to understand the potential impacts on the marine biodiversity as a correspondence between surveyed ports, port type (major vs minor ports), and latitudinal groups.

The APS surveyed a total of 39 ports; however, ports with low replicates and ports with species number less than 5 indicated in the provided dataset were rejected from the analyses to avoid underlying outliers. The data for the sampling method ‘Quadrat scrapping’ was used to analyse the hypotheses for this study. The presence/absence data rather than abundance were used as recommendations of severe transformations are required for species communities where rare species are present, otherwise may be lost between more common species (Clarke and Warwick 2001). Also, there were inadequacies in the abundance data of the species provided.

The data analyses were performed on 27 ports as a function of the surveyed port. The number of replicate sampling (sampling effort) varied across all surveyed ports. The dataset

with replicates (presence/absence) was further averaged for each port to analyse the community composition and species status (native, non-native, cryptogenic) for the factors; port type (major vs minor) and longitudinal groups. This standardisation approach was undertaken to eradicate the bias caused due to the different number of replicate sampling (sampling effort) (Table 2.2.1) conducted at each port.

Table 2.2.1. Ports sampled for the Australian Port Surveys with latitudinal and longitudinal groups, port type, and replicates (sampling effort).

Ports	Latitude	Longitude	Port Type	Replicates
Abbot Point	19° 53' S	148° 50' E	Minor	16
Adelaide	34° 47' S	138° 30' E	Major	66
Albany	35° 20' S	117° 54' E	Minor	59
Bunbury	33° 18' S	115° 39' E	Minor	52
Burnie	41° 30' S	145° 54' E	Minor	44
Devonport	41° 11' S	146° 21' E	Minor	22
Eden	37° 94' S	149° 56' E	Minor	31
Esperance	33° 52' S	121° 53' E	Minor	60
Fremantle	32° 30' S	115° 44' E	Major	250
Geelong	38° 70' S	144° 23' E	Minor	41
Geraldton	28° 47' S	114° 36' E	Minor	21
Gladstone	23° 50' S	151° 35' E	Minor	100
Hastings	38° 18' S	145° 13' E	Minor	18
Hay Point	21° 13' S	149° 20' E	Minor	44
Hobart	42° 52' S	147° 20' E	Major	106
Lady Barron	40° 12' S	148° 14' E	Minor	17
Launceston	41° 26′ S	147° 80′ E	Minor	78
Lucinda	18° 31' S	146° 21' E	Minor	18
Mackay	21° 80' S	149° 15' E	Minor	25
Melbourne	37° 49' S	144° 55' E	Major	135
Mourilyan	17° 37' S	146° 70' E	Minor	12
Newcastle	32° 55' S	151° 47' E	Minor	86
Port Hedland	20° 19' S	118° 36' E	Minor	52
Port Lincoln	34° 44' S	135° 56' E	Minor	45
Portland	38° 20' S	141° 36' E	Minor	15
Townsville	19° 15' S	146° 50' E	Minor	45
Weipa	12° 40' S	141° 52' E	Minor	18

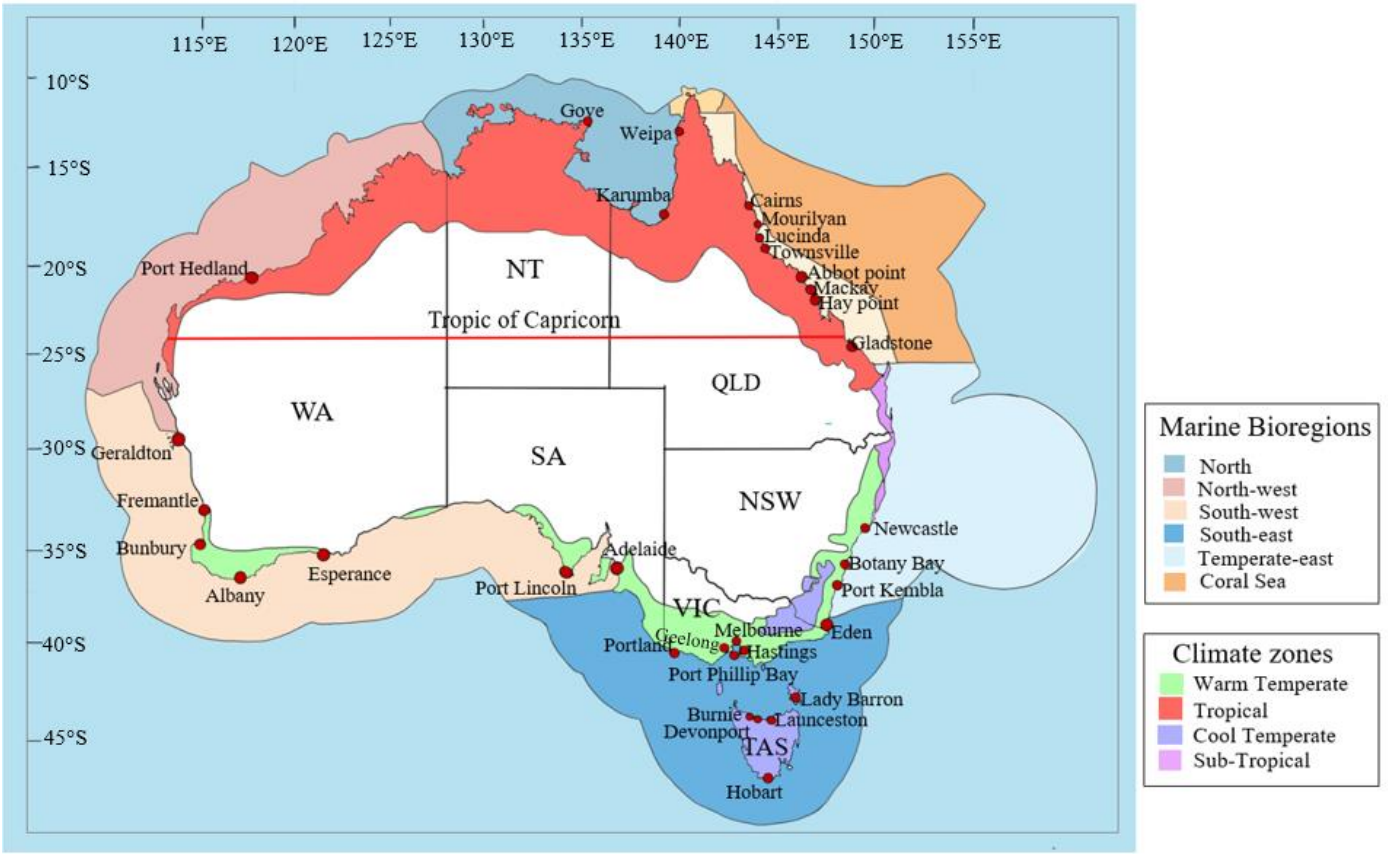


Figure 2.2.1. Map of Australia with commercial shipping ports surveyed for Australian Port Survey study. Map sourced from Hewitt & Martin (2001) and Commonwealth of Australia (2011).

B. New Zealand Port Biological Baseline Surveys (NZPS)

The data for 'pile scrapping method' was obtained from the Biosecurity New Zealand Technical papers available at https://www.marinebiosecurity.org.nz/ (Inglis et al. 2006, 2008). This baseline survey provided a preliminary inventory of native, non-native and cryptogenic species in New Zealand ports. The baseline surveys were performed at 15 ports (13 shipping ports and 2 marinas – from here on referred to as ports) in New Zealand (Table 2.2.2). The dataset assessed: to observe and interpret patterns of distribution of species status- native, non-native and cryptogenic, and to understand the potential impacts on the marine biodiversity as a correspondence between ports, port types (major vs minor ports) and latitudinal groups.

The data analyses were performed on 15 ports as a function of the surveyed port. The number of replicate sampling (sampling effort) varied across all the surveyed ports. The dataset with replicates was further averaged for each port to analyse the community composition and species status (native, non-native, cryptogenic) for the factors; port type (major vs minor) and longitudinal groups. The averaged dataset, i.e., the standardised dataset provided a non-bias

approach excluding the effects of variations in the number of replicate sampling (sampling effort) (Table 2.2.2).

The dataset was transformed into presence/absence rather than abundance because; recommendations of severe transformations are required for species communities where rare species are present, otherwise may be lost between more common species (Clarke and Warwick 2001). Also, not all species were quantified at each sampling time; therefore, the presence/absence coding approach was used. The presence/absence data of the replicates (sampling effort) were averaged for each port as the sampling effort was different for each port. The averaged dataset was further analysed to examine the community composition and species status (native, non-native, cryptogenic) as a function of the port type and latitudinal groups

Table 2.2.2. Ports sampled for the New Zealand Port Biological Baseline Surveys with latitudinal and longitudinal groups, port type and replicates (sampling effort).

Ports	Latitude	Longitude	Port type	Replicates
Auckland	36° 84' S	174° 78' E	Major	71
Bluff	46° 37' S	168° 18' E	Minor	53
Dunedin Harbour	45° 81' S	170° 62' E	Minor	47
Gisborne	38° 67' S	178° 02' E	Minor	31
Gulf Harbour Marina	36° 62' S	174° 78' E	Minor	58
Lyttelton	43° 61' S	172° 72' E	Major	50
Napier	39° 47' S	176° 91' E	Major	48
Nelson	41° 25' S	173° 17' E	Minor	94
Opua Marina	35° 31' S	174° 12' E	Minor	30
Picton	41° 28' S	174° 00' E	Minor	35
Taranaki	39° 05' S	174° 03' E	Minor	44
Tauranga	37° 64' S	176° 18' E	Major	68
Timaru	44° 39' S	171° 25' E	Minor	39
Wellington	41° 31' S	174° 81' E	Major	73
Whangarei	35° 75' S	174° 34' E	Minor	47

2.2.2. Statistical analysis

The total number of species community and species status at each surveyed port was divided with replicate numbers at each port due to varying sampling replicates at each survey port. The relative number of native, non-native cryptogenic species were regressed to observe the relationship between the number of native vs non-native species, non-native vs cryptogenic species, and native vs cryptogenic species. Regressions were plotted with 95% confidence intervals using the STATISTICA v.7 (Stat Soft Inc.) software. R^2 and *P* values were calculated for each association. The significance of these tests was set at $P < 0.05$.

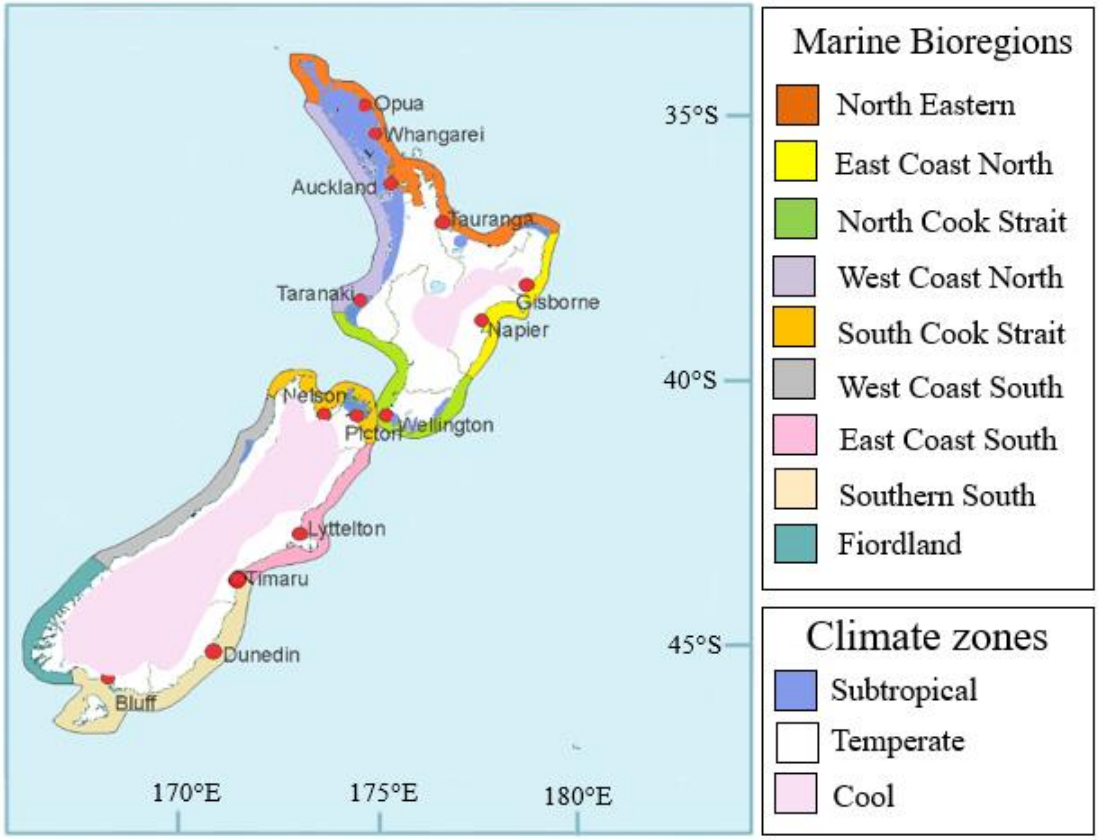


Figure 2.2.2. Map of Australia with commercial shipping ports surveyed for New Zealand Port Biological Baseline Survey study. Map sourced from Department of Conservation and Ministry of Fisheries (2011).

An initial, two-dimensional multidimensional scaling (MDS) ordination plot was performed to visualise the similarity in community composition and species status as a function of the port type and latitudinal and longitudinal groups. In MDS, similar samples, cluster together whereas samples which are dissimilar, cluster further apart. MDS plot stress values were used to interpret the reliability of the relationships; values < 0.15 = good representation between groups. The stress levels are also affected by the number of samples (Clarke 1993).

Data analyses for community composition and species status were performed using the statistical package Plymouth Routines in Multivariate Ecological Research (PRIMER v.6); with permutational multivariate analysis of variance (PERMANOVA) as an add-on package (Clarke & Gorley 2006; Anderson et al. 2008). The resemblance matrix based on Bray-Curtis similarity matrices was zero-adjusted (dummy variable) for clearer assemblages which were present across the presence/absence data. The replicates in each port were averaged and square root transformed to carry out further analyses. When species were tallied as per their status - native, non-native and cryptogenic, the dataset was square-root transformed to down-weight the dominant species (Clarke & Gorley 2006).

PERMANOVA analysis was used to determine any significant differences between surveyed ports, port type and latitudinal groups with a significance level of $P < 0.05$. PERMANOVA based on 9999 permutations with Type III (partial) sums of squares was performed for each factor. The independent factors were surveyed port, port type and latitudinal groups. PERMANOVA helps statistically test the differences between two and among multiple groups, and the effects of factors on the species communities with permutations to avoid possible biases. PERMANOVA was followed with *post-hoc* pairwise tests between factors – surveyed port, port type and latitudinal groups, respectively to indicate significant correlations between each factor group, within-group average similarity and between-group dissimilarity results

SIMPER (Similarity percentages) in PRIMER was employed to determine the species as well as species status, respectively contributing most to the overall patterns in community composition and species status (native, non-native and cryptogenic). The SIMPER analyses were restricted to top 5 species describing the location of differences leading to between-group dissimilarity.

2.3. Results (A)

AUSTRALIAN PORT SURVEY

2.3.1. Presence/absence data

A total of 1352 species were sampled across the 27 ports for the Australian port survey study. The species were grouped in 14 phyla: Chlorophyta, Ochrophyta, Rhodophyta, Annelida, Arthropoda, Bryozoa, Chordata, Cnidaria, Echinodermata, Mollusca, Platyhelminthes, Porifera, Sipuncula and Heterokontophyta (see Appendix – Table A2 for the species list). The most represented phyla in this survey were the Mollusca (272 species) followed by Annelida (260 species) and Arthropoda (234 species). The species were further grouped according to their status; native, non-native and cryptogenic. Of the 1352 species, 1181 were native species (88%), 126 non-native species (9%) and 45 cryptogenic species (3%) (Table 2.3.1).

Table 2.3.1. The total number of species noted in Australian Port Surveys grouped to Phylum and status (native, non-native and cryptogenic).

Phylum	Total	Native	Non-native	Cryptogenic
Chlorophyta	26	19	4	3
Ochrophyta	32	27	5	0
Rhodophyta	103	88	9	6
Annelida	260	239	14	7
Arthropoda	234	199	27	8
Bryozoa	126	93	24	9
Chordata	113	98	14	1
Cnidaria	126	102	16	8
Echinodermata	41	39	2	0
Mollusca	272	261	10	1
Platyhelminthes	1	1	0	0
Porifera	13	12	1	0
Sipuncula	3	3	0	0
Heterokontophyta	2	0	0	2
Total	1352	1181	126	45

2.3.2. Variations in the total presence of species as a function of replicates (sampling effort) at each surveyed port

The replication of surveys varied at each surveyed port, so to have a fair comparison of the presence of species between ports, the total number of species at each port was divided by the number of replicates to obtain the relative number of species (Table 2.3.2). The relative percent of species was highest at Abbot Point (9.13%) followed by Mourilyan (5.5%), and Lucinda (5.5%), and lowest relative percent of species were observed at Fremantle (0.54%) and Melbourne (0.56%) (Figure 2.3.1).

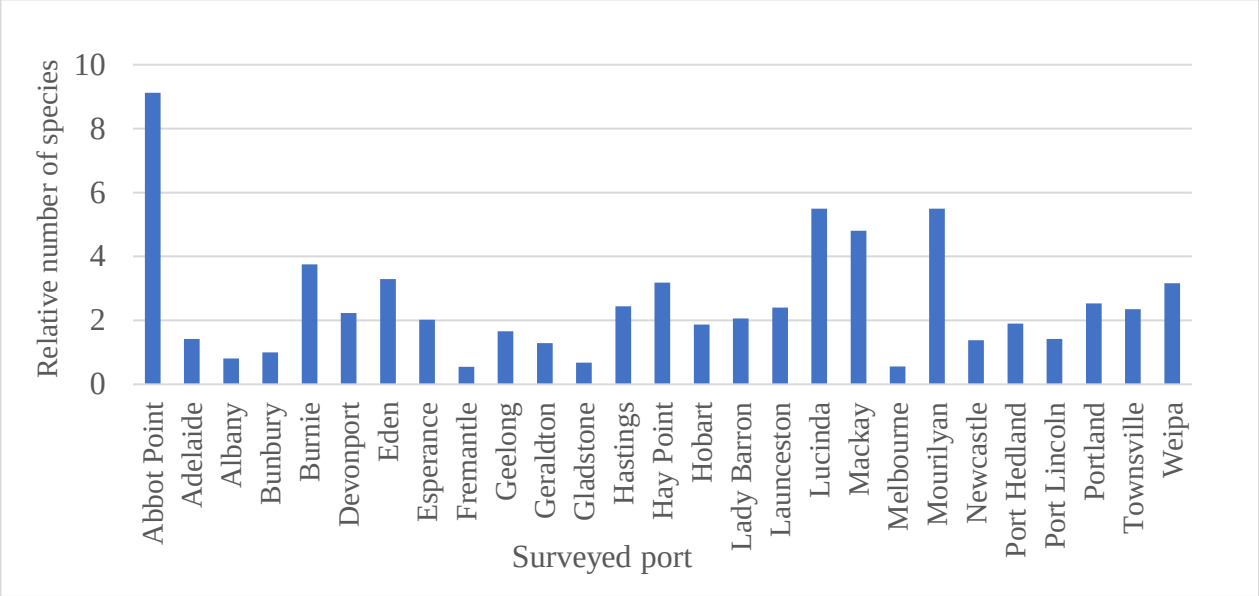


Figure 2.3.1. The total relative number of species across all 27 surveyed ports.

Table 2.3.2. The total number, sampling effort (replicates) and the relative number of species as a function of replicates at each surveyed port.

Ports	Total number	Replicates	Relative number
Abbot Point	146	16	9.13
Adelaide	94	66	1.42
Albany	48	59	0.81
Bunbury	52	52	1.00
Burnie	165	44	3.75
Devonport	49	22	2.23
Eden	102	31	3.29
Esperance	121	60	2.02
Fremantle	136	250	0.54
Geelong	68	41	1.66
Geraldton	27	21	1.29

Gladstone	68	100	0.68
Hastings	44	18	2.44
Hay Point	140	44	3.18
Hobart	198	106	1.87
Lady Barron	35	17	2.06
Launceston	187	78	2.40
Lucinda	99	18	5.50
Mackay	120	25	4.80
Melbourne	75	135	0.56
Mourilyan	66	12	5.50
Newcastle	119	86	1.38
Port Hedland	99	52	1.90
Port Lincoln	64	45	1.42
Portland	38	15	2.53
Townsville	106	45	2.36
Weipa	57	18	3.17

2.3.3. Variations in the community composition as a function of the surveyed port, port type and latitudinal groups

a) Surveyed ports

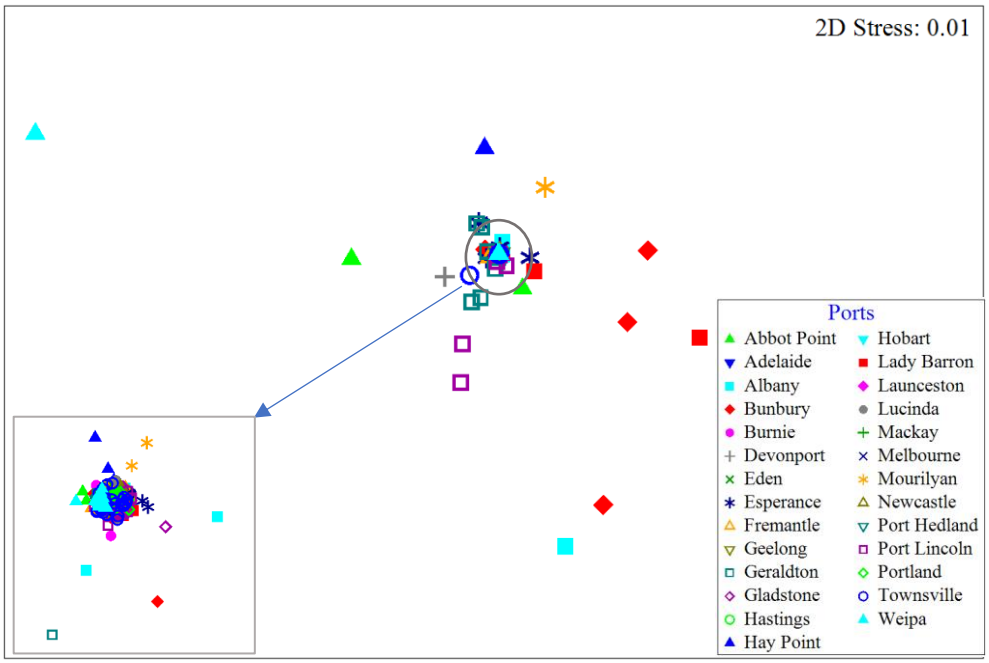


Figure 2.3.2. Multidimensional Scaling (MDS) plot. The proximity of surveyed ports to each other indicates similarity in species (based on presence/absence data).

The graphical representation of the MDS ordination of the presence of species (presence/absence data) as a function of surveyed port showed some patterns in clustering of ports with similar species. However, the patterns are not clear enough to state the groupings (Figure 2.3.2). The 2D stress result of 0.01 indicates that the MDS is an excellent representation of the data.

Multivariate analyses were carried out to observe patterns of community composition among/between ports. PERMANOVA based on presence/absence data as a function of surveyed ports indicates significant differences in community composition among 27 surveyed ports ($P < 0.001$; Table 2.3.3).

Table 2.3.3. Results of the PERMANOVA test performed on the presence/absence of species as a function of the surveyed port. Significance marked in bold ($P < 0.05$).

	df	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**	**Unique perms**
Surveyed port	26	2.3875E6	91828	30.718	**0.001**	9389
Residual	1449	4.3316E6	2989.4			
Total	1475	6.7192E6				

Pairwise comparisons also showed a high significance in community composition between surveyed ports ($P < 0.001$). The within-group similarity was relatively more robust at Port Geelong (40.69%) followed by Hobart (40.16%), and Esperance had the least within-group similarity (9.23%) (Table 2.3.4). The between-ports dissimilarity ranged from 75.86 - 100%, indicating high dissimilarity in the community composition between ports. The paired ports that showed less than 90% dissimilarity are; Geelong vs Melbourne (75.86%), Hastings vs Portland (85.95%), Fremantle vs Melbourne (86.02%), Eden vs Melbourne (87.21%), Geelong vs Hobart (88.09%), Geelong vs Portland (88.36%), Adelaide vs Melbourne (88.73%), Fremantle vs Newcastle (89.20%), Fremantle vs Geelong (89.71%) and Hay point vs Mackay (89.84%). Further, observing these paired ports, the between-ports dissimilarity is relatively low for ports at proximity.

Table 2.3.4. The average similarity of the presence/absence of species as a function of the surveyed port.

Ports	Avg. sim. (%)	Ports	Avg. sim. (%)	Ports	Avg. sim. (%)
Abbot Point	13.07	Devonport	19.68	Geraldton	27.66
Adelaide	28.34	Eden	25.48	Gladstone	28.27

Albany	13.81	Esperance	9.23	Hastings	38.67
Bunbury	13.50	Fremantle	24.87	Hay Point	21.26
Burnie	15.77	Geelong	40.69	Hobart	40.16
Lady Barron	11.22	Mackay	19.66	Newcastle	24.25
Launceston	35.17	Melbourne	34.38	Port Hedland	28.91
Lucinda	11.98	Mourilyan	15.15	Port Lincoln	15.68
Portland	32.76	Townsville	11.92	Weipa	9.65

SIMPER (similarity percentage) analysis was applied to identify the top 5 contributing and discriminating species between surveyed ports. It is important to note that red alga, *Jania adhaerens*, contributed 94.68% to the average similarity within Port Geraldton explaining the port as an outlier (Table 2.3.5). The SIMPER results indicated that the species contributing to the within-ports similarity also contributed to the between-ports dissimilarity (considering the top 5 species). There was no specific trend observed in terms of species contribution between surveyed ports highlighting the dissimilarities. However, the dissimilarity between ports was dependent on the average abundance of the species at each port.

Table 2.3.5. SIMPER analysis: average similarity in the presence/absence of species as a function of the surveyed port.

Abbot Point **Average similarity: 13.07%**				**Adelaide** **Average similarity: 28.34%**				**Burnie** **Average similarity: 15.77%**			
Species	Avg. Abund	C%	Cum.%	Species	Avg. Abund	C%	Cum.%	Species	Avg. Abund	C%	Cum.%
Ophiactis cf. savignyi	0.69	15.49	15.49	*Sabella spallanzanii*	0.67	12.69	12.69	*Xenostrobus pulex*	0.45	10.83	10.83
Chama fibula	0.56	11.86	27.35	*Hydroides elegans*	0.65	11.24	23.94	*Lasaea australis*	0.48	9.29	20.12
Pinctada sugillata	0.56	10.85	38.21	*Styela plicata*	0.56	8.85	32.78	*Celleporaria foliata*	0.45	7.82	27.94
Dendostrea folium	0.5	9.55	47.76	*Harmothoe waahli*	0.58	8.02	40.8	*Hiatella australis*	0.45	7.51	35.45
Pyura stolonifera	0.5	8.83	56.59	*Botryllus schlosseri*	0.47	7.13	47.94	*Paradexamine churinga*	0.43	6.99	42.44
Albany **Average similarity: 13.81%**				**Bunbury** **Average similarity: 13.50%**				**Devonport** **Average similarity: 19.68%**			
Species	Avg. Abund	C%	Cum.%	Species	Avg. Abund	C%	Cum.%	Species	Avg. Abund	C%	Cum.%
Bugula stolonifera	0.32	15.28	15.28	*Paracerceis sculpta*	0.46	56.77	56.77	*Thelepus extensus*	0.59	24.78	24.78
Sabella spallanzanii	0.34	14.21	29.49	*Sabella spallanzanii*	0.27	18.47	75.24	*Sertularella cf. robusta*	0.5	19.15	43.93
Watersipora subtorquata	0.29	13.55	43.03	*Leptochiton liratus*	0.21	9.32	84.56	*Tubularia cf. crocea*	0.45	15.73	59.66
Bugula neritina	0.27	8.42	51.46	*Herpetopoma aspersa*	0.17	4.51	89.07	*Bimeria australis*	0.36	8.81	68.47
Cryptosula pallasiana	0.24	7.73	59.19	*Hiatella australis*	0.13	3.03	92.1	*Sarsia cf. eximia*	0.32	6.04	74.5
Eden **Average similarity: 25.48%**				**Esperance** **Average similarity: 9.23%**				**Fremantle** **Average similarity: 24.87%**			
Species	Avg. Abund	C%	Cum.%	Species	Avg. Abund	C%	Cum.%	Species	Avg. Abund	C%	Cum.%
Balanus trigonus	0.71	23.01	23.01	*Hiatella australis*	0.45	26.42	26.42	*Balanus trigonus*	0.84	37.13	37.13
Podarkeopsis galangaui	0.74	21.7	44.71	*Pilumnus acer*	0.27	14.25	40.67	*Hiatella australis*	0.48	8.91	46.03
Mytilus edulis planulatus	0.61	14.29	58.99	*Halicarcinus ovatus*	0.28	11.23	51.91	*Pilumnus fissifrons*	0.45	8.83	54.87
Hiatella australis	0.48	6.9	65.89	*Alpheus socialis*	0.22	5.83	57.73	*Mytilus edulis planulatus*	0.46	8.06	62.93
Watersipora subtorquata	0.42	6	71.89	*Musculus cf. nanus*	0.23	5.02	62.76	*Celleporaria cf. nodulosa*	0.33	5.86	68.79

Geelong **Average similarity: 40.69%**				**Gladstone** **Average similarity: 28.27%**				**Hastings** **Average similarity: 38.67%**			
Species	Avg. Abund	C%	Cum.%	Species	Avg. Abund	C%	Cum.%	Species	Avg. Abund	C%	Cum.%
Mytilus galloprovincialis	0.85	16.44	16.44	*Pisidia gordoni*	0.78	38.14	38.14	*Stolonica australis*	0.83	20.34	20.34
Balanus trigonus	0.83	15.24	31.68	*Sphaeroma sculpta*	0.56	21.22	59.36	*Bugula dentata*	0.72	16.1	36.44
Pyura stolonifera	0.83	14.66	46.35	*Hiatella arctica*	0.39	8.03	67.39	*Triphyllozoon cf. moniliferum*	0.72	15.5	51.95
Ascidiella aspersa	0.66	9.04	55.39	*Scruparia ambigua*	0.33	6.81	74.2	*Amastigia cf. texta*	0.72	15.19	67.14
Platynereis antipoda	0.66	8.67	64.06	*Aora maculata*	0.36	6.16	80.36	*Cryptosula pallasiana*	0.56	8.95	76.09
Lady Barron **Average similarity: 11.22%**				**Hay Point** **Average similarity: 21.26%**				**Hobart** **Average similarity: 40.16%**			
Species	Avg. Abund	C%	Cum.%	Species	Avg. Abund	C%	Cum.%	Species	Avg. Abund	C%	Cum.%
Bugula dentata	0.41	46.7	46.7	*Chama lazarus*	0.64	15.06	15.06	*Monocorophium acherusicum*	0.92	9.81	9.81
Herdmania momus	0.35	18.34	65.04	*Pilumnus cf. tomentosus*	0.64	14.67	29.73	*Hiatella australis*	0.81	7.36	17.16
Amathia distans	0.29	11.98	77.01	*Striatobalanus amaryllis*	0.64	12	41.73	*Watersipora subtorquata*	0.79	6.87	24.03
Celleporaria fusca	0.18	4.25	81.26	*Lumbrineris coccinea*	0.45	5.29	47.02	*Mytilus galloprovincialis*	0.79	6.83	30.86
Stolonica australis	0.18	3.82	85.08	*Hyastenus cf. convexus*	0.43	5.12	52.13	*Crassostrea gigas*	0.79	6.77	37.63
Launceston **Average similarity: 35.17%**				**Lucinda** **Average similarity: 11.98%**				**Mackay** **Average similarity: 19.66%**			
Species	Avg. Abund	C%	Cum.%	Species	Avg. Abund	C%	Cum.%	Species	Avg. Abund	C%	Cum.%
Balanus trigonus	0.87	9.2	9.2	*Balanus reticulatus*	0.28	29.07	29.07	*Amathia distans*	0.72	16.78	16.78
Halicarcinus ovatus	0.76	6.46	15.66	*Isognomon nucleus*	0.5	15.35	44.42	*Eupolymnia koorangia*	0.64	11.57	28.36
Balanus variegatus	0.69	5.47	21.12	*Chama fibula*	0.44	9.98	54.4	*Thelepus robustus*	0.56	10.83	39.19
Achelia assimilis	0.69	5.13	26.25	*Brachidontes maritimus*	0.33	7.48	61.88	*Lumbrineris coccinea*	0.48	6.96	46.15
Molgula ficus	0.64	4.99	31.24	*Balanus amphitrite*	0.28	4.74	66.61	*Lumbrineris inflata*	0.44	5.59	51.75

Melbourne **Average similarity: 34.38%**				**Mourilyan** **Average similarity: 15.14%**				**Newcastle** **Average similarity: 24.25%**			
Species	Avg. Abund	C%	Cum.%	Species	Avg. Abund	C%	Cum.%	Species	Avg. Abund	C%	Cum.%
Balanus trigonus	0.7	28.86	28.86	*Dendostrea sandvichensis*	0.5	15.13	15.13	*Balanus variegatus*	0.67	29.1	29.1
Sabella spallanzanii	0.59	20.55	49.4	*Balanus amphitrite*	0.42	10.28	25.41	*Balanus trigonus*	0.62	15.52	44.62
Pyura stolonifera	0.52	13.84	63.24	*Leonnates decipens*	0.42	9.25	34.66	*Irus crebrelamellatus*	0.43	7.91	52.53
Mytilus edulis planulatus	0.48	13.16	76.4	*Chama fibula*	0.42	9.14	43.8	*Augeneria verdis*	0.38	5.54	58.07
Ascidiella aspersa	0.37	6.94	83.34	*Striostrea mytiloides*	0.33	7.13	50.93	*Bugula neritina*	0.34	4.61	62.68
Port Hedland **Average similarity: 28.91%**				**Port Lincoln** **Average similarity: 15.68%**				**Portland** **Average similarity: 32.76%**			
Species	Avg. Abund	C%	Cum.%	Species	Avg. Abund	C%	Cum.%	Species	Avg. Abund	C%	Cum.%
Lumbrineris inflata	0.73	19.23	19.23	*Hiatella australis*	0.56	36.63	36.63	*Bugula dentata*	0.8	24.58	24.58
Crisia cf. acropora	0.69	17.53	36.76	*Musculus impactus*	0.36	11.33	47.96	*Paratanais ignotus*	0.53	10.6	35.18
Syllis australiensis	0.52	9.92	46.68	*Ophiactis resiliens*	0.29	8.39	56.35	*Halicarcinus ovatus*	0.53	9.38	44.56
Microcosmus helleri	0.54	9.55	56.22	*Lasaea australis*	0.27	8.29	64.64	*Eucoelium mariae*	0.53	9.01	53.56
Pomatostegus stellatus	0.54	9.49	65.71	*Trichomusculus barbatus*	0.29	5.88	70.51	*Watersipora subtorquata*	0.53	8.52	62.09
Townsville **Average similarity: 11.92%**				**Weipa** **Average similarity: 9.65%**				**Geraldton** **Average similarity: 27.66%**			
Species	Avg. Abund	C%	Cum.%	Species	Avg. Abund	C%	Cum.%	Species	Avg. Abund	C%	Cum.%
Branchiomma nigromaculata	0.44	14.45	14.45	*Thelepus robustus*	0.44	28.23	28.23	*Jania adhaerens*	0.52	94.68	94.68
Lepidonotus carinulatus	0.4	9.02	23.46	*Striostrea mytiloides*	0.28	17.04	45.27				
Lumbrineris cf. coccinea	0.38	8.28	31.75	*Balanus amphitrite*	0.22	10.85	56.12				
Pseudopotamilla cf. laciniosa	0.36	7.54	39.29	*Lysidice collaris*	0.28	8.15	64.27				
Lysidice collaris	0.33	5.88	45.17	*Striatobalanus amaryllis*	0.28	6.9	71.17				

C% - Percent contribution; Cum.%- cumulative percentage

b) Port type (major and minor ports)

The graphical representation of the MDS ordination of the presence/absence data showed no distinct groupings of similar species composition as a function of port type, 4 major commercial shipping ports and 23 minor shipping ports (2D stress = 0.11; Figure 2.3.3).

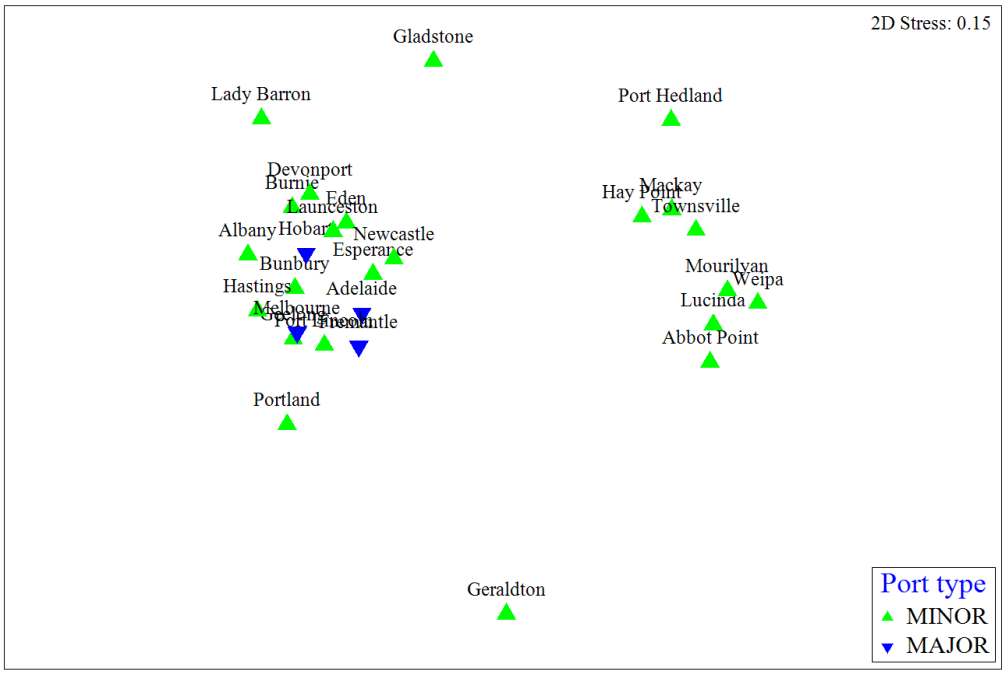


Figure 2.3.3. Multidimensional Scaling (MDS) Map. The proximity of surveyed ports to each other indicates similarity in community composition as a function of port type.

Further, multivariate analyses, PERMANOVA showed a significant difference in species community composition as a function of port type (P = 0.047; Table 2.3.6). Pairwise comparison, however, showed relatively more similar species composition at major ports (18.42%) than minor ports (6.84%) (Table 2.3.6).

Table 2.3.6. Results of the PERMANOVA and pairwise test performed as a function of port type (2 levels). Significance marked in bold ($P < 0.05$).

Source	df	SS	MS	Pseudo-*F*	*P* (perm)	Unique perms	t value	Avg. similarity	
								Major port	Minor port
Port type	1	5666.7	5666.7	1.3364	**0.047**	7541	1.156	18.42	6.84
Residual	25	1.06E+05	4240.2						
Total	26	1.116E+05							

SIMPER analysis showed 154 species contributing to the 50% dissimilarity between major and minor ports. The top 5 species contributing to the differences were: cryptogenic *Balanus trigonus* (1.44%), native *Mytilus edulis planulatus* (1.06%), non-native *Sabella spallanzanii* (1.05%), non-native *Ciona intestinalis* (0.89%) and native *Pyura stolonifera* (0.85%). The species at major ports were better discriminators (Table 2.3.7).

Table 2.3.7. SIMPER analysis: average similarity in the community composition as a function of port type. Species status, i.e., native (N), non-native (NN) and cryptogenic (C), is noted.

Minor ports Average similarity = 6.84%		**Major ports Average similarity = 18.42%**		**Minor & Major ports Average dissimilarity = 90.99%**			
Species	C%	Species	C%	Species	Minor	Major	C%
Hiatella australis (N)	8.07	*Balanus trigonus* (C)	12.91	*Balanus trigonus* (C)	0.18	0.75	1.44
Watersipora subtorquata (NN)	3.33	*Ciona intestinalis* (NN)	7.25	*Mytilus edulis planulatus* (N)	0.05	0.43	1.06
Bugula neritina (NN)	2.52	*Mytilus edulis planulatus* (N)	5.63	*Sabella spallanzanii* (NN)	0.1	0.45	1.05
Eupolymnia koorangia (N)	2.10	*Halicarcinus ovatus* (N)	5.07	*Ciona intestinalis* (NN)	0.02	0.42	0.89
Balanus amphitrite (C)	2.05	*Sabella spallanzanii* (NN)	4.92	*Pyura stolonifera* (N)	0.14	0.39	0.85

C% = percent contribution

c) Latitudinal groups

The surveyed ports were grouped as a function of their latitude forming 6 latitude groups ranging from 15°S to 40°S. The MDS plot is displayed in Figure 2.3.4; 2D stress = 0.15, showing the ordination patterns and overlaps between ports as a function of latitudinal groups. The ports at each latitudinal group clustered together but the ports at high (30°S, 35°S and 40°S) and low (15°S and 20°S) latitudinal groups showed distinct separation. Port Geraldton at latitude 25°S was an outlier and only port sampled from that latitude.

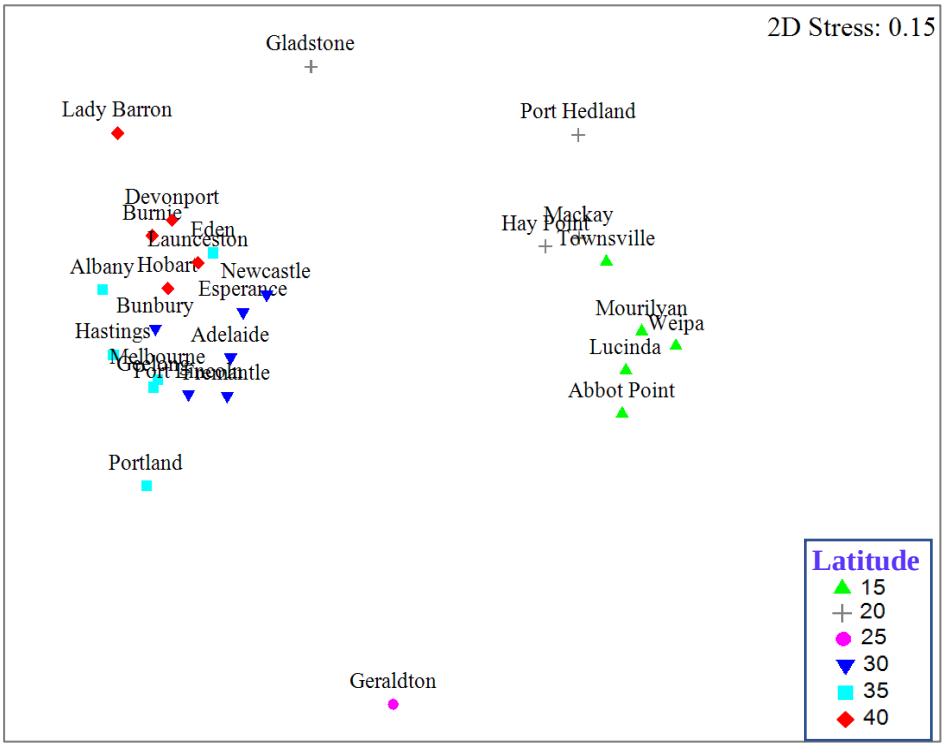


Figure 2.3.4. Multidimensional Scaling (MDS) plot. The proximity of surveyed ports to each other indicates similarity in community composition as a function of latitudinal groups.

The results of the PERMANOVA analysis showed a statistical significance in community composition as a function of latitude ($P < 0.001$; Table 2.3.8) indicating variations in community composition for ports at each latitudinal group. Pairwise tests indicated significance ($P < 0.05$) between latitudes (15, 20, 30, 35, 40°S) except for 25°S, i.e. Port Geraldton, which is an outlier (Table 2.3.9).

Table 2.3.8. Results of the PERMANOVA test performed as a function of latitude (7 levels). Significance ($P < 0.05$) marked in bold.

	df	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**	**Unique perms**
Latitude	6	42473	7078.8	2.046	**0.0001**	9661
Residual	20	69201	3460			
Total	26	1.1167E+05				

Table 2.3.9. Results of pairwise PERMANOVA test performed as a function of latitudinal groups with only significant paired latitudes. Significance ($P < 0.05$) marked in bold.

Latitude (°S)	**t**	***P* (perm)**	**Unique perms**
15 vs 30	1.6903	**0.0052**	210
15 vs 35	1.7544	**0.0049**	210
15 vs 40	1.7009	**0.0081**	126
15 vs 20	1.3609	**0.0309**	35
30 vs 35	1.2686	**0.0179**	462
30 vs 40	1.3786	**0.0026**	461
30 vs 20	1.5535	**0.0062**	210
35 vs 40	1.3431	**0.0065**	462
35 vs 20	1.6481	**0.0043**	210
40 vs 20	1.5486	**0.0089**	126

SIMPER was performed to identify the species (top 5) that contributed to the significant dissimilarity between paired latitudes (Table 2.3.11). The species at 15°S were better discriminators leading to the dissimilarity between latitude 15°S and other latitudes, i.e., 20, 30, 35, 40°S. The top species contributing to the dissimilarity are; *Chama fibula* (NN), *Ophiactis cf. savignyi* (N), *Dendostrea folium* (N) and *Eunice tubifex* (N). Species that explained the dissimilarity between latitude 20°S and latitudes 30, 35 and 40°S are; *Lumbrineris inflata (N)*, *Chama lazarus (N)* and *Thelepus robustus (N).* The species at latitude 20°S were the better discriminators. The dissimilarity for latitudinal groups 30°S vs 35°S was contributed by species; *Balanus trigonus* (C), *Bugula dentata* (N), *Cryptosula pallasiana* (NN) and *Watersipora subtorquata* (NN) with species at 35°S being the better discriminators. Lastly, the dissimilarity between latitudes 30°S and 40°S were explained by species; *Pomatoceros taeniata* (N), *Balanus trigonus* (C), *Crassotrea gigas* (NN), *Bimeria australis* (N) and *Bugula dentata* (N). The species at 40°S latitude being the better discriminators (Table 2.3.10).

To summarize, the percentage contribution (C%) of each species to the dissimilarities between the latitudes was less than 2%. Also, the results indicated no specific trend in species contribution between latitudinal groups. However, the species at lower latitudes, i.e., 15°S and 20°S were better discriminators compared to higher latitudes, i.e., 30°S, 35°S, 40°S.

Table 2.3.10. SIMPER analysis: average dissimilarity for the community composition as a function of latitude with only significant paired latitudes. Species status, i.e., native (N), non-native (NN) and cryptogenic (C), is noted.

15 & 30°S Average dissimilarity = 97.48%					15 & 35°S Average dissimilarity = 98.40%				
	15	30				15	35		
Species	Avg. Abund.	Avg. Abund	C%	Cum.%	Species	Avg. Abund.	Avg. Abund	C%	Cum.%
Chama fibula (NN)	0.52	0	0.97	0.97	*Watersipora subtorquata* (NN)	0	0.52	1.03	1.03
Ophiactis cf. savignyi (N)	0.51	0	0.96	1.93	*Chama fibula* (NN)	0.52	0	1.02	2.04
Hiatella australis (N)	0.06	0.56	0.95	2.88	*Ophiactis cf. savignyi* (N)	0.51	0	1	3.04
Dendostrea folium (N)	0.49	0.01	0.89	3.77	*Dendostrea folium* (N)	0.49	0	0.95	3.99
Eunice tubifex (N)	0.45	0	0.87	4.64	*Eunice tubifex* (N)	0.45	0	0.90	4.89
15 & 40°S Average dissimilarity = 98.21%					15 & 20°S Average dissimilarity = 92.19%				
	15	40				15	20		
Species	Avg. Abund.	Avg. Abund	C%	Cum.%	Species	Avg. Abund.	Avg. Abund	C%	Cum.%
Chama fibula (NN)	0.52	0	0.83	0.83	*Chama fibula* (NN)	0.52	0	0.91	0.91
Ophiactis cf. savignyi (N)	0.51	0	0.82	1.65	*Ophiactis cf. savignyi* (N)	0.51	0	0.9	1.81
Dendostrea folium (N)	0.49	0	0.78	2.43	*Lumbrineris inflata* (N)	0	0.53	0.88	2.70
Eunice tubifex (N)	0.45	0	0.74	3.16	*Eunice tubifex* (N)	0.45	0	0.81	3.51
Pomatoceros taeniata (N)	0	0.47	0.73	3.89	*Dendostrea folium* (N)	0.49	0.04	0.8	4.3
35 & 20°S Average dissimilarity = 97.79%					30 & 20°S Average dissimilarity = 96.13%				
	35	20				30	20		
Species	Avg. Abund.	Avg. Abund	C%	Cum.%	Species	Avg. Abund.	Avg. Abund	C%	Cum.%
Watersipora subtorquata (NN)	0.52	0	1.15	1.15	*Hiatella australis* (N)	0.56	0.07	1.08	1.08
Lumbrineris inflata (N)	0	0.53	1.07	2.22	*Lumbrineris inflata* (N)	0	0.53	1.04	2.12
Chama lazarus (N)	0	0.47	0.98	3.19	*Chama lazarus* (N)	0	0.47	0.94	3.06
Cryptosula pallasiana (NN)	0.43	0	0.96	4.15	*Balanus trigonus* (C)	0.45	0	0.91	3.97
Thelepus robustus (N)	0	0.45	0.92	5.07	*Thelepus robustus* (N)	0	0.45	0.89	4.85

40 & 20°S Average dissimilarity = 96.40%					35 & 40°S Average dissimilarity = 88.37%				
	40	20				35	40		
Species	Avg. Abund.	Avg. Abund	C%	Cum.%	Species	Avg. Abund.	Avg. Abund	C%	Cum.%
Lumbrineris inflata (N)	0	0.53	0.89	0.89	*Balanus trigonus* (C)	0.43	0.35	1.04	1.04
Pomatoceros taeniata (N)	0.47	0	0.81	1.69	*Cryptosula pallasiana* (NN)	0.43	0.13	0.99	2.03
Chama lazarus (N)	0	0.47	0.80	2.49	*Pomatoceros taeniata* (N)	0.07	0.47	0.97	2.99
Thelepus robustus (N)	0	0.45	0.76	3.25	*Bugula dentata* (N)	0.41	0.31	0.93	3.92
Hiatella australis (N)	0.53	0.07	0.75	4	*Sabella spallanzanii* (NN)	0.36	0	0.91	4.83
30 & 40°S Average dissimilarity = 89.63%					30 & 35°S Average dissimilarity = 86.99%				
	30	40				30	35		
Species	Avg. Abund.	Avg. Abund	C%	Cum.%	Species	Avg. Abund.	Avg. Abund	C%	Cum.%
Pomatoceros taeniata (N)	0	0.47	0.99	0.99	*Balanus trigonus* (C)	0.45	0.43	1.29	1.29
Balanus trigonus (C)	0.45	0.35	0.86	1.85	*Bugula dentata* (N)	0	0.41	1.20	2.49
Crassotrea gigas (NN)	0	0.43	0.78	2.63	*Cryptosula pallasiana* (NN)	0.04	0.43	1.17	3.67
Bimeria australis (N)	0	0.29	0.77	3.40	*Watersipora subtorquata* (NN)	0.17	0.52	1.14	4.80
Bugula dentata (N)	0	0.31	0.75	4.15	*Sabella spallanzanii* (NN)	0.31	0.36	1.10	5.90

C% = Per cent Contribution, Cum. % = Cumulative percentage

In summary, statistically significant differences in the presence of species were observed as a function of the surveyed port. The average dissimilarities between ports was more than 75%. The results indicated no specific trend in species contribution to the dissimilarities between ports; except for, Port Geraldton where the red alga, *Jania adhaerens*, contributed 94.68%. The community composition as a function of port type (major vs minor ports) indicated significant differences. The minor ports had relatively diverse species when compared to major ports. However, this could be because of 4 major and 23 minor ports in the dataset. The latitudinal groups indicated significance between latitude groups, except for 25°S, i.e., Port Geraldton. The species at lower latitudes, i.e., 15°S and 20°S were better discriminators compared to species at higher latitudes (30, 35, 40°S). The top species are contributing to the between-group dissimilarities for the factors, port type and latitudinal groupsare listed below; Table 2.3.11.

Table 2.3.11. The list of species that indicated variations as a function of the port type and latitudinal groups.

Species	**Phyla**	**Species status**
Balanus trigonus	Arthropoda	Cryptogenic
Bugula dentata	Bryozoa	Native
Bugula neritina	Bryozoa	Non-native
Chama fibula	Mollusca	Non-native
Chama lazarus	Mollusca	Native
Ciona intestinalis	Chordata	Non-native
Crassotrea gigas	Mollusca	Non-native
Cryptosula pallasiana	Bryozoa	Non-native
Dendostrea folium	Mollusca	Native
Eunice tubifex	Annelida	Native
Hiatella australis	Mollusca	Native
Jania adhaerens	Rhodophyta	Native
Lumbrineris inflata	Annelida	Native
Mytilus edulis planulatus	Mollusca	Native
Ophiactis cf. savignyi	Echinodermata	Native
Pomatoceros taeniata	Annelida	Native
Sabella spallanzanii	Annelida	Native
Thelepus extensus	Annelida	Native
Watersipora subtorquata	Bryozoa	Non-native

2.3.4. Variations in species status - native, non-native and cryptogenic species as a function of the surveyed port, port type and latitudinal groups

a) Surveyed ports

To eliminate the bias due to differences in the replicates (sampling effort) at each port; the total number of species status (native, non-native and cryptogenic) was divided by the number of replicates at each surveyed port. The total relative number of species (total number/number of replicates) at each surveyed port showed relatively higher percentages of native species, followed by non-native and cryptogenic species (Figure 2.3.5). The relative number of native species was highest at Abbot point (8.44), and lowest at Melbourne (0.33) whereas the non-native species were highest at Lucinda (0.5%) and lowest at Port Gladstone. The number of cryptogenic species was relatively lower compared to native and non-native species (Table 2.3.12).

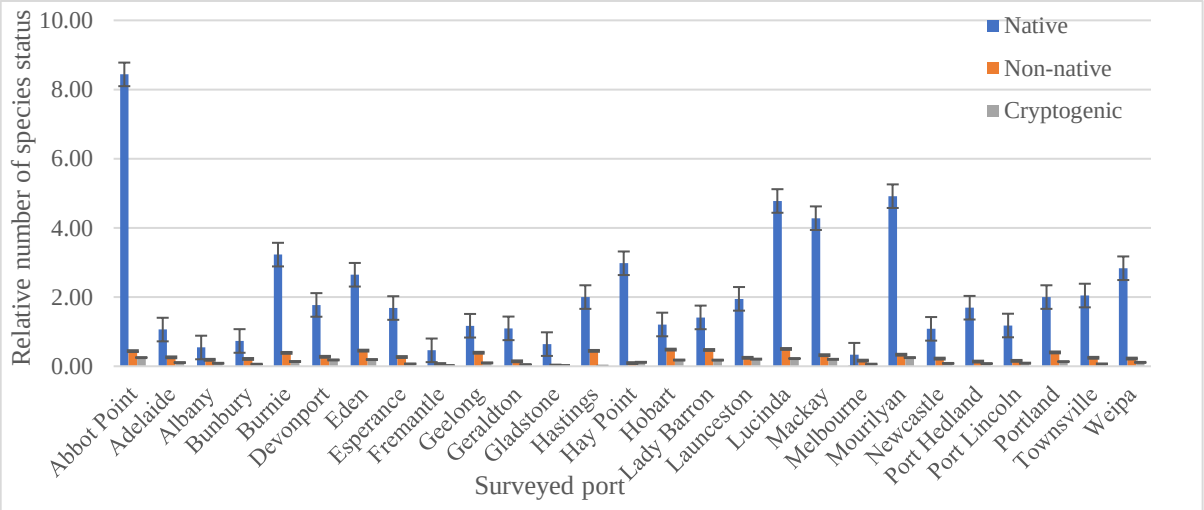


Figure 2.3.5. The total relative number of species status - native (blue), non-native (orange) and cryptogenic (grey) species across 27 surveyed ports.

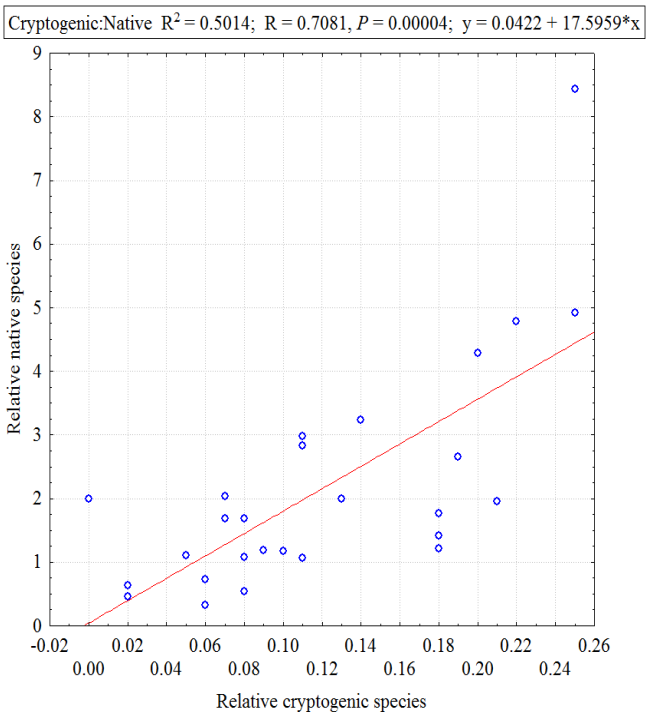
Table 2.3.12. The total number of species, species status, replicates (sampling effort) and the relative number of native, non-native and cryptogenic species - across 27 surveyed ports.

Surveyed port	Native species	Non-native species	Cryptogenic species	Survey Replicates	Relative Native	Relative Non-native	Relative Cryptogenic
Abbot Point	135	7	4	16	8.44	0.44	0.25
Adelaide	70	17	7	66	1.06	0.26	0.11
Albany	31	10	7	59	0.54	0.19	0.08
Bunbury	37	11	4	52	0.73	0.21	0.06

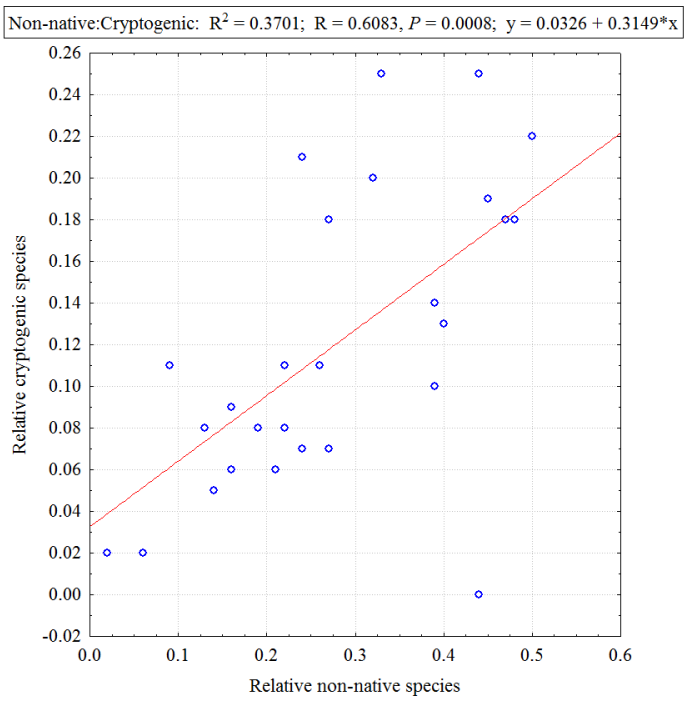
Burnie	140	19	6	44	3.23	0.39	0.14
Devonport	39	7	3	22	1.77	0.27	0.18
Eden	82	14	6	31	2.65	0.45	0.19
Esperance	103	14	4	60	1.68	0.27	0.07
Fremantle	116	16	4	250	0.46	0.06	0.02
Geelong	49	16	3	41	1.17	0.39	0.10
Geraldton	23	3	1	21	1.10	0.14	0.05
Gladstone	62	2	4	100	0.64	0.02	0.02
Hastings	37	7	0	18	2.00	0.44	0.00
Hay Point	131	6	3	44	2.98	0.09	0.11
Hobart	129	50	19	106	1.21	0.48	0.18
Lady Barron	25	7	3	17	1.41	0.47	0.18
Launceston	153	22	12	78	1.95	0.24	0.21
Lucinda	85	11	3	18	4.78	0.50	0.22
Mackay	109	8	3	25	4.28	0.32	0.20
Melbourne	50	17	8	135	0.33	0.16	0.06
Mourilyan	60	4	2	12	4.92	0.33	0.25
Newcastle	92	22	5	86	1.08	0.22	0.08
Port Hedland	89	7	3	52	1.69	0.13	0.08
Port Lincoln	53	9	2	45	1.18	0.16	0.09
Portland	31	5	2	15	2.00	0.40	0.13
Townsville	96	8	2	45	2.04	0.24	0.07
Weipa	51	4	2	18	2.83	0.22	0.11

Furthermore, the number of species status was correlated against each other to observe the interaction between the number of native, non-native and cryptogenic species across all surveyed ports. The results revealed high significance and a strong positive relationship between species status (Figure 2.3.6). The correlation between the number of native and cryptogenic ($R^2 = 0.50$; $P < 0.0001$) (Figure 2.3.6 a) species was relatively stronger compared to correlation of the number of cryptogenic and non-native ($R^2 = 0.37$; $P < 0.0001$) (Figure 2.3.6 b) species and number of native and non-native species ($R^2 = 0.22$; $P < 0.05$) (Figure 2.3.6 c).

a)



b)



c)

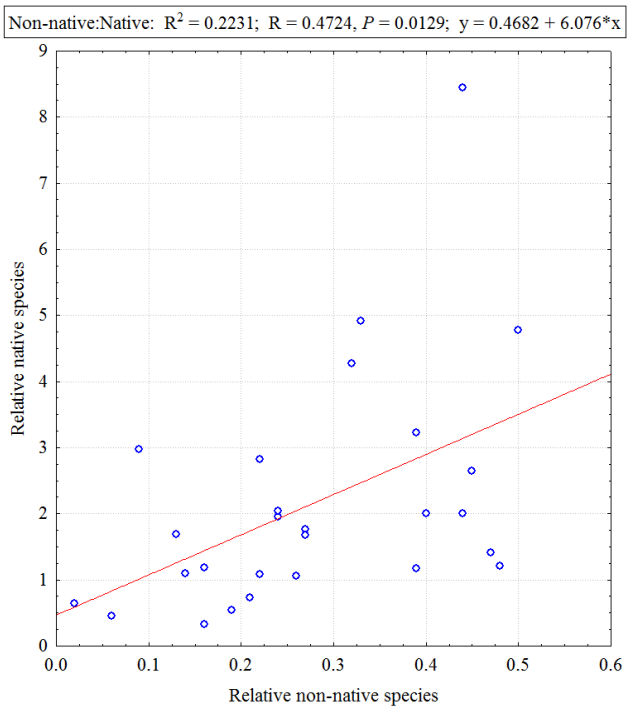


Figure 2.3.6. Regression between relative native and non-native species across 27 surveyed ports; a) Native vs Cryptogenic species, b) Cryptogenic vs Non-native species and c) Native vs Non-native species.

Multivariate analysis, PERMANOVA was performed to indicate variations in the species status (native, non-native and cryptogenic) as a function of the surveyed port. The species status varied significantly among surveyed ports (PERMANOVA; $P < 0.0001$; Table 2.3.13). The pairwise tests revealed significance between most of the ports with more than 50% average similarities.

Table 2.3.13. Results of the PERMANOVA test performed on the species status as a function of the surveyed port. Significant value in bold ($P < 0.05$).

	df	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**	**Unique perms**
Surveyed port	26	5.43E+05	20878	33.983	**0.0001**	9845
Residuals	1449	8.90E+05	614.36			
Total	1475	1.43E+06				

SIMPER results revealed more than 50% average similarity at all ports, with native species to be the highest contributing species status (Table 2.3.19; Figure 2.3.7). At ports such as Hobart, Geelong, Albany and Melbourne, the difference in percent contribution of native and non-native species was significantly similar. To note, native red alga, *Jania adherens* was the only contributor to the average similarity at Port Geraldton (Table A1). The between-group dissimilarities were mostly contributed by native species followed by non-native and cryptogenic species, except for ports Eden, Fremantle, Launceston and Weipa where cryptogenic species contributed more than non-native species (Figure 2.3.7).

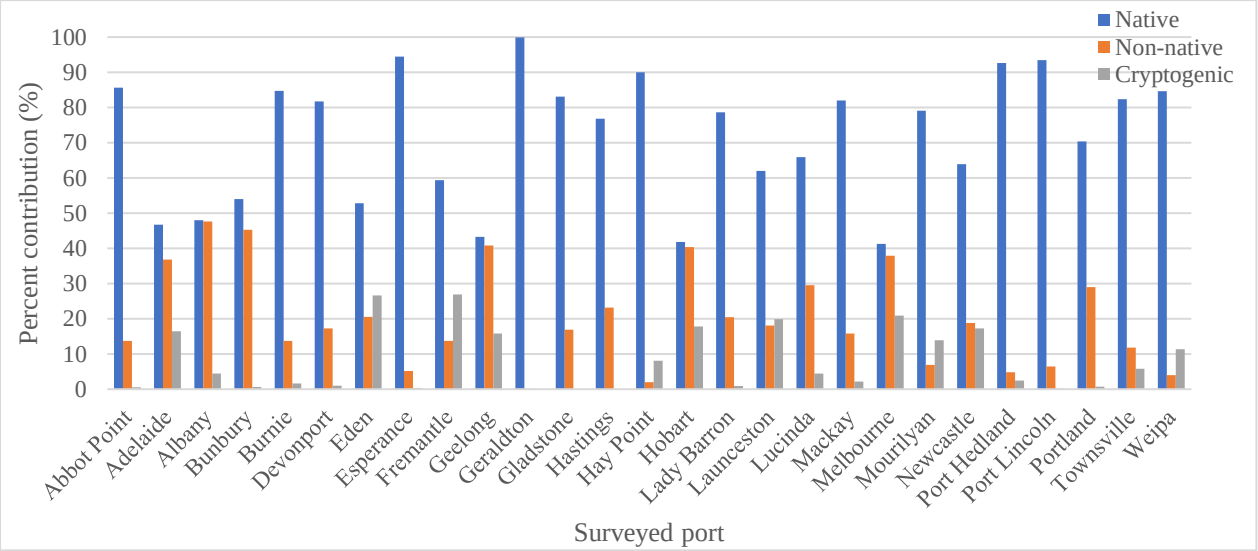


Figure 2.3.7. SIMPER analysis: Percent contribution of species status - native, non-native, cryptogenic to the average similarity as a function of surveyed port.

b) Port type

The graphical representation of the MDS ordination of the species status- native, non-native and cryptogenic show no distinct groupings between major and minor ports (2D stress = 0.17; Figure 2.3.8).

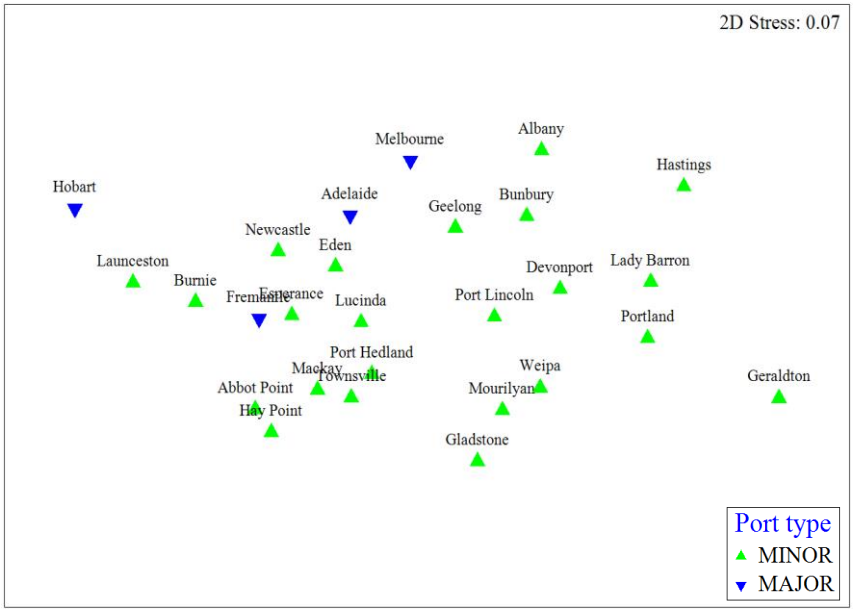


Figure 2.3.8. Multidimensional Scaling (MDS) plot. The proximity of surveyed ports to each other indicates similarity in species status (native, non-native, cryptogenic) as a function of port type.

The PERMANOVA tests were carried out to reveal significant differences in the number of species status as a function of port type. The results showed significant differences ($P < 0.05$; Table 2.3.14) with relatively higher within-group similarity at major ports (85.11%) than the major ports (82.87%). However, the high average similarity (80.96%) between contribution percent of species status at major and minor ports indicates not many variations in terms of species status as a function of port type (Table 2.3.14).

Table 2.3.14. Results of the PERMANOVA and pairwise test performed on the species status as a function of port type (2 levels). Significance marked in bold ($P < 0.05$).

	df	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**	**Unique perms**	**Average similarity (%)**		
Port type	1	647.89	647.89	3.6703	**0.044**	7637	**Major**	**Minor**	**Minor x Major**
Residual	25	4413.1	176.52				85.114	82.867	80.96
Total	26	5060.9							

SIMPER analyses indicate the native species to be the most contributing species status within-group similarity (Minor port = 63.31%; Major = 55.59%) followed by non-native (Minor port = 22.94%; Major = 28.14%) and cryptogenic species (Minor port = 13.35%; Major = 16.27%). The species at major ports were better discriminators between major and minor ports (19.04%). The native species contributed the highest (45.13%) followed by non-native (33.13%) and cryptogenic species (21.74%) to the differences between major and minor ports (Table 2.3.15).

Table 2.3.15. SIMPER analysis: percent contribution of species status as a function of the port type.

Port type	**Minor ports**		**Major ports**		**Minor & Major ports** Average dissimilarity = 19.04%		
	Average similarity = 82.87%		Average similarity = 85.11%				
Species status	**C%**	**Cum.%**	**C%**	**Cum.%**	**Minor ports Av. Abund.**	**Major ports Av. Abund.**	**C%**
Native	63.71	63.71	55.59	55.59	8.32	9.39	45.13
Non-native	22.94	86.65	28.14	83.73	2.99	4.83	33.13
Cryptogenic	13.35	100	16.27	100	1.8	2.96	21.74

C% = Per cent Contribution.

c) Latitudinal groups

The surveyed ports were grouped as a function of their latitude forming 6 latitude groups ranging from 15°S to 40°S. The MDS plot is displayed in Figure 2.3.9; 2D stress = 0.07, showing the ordination patterns and overlaps between ports as a function of latitudinal groups. Ports at 30°S, 35°S and 40°S latitudinal groups showed patterns of grouping and ports at 15°S and 20°S formed another group. This indicates variations in a number of species status between low (15°S and 20°S) and high (30°S, 35°S and 40°S) latitudinal groups. Port Geraldton at latitude 25°S, the only port sampled from that latitude is an outlier.

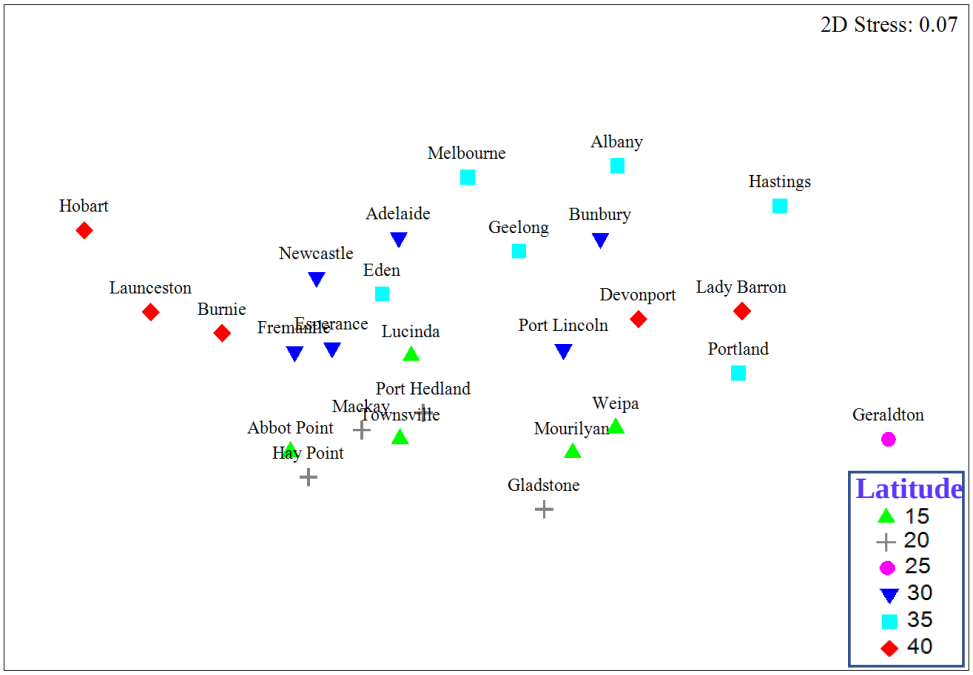


Figure 2.3.9. Multidimensional Scaling (MDS) plot. The proximity of surveyed ports to each other indicates similarity in species status (native, non-native, cryptogenic) as a function of latitudinal groups.

The multivariate PERMANOVA tests revealed statistical significance ($P < 0.05$) in the number of species status as a function of the latitudinal groups (Table 2.3.16). The pairwise PERMANOVA indicated significance ($P < 0.05$) between only 15°S vs 35°S and 35°S vs 20°S latitudinal groups (Table 2.3.17).

Table 2.3.16. Results of the PERMANOVA test performed on the status of the species as a function of latitude (6 levels), Significant value in bold ($P < 0.05$).

	df	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**	**Unique perm**
Latitudinal group	5	1839.6	367.92	2.3984	**0.0342**	9945
Residuals	21	3221.4	153.4			
Total	26	5060.9				

Table 2.3.17. Results of pairwise PERMANOVA test performed on status of the species as a function of latitude, Significant value in bold ($P < 0.05$).

Latitude °S	**t**	***P* (perm)**	**Unique perms**	**Average similarity (%)**
15 vs 30	1.4962	0.1139	462	86.604
15 vs 35	1.9003	**0.0326**	462	82.375
15 vs 40	1.0301	0.331	126	79.657
15 vs 25	2.6089	0.1678	6	73.196

15 vs 20	0.57764	0.6894	126	89.853
30 vs 35	1.7398	0.0865	462	84.548
30 vs 40	0.44573	0.7151	462	81.929
30 vs 25	3.0893	0.147	7	68.861
30 vs 20	1.5833	0.0975	210	86.519
35 vs 40	1.3764	0.1796	462	78.154
35 vs 25	1.7008	0.1423	7	76.691
35 vs 20	2.2963	**0.0193**	210	80.101
40 vs 25	1.5328	0.1654	6	66.575
40 vs 20	0.73562	0.4962	126	80.52
25 vs 20	3.1916	0.195	5	69.76

SIMPER results revealed the native species to be the highest contributor to the within-group average similarity followed by non-native and cryptogenic species as a function of the latitudinal group (Table 2.3.18). The between-group dissimilarity between latitudes 15 vs 35°S and 35 vs 20°S was explained by the high contribution of native species followed by non-native and cryptogenic species (Table 2.3.19).

Table 2.3.18. SIMPER analysis: percent contribution (C%) of species status to average similarity as a function of the latitudinal groups.

Latitude	**15°S**	**20°S**	**30°S**	**35°S**	**40°S**
Average similarity	**89.57%**	**72.97%**	**87.98%**	**84.21%**	**75.91%**
Species status	**C%**	**C%**	**C%**	**C%**	**C%**
Native	70.51	71.53	58.95	60.1	57.71
Non-native	15.55	14.62	26.85	28.34	25.73
Cryptogenic	13.95	13.85	14.2	11.56	16.56

Table 2.3.19. SIMPER analysis: species status contributing (C%)to the average dissimilarity as a function of the latitude that indicated significant differences.

Latitude °S	**15 & 35°S**			**35 & 20°S**		
Avg. dissimilarity (%)	17.62%			19.90%		
Avg. Abundance	**15**	**35**	**C%**	**35**	**20**	**C%**
Native	9.1	6.72	58.43	6.72	9.8	62.56
Non-native	2.56	3.32	21.75	3.32	2.33	21.34
Cryptogenic	1.59	1.84	19.82	1.84	1.8	16.1

To summarise, the number of species status, i.e., native, non-native and cryptogenic species significantly varied across **surveyed ports**. The native species were the most contributing species status across all surveyed ports. However, a high percentage of non-native species was observed at ports; Hobart, Geelong, Albany and Melbourne and cryptogenic species at ports; Eden, Fremantle, Launceston and Weipa. Native red alga, *Jania adherens* was the only contributor at Port Geraldton. The species status as a function of **port type** significantly varied between major and minor ports with a relatively high percentage of native species at minor ports than major ports. But, non-native and cryptogenic species had relatively higher percentages at major ports than at minor ports. Therefore, accepting the hypothesis that occurrences of non-native and cryptogenic species will be relatively greater at major commercial ports than at minor ports because of increased international marine traffic at the major ports. Lastly, species status significantly varied as a function of latitudinal groups. The native species had a relatively high percentage across all latitudinal groups. However, when comparing the non-native and cryptogenic across the latitudinal groups; the results are in coherence with my hypothesis that frequencies of non-native and cryptogenic species increase with the increase in latitude (15 - 40°S).

2.4. Results (B)

New Zealand Port Biological Baseline survey (NZPS)

2.4.1. Presence/absence data

A total of 585 species were identified across the 15 surveyed ports. The species were grouped in 11 phyla groups: Chlorophyta, Ochrophyta, Rhodophyta, Annelida, Arthropoda, Bryozoa, Chordata, Cnidaria, Echinodermata, Mollusca and Porifera (see Appendix - Table A3) for the species list). The most represented phyla in this survey were Arthropoda (128 species) followed by Annelida (84 species) and Mollusca (73 species). The species were further grouped as per their species status; native, non-native and cryptogenic. Of the 585 species, 461 were native species (78.80%), 65 non-native species (11.11%) and 59 cryptogenic species (10.09%) (Table 2.4.1).

Table 2.4.1. The total number of species noted in New Zealand port surveys grouped as per their Phyla and species status (native, non-native and cryptogenic).

Phyla	Total	Native	Non-native	Cryptogenic
Chlorophyta	7	7	0	0
Ochrophyta	16	14	2	0
Rhodophyta	65	56	4	5
Annelida	84	74	8	2
Arthropoda	128	100	13	15
Bryozoa	51	34	14	3
Chordata	56	43	3	10
Cnidaria	35	19	9	7
Echinodermata	11	9	1	1
Mollusca	73	68	3	2
Porifera	59	37	8	14
Total	585	461	65	59

2.4.2. Variations in total presence of species as a function of replicates (sampling effort) at each surveyed port

The total number of species at each port was divided with the number of replicates to obtain the relative number of species (Table 2.4.2). The relative number of species excludes the bias caused due to the differences in replicates (sampling effort). The relative total number of species was relatively highest at Picton 2005 (10.76%) followed by Timaru 2005 (8.29%), and lowest at Gulf Harbour Marina (3.73%) (Figure 2.4.1).

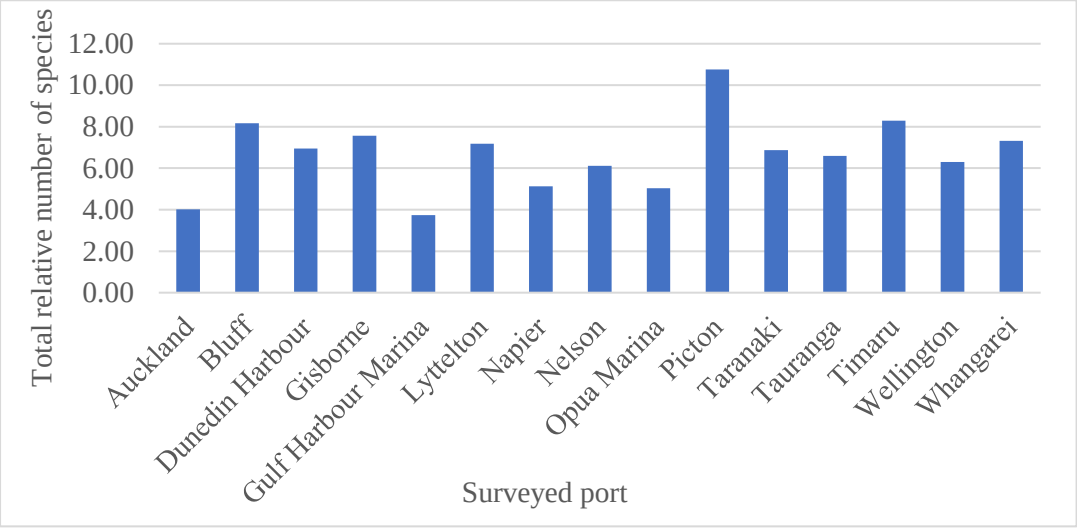


Figure 2.4.1. The total relative number of species across 15 surveyed ports.

Table 2.4.2. The total relative number of species as a function of replicates (sampling effort) at each surveyed port.

Surveyed ports	Total number	Replicates	Relative Total	Total percent (%)
Auckland	96	71	1.35	4.01
Bluff	146	53	2.75	8.17
Dunedin Harbour	110	47	2.34	6.94
Gisborne	79	31	2.55	7.56
Gulf Harbour Marina	73	58	1.26	3.73
Lyttelton	121	50	2.42	7.18
Napier	83	48	1.73	5.13
Nelson	194	94	2.06	6.12
Opua Marina	51	30	1.70	5.04
Picton	127	35	3.63	10.76
Taranaki	102	44	2.32	6.87
Tauranga	151	68	2.22	6.59
Timaru	109	39	2.79	8.29
Wellington	155	73	2.12	6.30
Whangarei	116	47	2.47	7.32

2.4.3. Occurrences of species

The presence of each species was calculated across all surveyed ports to observe the high occurring species in the New Zealand port survey (NZPS). The cryptogenic tunicates, *Asterocarpa cerea* and *Corella eumyota* occurred at all surveyed ports. The top 10 species occurring in most of the surveyed ports are listed in Table 2.4.3.

Table 2.4.3. Total occurrences of top 10 species across 15 surveyed ports.

Species	Phyla	Species status	Total port occurrences
Asterocarpa cerea	Chordata	Cryptogenic	15
Corella eumyota	Chordata	Cryptogenic	15
Notomithrax minor	Arthropoda	Native	14
Austrominius modestus	Arthropoda	Native	13
Bugula flabellata	Bryozoa	Non-native	13
Cnemidocarpa bicornuta	Chordata	Native	13
Cnemidocarpa nisiotus	Chordata	Native	13
Molgula mortenseni	Chordata	Native	13
Lepidonotus polychromus	Annelida	Native	12
Modiolarca impacta	Mollusca	Native	12

2.4.4. Variations in the community composition as a function of the surveyed port, port type and latitudinal groups

a) Surveyed ports

The multivariate PERMANOVA was performed to indicate patterns in species composition as a function of the surveyed port. The results revealed high significance ($P < 0.0001$; Table 2.4.4) as a function of the surveyed port. The pairwise PERMANOVA also revealed high significance between the ports ($P < 0.0001$). The ports; Picton (26.45%) had the most similar species followed by Opua Marina (26.11%) and least within-group similarity at Port Nelson (8.88%) (Table 2.4.5). The between-group dissimilarity in species composition between surveyed ports ranged from 80.05% (Picton vs Wellington) to 98.37% (Dunedin vs Gisborne).

Table 2.4.4. Results of the PERMANOVA test performed on the presence/absence of species as a function of the surveyed port. Significance marked in bold ($P < 0.05$).

	df	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**	**Unique perms**
Surveyed port	14	6.49E+05	46329	12.862	**0.0001**	9606
Residual	773	2.78E+06	3602			
Total	787	3.43E+06				

SIMPER results revealed the top 5 species to contribute to more than 50% average within-group similarity as a function of surveyed ports (Table 2.4.5). Native barnacle, *Austrominius modestus* was observed to be the highest contributing species at ports, Auckland (21.57%), Bluff (22.59%), Dunedin (19.54%), Nelson (27.54%), Opua Marina (58.6%) and Tauranga (20.48%). The non-native bryozoan, *Bugula neritina* contributed relatively highest at ports Gisborne (25.11%), Napier (19.04%) and Whangarei (17.70%). The non-native bryozoan, *Watersipora subtorquata* contributed highest at ports, Timaru (24.79%) and Lyttelton (22.04%). The average between-group dissimilarities ranged from 80.05% (Picton vs Wellington) to 98.37% (Dunedin vs Gisborne). SIMPER results revealed that the species that contributed to the within-group similarity also contributed to the between-group similarity, but the average abundance contribution from each port varied, leading to the dissimilarities in community composition between surveyed ports.

Table 2.4.5. SIMPER analysis: average similarity in the presence/absence of species as a function of the surveyed port.

Auckland **Average similarity: 17.69**				**Bluff** **Average similarity: 11.84**				**Dunedin Habour** **Average similarity: 14.95**			
Species	Avg. Abund	C%	Cum.%	Species	Avg. Abund	C%	Cum.%	Species	Avg. Abund	C%	Cum.%
Austrominius modestus	0.42	21.57	21.57	*Austrominius modestus*	0.28	22.59	22.59	*Austrominius modestus*	0.38	19.54	19.54
Caberea rostrata	0.52	15.58	37.15	*Corella eumyota*	0.47	15.21	37.8	*Haplocheira barbimana*	0.53	16.21	35.75
Crassostrea gigas	0.46	13.72	50.87	*Phycodrys quercifolia*	0.36	7.72	45.52	*Nereis falcaria*	0.4	9.06	44.81
Ostrea chilensis	0.37	6.5	57.38	*Galeolaria hystrix*	0.32	6.22	51.74	*Asterocarpa cerea*	0.34	5.92	50.74
Pyura picta	0.34	5.39	62.77	*Nereis falcaria*	0.3	5.3	57.04	*Aplidium adamsi*	0.3	4.55	55.28
Gisborne **Average similarity: 13.59**				**Gulf Harbour Marina** **Average similarity: 16.16**				**Lyttelton** **Average similarity: 23.89**			
Species	Avg. Abund	C%	Cum.%	Species	Avg. Abund	C%	Cum.%	Species	Avg. Abund	C%	Cum.%
Bugula neritina	0.55	25.11	25.11	*Styela plicata*	0.4	12.48	12.48	*Watersipora subtorquata*	0.76	22.04	22.04
Scrupocellaria ornithorhyncus	0.45	14.41	39.51	*Balanus trigonus*	0.36	11.31	23.79	*Branchiomma curta*	0.6	10.62	32.66
Leptograpsus variegatus	0.26	5.85	45.36	*Schizoporella errata*	0.29	9.07	32.86	*Austrominius modestus*	0.44	9.03	41.69
Cnemidocarpa nisiotus	0.29	5.43	50.8	*Dictyota dichotoma*	0.36	8.1	40.97	*Asterocarpa cerea*	0.52	7.83	49.52
Paguristes setosus	0.29	5.34	56.14	*Asterocarpa cerea*	0.34	7.78	48.75	*Leucothoe trailli*	0.46	5.65	55.18
Napier **Average similarity: 13.15**				**Nelson** **Average similarity: 8.92**				**Opua Marina** **Average similarity: 26.11**			
Species	Avg. Abund	C%	Cum.%	Species	Avg. Abund	C%	Cum.%	Species	Avg. Abund	C%	Cum.%
Bugula neritina	0.44	19.04	19.04	*Austrominius modestus*	0.38	27.54	27.54	*Austrominius modestus*	0.53	58.6	58.6
Bugula flabellata	0.4	12.89	31.93	*Asterocarpa cerea*	0.35	10.8	38.35	*Asterocarpa cerea*	0.43	6.41	65
Proscoloplos bondi	0.31	7.39	39.32	*Petrolisthes novaezealandiae*	0.3	9.07	47.42	*Balanus trigonus*	0.4	6.2	71.2
Austrominius modestus	0.25	7.23	46.55	*Haplocheira barbimana*	0.24	5.93	53.35	*Neanthes kerguelensis*	0.4	6.18	77.38
Pterocirrus brevicornis	0.29	6.73	53.27	*Xenostrobus pulex*	0.15	3.69	57.04	*Halicarcinus varius*	0.33	3.68	81.06

Picton **Average similarity: 26.45**				**Taranaki** **Average similarity: 19.71**				**Tauranga** **Average similarity: 18.95**			
Species	Avg. Abund	C%	Cum.%	Species	Avg. Abund	C%	Cum.%	Species	Avg. Abund	C%	Cum.%
Aulacomya atra maoriana	0.86	15.27	15.27	*Chaemosipho columna*	0.66	31.49	31.49	*Molgula mortenseni*	0.59	10.5	10.5
Ostrea chilensis	0.71	10.38	25.66	*Xenostrobus pulex*	0.57	23.27	54.76	*Austrominius modestus*	0.29	9.99	20.48
Petrolisthes elongatus	0.66	8.16	33.82	*Austrominius modestus*	0.3	7.34	62.1	*Balanus trigonus*	0.51	8.18	28.66
Perna canaliculus	0.57	6.01	39.83	*Watersipora subtorquata*	0.36	7.01	69.11	*Lepidonotus polychromus*	0.46	6.49	35.15
Nicolea armilla	0.54	5.14	44.97	*Lumbrineris sphaerocephala*	0.25	2.15	71.26	*Maoricrypta costata*	0.47	6.45	41.6
Timaru **Average similarity: 22.15**				**Wellington** **Average similarity: 21.72**				**Whangarei** **Average similarity: 12.91**			
Species	Avg. Abund	C%	Cum.%	Species	Avg. Abund	C%	Cum.%	Species	Avg. Abund	C%	Cum.%
Watersipora subtorquata	0.74	24.79	24.79	*Petrolisthes elongatus*	0.63	9.18	9.18	*Bugula neritina*	0.45	17.7	17.7
Branchiomma curta	0.59	11.54	36.32	*Mytilus galloprovincialis*	0.6	8.34	17.53	*Austrominius modestus*	0.28	12.31	30.01
Austrominius modestus	0.44	9.94	46.27	*Aulacomya atra maoriana*	0.6	7.56	25.09	*Ostrea aupouria*	0.45	12.03	42.03
Cryptosula pallasiana	0.41	7.58	53.85	*Ostrea chilensis*	0.53	5.75	30.84	*Balanus trigonus*	0.43	11.36	53.39
Pseudosphaeroma campbellense	0.33	6.88	60.73	*Petrolisthes novaezealandiae*	0.49	5.14	35.99	*Bugula flabellata*	0.3	4.83	58.22

b) Port type (major and minor ports)

The graphical representation of the MDS ordination of the presence/absence data showed no groupings of similar species composition as a function of port type, 5 major commercial shipping ports and 10 minor shipping ports (2D stress = 0.13; Figure 2.4.2). The PERMANOVA tests results were in coherence with the MDS ordination and indicated no significant (P = 0.96) variations in community composition as a function of port type (Table 2.4.6).

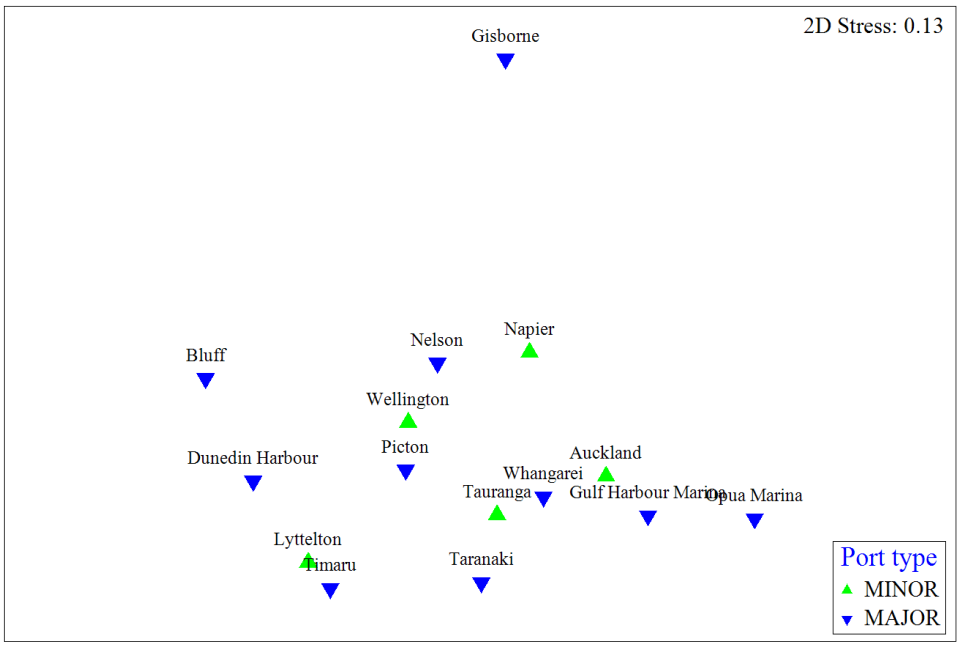


Figure 2.4.2 Multidimensional Scaling (MDS) plot. The proximity of surveyed ports to each other indicates similarity in community composition as a function of port type.

Table 2.4.6. Results of the PERMANOVA analysis and pairwise test performed on the presence of species as a function of port type (2 levels). Significance marked in bold (P < 0.05).

Source	df	SS	MS	Pseudo-*F*	*P* (perm)	Unique perms	Average similarity (%)		
Port type	1	1500.1	1500.1	0.63315	0.967	2889	**Major**	**Minor**	**Minor x Major**
Residual	13	30799	2369.2				35.53	29.84	34.47
Total	14	32300							

c) Latitudinal groups

The surveyed ports at each latitude were grouped, forming 3 latitudinal groups; 35°S, 40°S and 45°S. The MDS plot showed the ordination patterns as a function of the latitudinal groups (35, 40, 45°S) (Figure 2.4.3; 2D stress = 0.13).

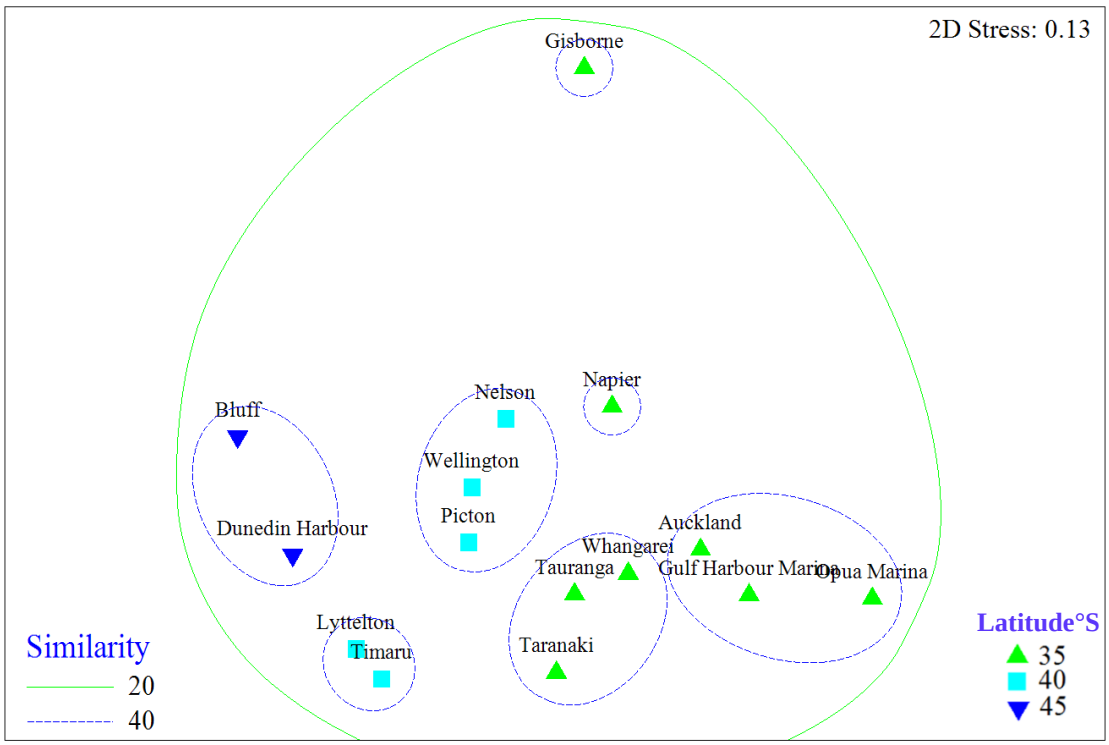


Figure 2.4.3. Multidimensional Scaling (MDS) plot. The proximity of latitudes to each other indicates similarity in the community composition.

The PERMANOVA tests, as a function of latitude, revealed high significance ($P < 0.0001$) (Table 2.4.7). The pairwise PERMANOVA test revealed significant differences between 35 vs 45°S ($P = 0.02$) and 35 vs 40°S ($P = 0.002$) but not between 40 vs 45°S ($P = 0.14$) (Table 2.4.8).

Table 2.4.7. Results of the PERMANOVA test performed as a function of latitude (3 levels). Significance ($P < 0.05$) marked in bold.

	df	SS	MS	Pseudo-*F*	*P* (perm)	Unique perms
Latitude	2	8279.5	4139.7	2.0681	**0.0001**	9499
Residual	12	24020	2001.7			
Total	14	32300				

Table 2.4.8. Results of the PERMANOVA and pairwise test as a function of port type (2 levels). Significance marked in bold ($P < 0.05$).

Latitude	t	P (perm)	Unique perms
35 vs 45 °S	1.48	**0.022**	45
35 vs 40 °S	1.45	**0.003**	1282
45 vs 40 °S	1.32	0.139	21

SIMPER analysis for latitudinal groups indicated latitudes 35 vs 45°S to have the highest average dissimilarity (76.09%). The species that indicated the dissimilarities are; *Bugula flabellata* (NN), *Forsterygion lapillum* (N), *Nereiphylla castanea* (N), *Halisarca dujardini* (NN) and *Leuconopsis obsoleta* (N). The species at latitude 45°S were better discriminators. The species indicating dissimilarities between latitudes 35 vs 40°S (71.28%) are; *Petrolisthes elongatus* (N), *Asterocarpa coerulea* (N), *Watersipora subtorquata* (NN), *Undaria pinnatifida* (NN) and *Bougainvillia muscus* (C) (Table 2.4.9).

Table 2.4.9. SIMPER analysis: average dissimilarity of community composition as a function of latitude. Species status – native (N), non-native (NN) and cryptogenic (C).

35 & 45 °S Average dissimilarity = 76.09%				**35 & 40 °S** Average dissimilarity = 71.28%			
Species	**35**	**45**	**C%**	**Species**	**35**	**40**	**C%**
Bugula flabellata (NN)	0.47	0	1.14	*Petrolisthes elongatus* (N)	0.07	0.5	0.99
Forsterygion lapillum (N)	0.06	0.5	1.06	*Asterocarpa coerulea* (N)	0.03	0.43	0.94
Nereiphylla castanea (N)	0.2	0.59	0.98	*Watersipora subtorquata* (NN)	0.24	0.52	0.94
Halisarca dujardini (NN)	0.2	0.55	0.97	*Undaria pinnatifida* (NN)	0	0.35	0.81
Leuconopsis obsoleta (N)	0	0.41	0.97	*Bougainvillia muscus* (C)	0.1	0.31	0.80

C% = Per cent Contribution.

In summary, the presence of species as a function of surveyed ports showed significance; however, the community composition as a function of port type did not show the significance. The latitudinal groups indicated significant differences for groups; 35 vs 40°S and 35 vs 45°S. The species at higher latitudes (40, 45°S) being better discriminators explaining the differences. A strong association in the community composition between ports; i) Auckland, Gulf Harbour and Opua Marina (native barnacle *Austrominius modestus*, cryptogenic tunicate *Asterocarpa cerea*, cryptogenic barnacle *Balanus trigonus*), ii) Tauranga,

Whangarei, Taranaki and Napier (native barnacle *Austrominius modestus*, cryptogenic barnacle *Balanus trigonus*), iii) Wellington, Picton and Nelson (native mollusc *Aulacomya atra maoriana*, native false crab *Petrolisthes elongatus* and native molluscs *Ostrea chilensis*) iv) Lyttelton and Timaru (non-native bryozoan *Watersipora subtorquata*, native polychaete *Branchiomma curta* and native barnacle *Austrominius modestus*, v) Bluff and Dunedin (native barnacle *Austrominius modestus* and cryptogenic tunicate *Corella eumyota*), was observed. The results indicated similar high contributing species at proximity ports. The species showing variations as a function of surveyed ports and latitudinal groups are stated in Table 2.4.10.

Table 2.4.10. The list of species that indicated variations as a function of surveyed ports and latitudinal groups.

Species	Phyla	Species status
Asterocarpa cerea	Chordata	Cryptogenic
Aulacomya atra maoriana	Mollusca	Native
Austrominius modestus	Arthropoda	Native
Balanus trigonus	Arthropoda	Native
Bougainvillia muscus	Cnidaria	Cryptogenic
Bugula flabellata	Bryozoa	Non-native
Bugula neritina	Bryozoa	Non-native
Chaemosipho columna	Arthropoda	Native
Corella eumyota	Chordata	Cryptogenic
Halisarca dujardini	Porifera	Non-native
Molgula mortenseni	Chordata	Native
Mytilus galloprovincialis	Mollusca	Cryptogenic
Nereiphylla castanea	Annelida	Native
Ostrea chilensis	Mollusca	Native
Petrolisthes elongatus	Arthropoda	Native
Petrolisthes novaezealandiae	Arthropoda	Native
Styela plicata	Chordata	Cryptogenic
Watersipora subtorquata	Bryozoa	Non-native
Xenostrobus pulex	Mollusca	Native

2.4.5. Variations in the species status - native, non-native and cryptogenic species as a function of surveyed ports, port type and latitudinal groups

a) Surveyed ports

The total number of species at each port was divided with the number of replicates to obtain the relative number of species (Table 2.4.11). The native species were relatively observed in higher percentages, followed by non-native and cryptogenic species (Figure 2.4.4). The relatively high levels of native species were highest at Port Picton (15.20) and lowest at Melbourne (0.33%). In contrast, the non-native species were highest at Lyttelton (2.62%), Timaru (2.51%) and lowest at Port Picton (0.51). The cryptogenic species were relatively in high levels at Wellington (2.11) and lowest at Port Taranaki (0.45) (Table 2.4.11).

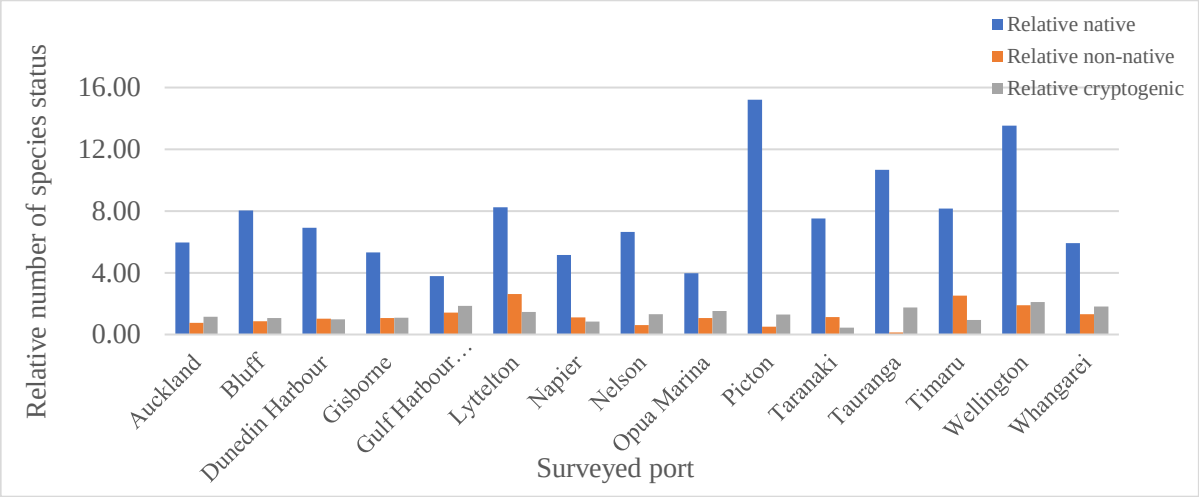


Figure 2.4.4. The total relative number of species status - native (blue), non-native (orange) and cryptogenic (grey) species across 15 surveyed ports.

Table 2.4.11. The total number of species as a function of status - native, non-native and cryptogenic species - across 15 surveyed ports.

Surveyed port	Total Native	Total Non-native	Total Cryptogenic	Replicates	Relative native	Relative non-native	Relative cryptogenic
Auckland	423	53	81	71	5.96	0.75	1.14
Bluff	426	46	57	53	8.04	0.87	1.08
Dunedin Harbour	325	48	46	47	6.91	1.02	0.98
Gisborne	165	33	34	31	5.32	1.06	1.10
Gulf Harbour Marina	219	82	108	58	3.78	1.41	1.86
Lyttelton	412	131	73	50	8.24	2.62	1.46
Napier	247	53	40	48	5.15	1.10	0.83
Nelson	625	58	123	94	6.65	0.62	1.31

Opua Marina	119	32	46	30	3.97	1.07	1.53
Picton	532	18	45	35	15.20	0.51	1.29
Taranaki	331	50	20	44	7.52	1.14	0.45
Tauranga	725	9	119	68	10.66	0.13	1.75
Timaru	318	98	37	39	8.15	2.51	0.95
Wellington	987	138	154	73	13.52	1.89	2.11
Whangarei	278	62	85	47	5.91	1.32	1.81

Furthermore, the species status, i.e., native, non-native and cryptogenic, were regressed to observe the relationship between species status across all surveyed ports. However, no significant relationship was observed between native vs non-native ($P = 0.08$), cryptogenic vs non-native ($P = 0.47$), and cryptogenic vs non-native ($P = 0.79$) (Table 2.4.12).

Table 2.4.12. Results for regression for species status - native, non-native and cryptogenic species (significance = $P < 0.05$, marked in bold).

Species status	R^2	R	*P*	y
Native vs Non-native	0.002	-0.046	0.0868	7.9319 + 0.2216*x
Cryptogenic vs Non-native	0.042	0.204	0.466	5.7133 + 1.4906*x
Cryptogenic vs Non-native	0.006	0.076	0.788	1.2501 + 0.0497*x

Multivariate analysis, PERMANOVA was performed to indicate variations in the number of species status as a function of the surveyed port. The number of species (native, non-native and cryptogenic) was found to vary significantly among surveyed ports (PERMANOVA; $P < 0.0001$; Table 2.4.13).

Table 2.4.13. Results of the PERMANOVA test performed on the species status as a function of surveyed port (15 levels). Significance marked in bold ($P < 0.05$).

Source	**df**	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**	**Unique perms**
Port	14	89881	6420.1	5.6423	**0.0001**	9839
Residual	773	8.80E+05	1137.8			
Total	787	9.69E+05				

The pairwise tests revealed significance ($P < 0.05$) between most of the ports with more than 50% average similarities. The native species contributed the most to the within-port similarity and between-port dissimilarity followed by non-native species (Table 2.4.14).

However, a relatively high percent of cryptogenic species was observed at ports; Nelson, Wellington, Tauranga and Picton.

Table 2.4.14. SIMPER analysis: percent contribution of species status - native, non-native and cryptogenic species, as a function of the surveyed port.

Surveyed port	Avg. similarity (%)	Native (%)	Non-native (%)	Cryptogenic (%)
Auckland	56.95	72.56	16.3	11.13
Bluff	61.52	76.97	12.19	10.83
Dunedin Harbour	65.63	71.3	14.98	13.72
Gisborne	62.96	61.76	21.54	16.7
Gulf Harbour Marina	51.35	50.34	26.98	22.68
Lyttelton	76.17	58.18	30.59	11.23
Napier	53.49	71.45	17.2	11.35
Nelson	56.71	78.98	4.76	16.26
Opua Marina	55.85	77.91	12.98	9.11
Picton	72.3	75.9	8.84	15.27
Taranaki	70.74	87.1	12.14	0.76
Tauranga	65.61	80.36	3.11	16.53
Timaru	72.09	65.45	27.87	6.69
Wellington	58.92	57.29	19.22	23.49
Whangarei	55.43	57.5	22.88	19.62

b) Port type

The PERMANOVA results for species status revealed no statistical significance ($P = 0.09$) as a function of port type (Table 2.4.15). Therefore, rejecting my hypothesis that occurrences of non-native and cryptogenic species will be relatively greater at major commercial ports than at minor ports.

Table 2.4.15. The PERMANOVA analysis used to determine differences in the species status as a function of port type (2 levels), Significant value in bold ($P < 0.05$).

Source	**df**	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**	**Unique perms**
Port type	1	76.872	76.872	2.514	0.091	2881
Residual	13	397.51	30.578			
Total	14	474.38				

c) Latitudinal groups

PERMANOVA results revealed no significance ($P = 0.37$) between the number of the status of the species as a function of latitude (Table 2.4.16). Therefore, rejecting my hypothesis that frequencies of non-native and cryptogenic species increase with increase in latitude.

Table 2.4.16. The PERMANOVA analysis used to determine differences in the species status as a function of latitude (3 levels), Significant value in bold ($P < 0.05$).

Source	df	SS	MS	Pseudo-*F*	*P* (perm)	Unique perm
Latitude	2	74.818	37.409	1.1235	0.3681	9593
Residuals	12	399.56	33.297			
Total	14	474.38				

To summarise, the species status – native, non-native and cryptogenic species showed significance as a function of surveyed ports. The relatively high percentages of native species compared to non-native and cryptogenic species were observed at all ports. However, no significance was observed as a function of the port type and latitudinal groups. For NZPS, I reject both my hypotheses based on the factors; port type and latitudinal groups.

2.5. Discussion

2.5.1. Background

Marine organisms have spread from their native range to another through human transport such as shipping (ballast water exchange, hull fouling, dry ballast, etc.), aquaculture (intentional or unintentional), trade escape and man-made canals where species move from one place to another (Ruiz et al. 2000; Hewitt & Hayes 2002). The rate of bioinvasions has immensely increased during the last decade and most likely be increasing due to accelerated global trade, transport and tourism. Marine traffic plays a key role as transport hubs facilitating the spread of species through hitchhiking on cargo ships (Hulme 2009; Seebens et al. 2013). Although not all species survive the range expansion, some die during transit whilst some cannot withstand the new environmental conditions. However, the species that survive and establish can cause immense impacts on ecological and socio-economic ecosystems. Therefore, understanding the pathway and predicting potential invasive species' entry point is likely to be the first step towards strategising any rapid management and eradication plans. This chapter, for this reason, analysed two large national-scale baseline port surveys (the Australian Port Survey dataset [APS] and the New Zealand Port Biological Baseline Survey dataset [NZPS]) to determine the

community structure and the species status – native, non-native and cryptogenic – at the surveyed ports and tested factors of port type (major vs minor ports) and latitudinal groups - explain the occurrence of non-native species. The results of this study highlighted the major commercial shipping ports being the hotspots for non-native species and latitudinal separation with regard to occurrences of non-native species.

2.5.2. Australian Port Surveys (APS)

The extensive sampling of Australian port surveys indicated 88% native species, 9% non-native and 3% cryptogenic species. The species composition amongst surveyed ports significantly differed, with relatively stronger species composition (within-group similarity) at Port Geelong (40.69%) followed by Hobart (40.16%) whereas weak species composition among Port Esperance (9.23%). Port Geraldton sat as an outlier as a native red alga, *Jania adherens* was the only species contributing to its within-group similarity. This led to high dissimilarities between Port Geraldton and other surveyed ports. Port Geelong and Port Melbourne however, had the average lead dissimilarity indicating a similar set of species contributing at each port.

It is interesting to observe that ports in the southern region of Australia such as Geelong, Melbourne, Hobart, Portland, Fremantle, Newcastle, Eden, Adelaide and two ports in the north region of Australia, Port Hay point and Mackay had relatively low between ports dissimilarity. These ports are located within close proximity to each other and experience immense domestic traffic which may likely be the reason for the sharing of species. These results for the factor latitudinal groups supported these assumptions. The ports in the north of Australia at 15°S and 20°S formed one group whereas ports at 30°S, 35°S and 40°S formed another (MDS plot). A strong separation between northern (low latitudes) and southern (high latitudes) of Australia was observed with regards to species composition. Similarly, the species status- native, non-native and cryptogenic significantly varied among latitude groups with a strong association between species status at high latitudes and low latitudes. Although native species were the main species status explaining similarity and dissimilarity among and between latitude groups, the non-native species were relatively abundant at higher latitudes. These results were explained by the top 5 species explaining similarity for low latitudes are cryptogenic barnacle *Balanus amphitrite*, native barnacle *Striatobalanus amaryllis*, native polychaete *Thelepus robustus*, cryptogenic polychaete *Lysidice collaris* and native oyster *Dendostrea folium*. In contrast, species such as native clam *Hiatella australis*, non-native bryozoan *Watersipora*

subtorquata, native sea spider *Halicarcinus ovatus*, non-native bryozoan *Bugula neritina* and cryptogenic barnacle *Balanus trigonus* at higher latitudes.

The species, however, did not show significance, but pairwise tests showed a difference in species composition between major and minor ports. The species at major ports had stronger within-group similarity than at minor ports (SIMPER). Similarly, the species status significantly differed between port types with native species as the main species contributing to within-group and between-group similarity. For non-native species, the major ports had high levels of non-native species compared to minor ports. The species (top 5) explaining the similarities within minor ports are native clam *Hiatella australis*, non-native bryozoan *Watersipora subtorquata*, cryptogenic barnacle *Balanus amphitrite*, non-native bryozoan *Bugula neritina* and native tunicate *Pyura stolonifera* whereas species such as cryptogenic barnacle *Balanus trigonus*, non-native tunicate *Ciona intestinalis*, native sea spider *Halicarcinus ovatus*, native brittle star *Amphipholis squamata* and non-native mussel *Musculista senhousia* at major ports.

Given these results, the major ports analysed - Adelaide, Fremantle, Hobart and Melbourne are in the south of Australia explaining a high number of non-native species at high latitudes. These results highlight several on-going challenges such as major commercial ports being hotspots for marine invasions and the role of shipping as the main pathway for introductions and thereby spread of species (especially non-native species) through regional transport connecting ports for domestic trade or recreational activities.

2.5.3. New Zealand Port Biological Baseline survey (NZPS)

The analysis of the NZPS dataset identified 78.80% native species, 11.11% non-native species and 10.09% cryptogenic species. The species composition significantly differed amongst 15 surveyed ports. The MDS plots, in this study, indicated close species interaction between ports forming groups such as; i) Nelson, Wellington and Picton, ii) Bluff and Dunedin Harbour, iii) Lyttelton and Timaru, iv) Whangarei, Tauranga and Taranaki, v) Auckland, Gulf Harbour Marina and Opua Marina. The major ports Auckland, Lyttelton, Napier, Tauranga and Wellington grouped with minor ports. The multivariate analyses supported the MDS patterns, the species composition and species status did not vary as a function of major and minor port types. The port groups observed are located at proximity distance. These results indicate the domestic transfer of species presumably due to local or regional marine traffic with hull fouling

being the important pathway for the spread of species at regional scales (Coutts & Taylor 2004; Floerl et al. 2004; Floerl & Inglis 2005).

Considering the factor; latitudinal groups (35°S, 40°S and 45°S) of New Zealand, the species composition significantly differed amongst latitudinal groups with high similarity in species composition between higher latitudes (33.39%) (40°S vs 45°S) than between low latitudes (35°S vs 40°S = 31.51%; 35°S vs 45°S = 25.58%). Considering the species status analyses, species status did not show a significant difference between latitudinal groups. As seen above, with the species contributing to the similarity among each latitudinal group, the native species were the main species representing latitude groups followed by cryptogenic and lastly the non-native species. These results were explained by the top 5 species explaining similarity with 35°S latitudes were cryptogenic tunicate *Asterocarpa cerea,* non-native bryozoan *Bugula neritina,* cryptogenic tunicate *Corella eumyota*, native sea spider *Halicarcinus cookii* and native sea spider N*otomithrax minor.* At 40°S latitude, species contributing to the within-group similarity are cryptogenic tunicate *Asterocarpa cerea*, native barnacle *Austrominius modestus,* non-native bryozoan *Bugula flabellata*, native tunicate *Cnemidocarpa bicornuta* and native tunicate *Cnemidocarpa nisiotus*. In contrast, species such as native red algae *Adamsiella chauvinii,* native amphipod *Amaryllis macrophthalma,* native tunicate *Aplidium adamsi,* cryptogenic tunicate *Aplidium phortax* and cryptogenic tunicate *Asterocarpa cerea* explained similarity at 45°S latitude. These species consist of biofouling species which commonly encrust on the hull of the ships, engine or port equipment that may result in the domestic transfer of species. These results highlight the complexity of human-mediated transfer of species from one port to another or even port to marinas (Floerl et al. 2004).

2.5.4. Defining pathways

Marine traffic has been highlighted as the potential vector to transfer non-native marine species across the world (Hewitt et al. 2009; Seebens et al. 2016; Ziako et al. 2016; O'Brien et al. 2017). Marine traffic arriving at major international shipping ports are the main access points (Campbell & Hewitt 2007). The marine vessels dock at ports and harbours for extended periods and are a substantial time for fouling to occur (Hewitt et al. 2009). Regarding invasion success at major ports, the commercial ports receiving large volumes of international trade as well as propagules of non-native species. The release of a large number of propagules will increase the chance of non-native species to survive and reproduction at new environments, i.e. ports. Therefore, the heavily invaded areas may serve as hubs for the transfer of species from

major ports to nearby minor ports (Lockwood et al. 2009; Firth et al. 2016; Olenin et al. 2016; Johnston et al. 2017). This is in consistence with the results of this study indicating similar species between major ports and nearby minor ports where the marine vessels frequently travel to and from. With an increase in human activities over the past 50 years, maritime traffic has increased risks of transfer of species from one region to another.

Recent changes to the climatic conditions with increasing global warming, the species from warm regions (low latitudes) spread to colder regions (high latitudes) consequently changing their geographical ranges thereby affecting the ecological ecosystems (Walther et al. 2002, 2009). There a climate-mediated invasion process follows a classic invasion process (Walther et al. 2009). Human mediated vectors and climate change are the two most prevalent problems impacting marine biodiversity (Rahel & Olden 2008). The altered habitats put stress on the native species to adapt new conditions; in contrast, the non-native species are excellent in adapting, establishing and spreading. Combination of the number of major ports at high latitudes increases invasion pressure.

The ports and marinas receiving a high frequency of marine traffic are the focal point of entry for marine bioinvasions (Firth et al. 2016; Olenin et al. 2016; Johnston et al. 2017). Commercial shipping vessels have also been associated with non-native species in other studies (Hopkins and Forrest 2010; Lo et al. 2012). As such, major shipping ports supporting a high number of non-native species was not surprising, especially in the south of Australia where the shipping traffic is relatively high (Commonwealth of Australia 2015). Domestic marine traffic poses a threat to the intra-regional transfer of non-native species from port to port within a region (Forrest et al. 2009; Clarke Murray 2011; Hänfling et al. 2011). Domestic trade vessels, fishing vessels, pleasure boats and tour boats move extensively among harbours connecting the major port to other harbours or marinas. The southern regions of Australia are home to some of Australia's busiest shipping routes including Bass Strait, east-west and west-east international shipping routes (Commonwealth of Australia 2015). The marine traffic comprises of international and coastal cargo trading ships, passenger shipping, and ferry services across the Bass Strait. These regions are also productive for fisheries, and commercial fishing is concentrated in inshore coastal waters, and most of the recreational fishing occurs inland, near the coasts and bays. Major ports and adjacent marinas in these areas have numerous marine-based industries and are connected to various minor ports through commercial and recreational fishing, yachts or pleasure crafts.

The main shipping routes for international and domestic marine traffic in New Zealand and the frequency of marine vessels increase the risk of inter-port transfer of non-native species. However, the frequency of vessels is not the only factor facilitating invasions; the marine vessels carrying high volumes of ballast water - non-native discharge species. For instance, Auckland is the busiest port in New Zealand; however, Port Taranaki receives high volumes of bulk carriers and tankers carrying petroleum. Coutts & Taylor (2004) examined 30 merchant ships arriving New Zealand and concluded that hulls of the ships are more susceptible to fouling and spread of species on vessels. Biosecurity New Zealand and Cawthron Institute have developed a database to record international cargo vessels and ballast water operations (Dodgshun et al. 2007). However, domestic vessels operating exclusively between NZ domestic ports are not required to report the ballast water discharge, the introduction of non-native species via ballast water is most likely.

Domestic vessels and local crafts such as fishing vessels and pleasure crafts put a significant pressure of transfer of non-native species through hull fouling (Forrest et al. 2009; Clarke & Johnston 2011; Hänfling et al. 2011). A report on eradication measures of *Undaria pinnatifida*, spread from Wellington to South Island revealed fishing vessels to be the primary vector for the transfer of the seaweed (Department of Conservation 2005). Facilities such as marinas, harbours and berths are exposed to frequent movements of recreational and fishing vessels along the coastline. Additionally, these pleasure boats dock in marinas and harbours for a long period – become heavily exposed to hull fouling and being potential vectors for non-native species. For example, about 47% yachts and 30% of launches in ports between Timaru and Bluff, New Zealand were heavily fouled by non-native seaweed, *Undaria pinnatifida* (Department of Conservation 2005). New Zealand in recent years has implemented regulations for recreational vessels posing risks on intra-coastal species transfer are required to follow Craft Risk Management Standard (CRMS) and IMO guidelines (i.e. Biofouling Management Plan and BioFouling Record Book), provide evidence of records of non-permanent ballast water, vessel hull cleaning and use of appropriate antifouling treatment (MPI 2014; IMO 2015).

2.5.5. Management implications

As outlined in this study, human-mediated pathways at a regional scale also indicate as high-risk pathways linking major and minor ports (Coutts & Forrest 2007). Connectivity between ports has increased in recent years – increasing the possibility of introduction of non-native species. Progress has recently been made by Australia and New Zealand to develop region-based surveillance programmes for the spread of non-native species. Examples include Marine High-

Risk Site Surveillance (MHRSS, NZ) (Woods et al. 2015), Australian State government and Commonwealth government department led regional surveillance and legislation with regard to non-native species (DAFF 2015).

With changing environments, significant new path risks may emerge for specific non-native species even where the introduction of species is managed. The propagule pressure primarily correlate to invasion success (Ruiz et al. 2000; Floerl & Inglis 2005; Lockwood et al. 2005). Many scientists have explained the importance of propagule pressure with regard to non-native species and its management measures; however, it is hard to predict parameter (Johnston et al. 2009). For example, evaluation in Port Phillip Bay, Australia indicates a new introduction every 41.5 weeks (Thresher et al. 1999). The issues of non-native species have grown in recent years – controlling and eradication are quite complicated. Government around the world have taken up national priorities to establish programs and management protocols for prevention (pre and post borders), early detection and management of non-native species. Examples include EU Biodiversity Strategy and the Marine Strategy Framework Directive (Lehtiniemi et al. 2015), Australian National System for the Prevention and Management of Marine Pest Incursions (DAFF 2015), Marine Biosecurity Programme of New Zealand, Aquatic Nuisance Species Task Force (ANSTF) in the United States.

Prevention, early detection and rapid management response reduce the potential introduction of non-native species and their impacts on ecosystems. Australia and New Zealand have established some of the world's strongest biosecurity and management measures, i.e. a comprehensive pre-border, at-border and post-border management responses (Hewitt & Campbell 2007; Commonwealth of Australia 2013; Ojaveer et al. 2015). Both countries have adopted and implemented international pre-border measures for ballast water management, i.e. the International Maritime Organization, the Ballast Water Management Convention, to control and minimise the spread of non-native species. The Biosecurity Act, NZ (1993) and the Biosecurity Act, AUS (2015), are oriented towards the management of the unintentional introduction of non-native species and post-border incursion measures and long-term management. Ballast water management following the International Maritime Organisation (IMO) protocols and ballast water treatment in the mid-ocean measures are undertaken to reduce the risks of invasions (Hewitt and Campbell 2007; Tamelander et al. 2010; IMO 2017). Recent measures have been focussed on biofouling management; IMO proposed protocols to clean marine vessels, using appropriate anti-fouling agents, evidence of biofouling maintenance and record books (Ministry of Primary Industries 2018; Australian Government

Department of Agriculture and Water Resources 2019). These countries have also undertaken long term management plans of non-native species conducted by regional councils for baseline evaluations. Australia and New Zealand led many countries across the world in establishing management strategies for non-native species (Hayes et al. 2005; Hewitt and Campbell 2007).

2.5.6. Pros and cons of large-scale studies

The passive sampling devices used in APS and NZPS includes dive surveys, fouling panels traps settlement trays for sediment infauna (Hewitt & Martin 2001). Such sampling designs provide the opportunity to sample biofouling species at large scale locations; however, there are still drawbacks for such sampling designs. The 'snapshot' data capture only provides real-time information; organisms may settle selectively depending on design flaws or environmental conditions such as temperature or wave exposure. Advantage of such passive sampling is that it can acquire samples of species at larval/juvenile stages which thereby impacts the development of species structure. However, the success of such samples depends on taxonomic expertise; the identification of species plays an important role for such large datasets with numerous species collection. Poor identification of species may lead to confusion between congeners or identifying non-native species as native species (Ponchon et al. 2013). Lastly, such large datasets (APS and NZPS) are time consuming and expensive task. Re-surveys may be an option to observe the effectiveness of management plans or identify new introductions, but it highly depends on the funding on such large-scale projects.

While the usefulness of large-scale datasets for a broad sense of potential vectors of the introduction of non-native species to aid with rapid management measures is undeniable, this study provides an overall perspective of major commercial shipping ports being the hotspots for non-native species. Ports as entry points for invaders is established, but the second key result indicates the regional transfer of non-native species through domestic vectors. Nonetheless, marine traffic being transport hubs of non-native species is evident. Increased maritime traffic leads to continuous transfer of non-native species. Another factor considered for this study was latitude groups. Relatively abundant non-native species were observed at high latitudes (35°S, 40°S, 45°S) but these results are in an argument with the locations of major ports at high latitudes. Most of the species observed were biofouling species which further indicate strict management plans towards the eradication of non-native biofouling species. Such species easily attach on vessels' hulls, engines or crevices of the ship which is not easily visible. Australia and New Zealand have developed several guidelines for biofouling

considering IMO Biofouling Management Plan 2011 (MEPC.207[62]) and are in the process of considering biofouling regulations.

The Australian Port surveys and New Zealand Port Biological Baseline Surveys offered as good datasets to identify the potential factors, i.e. major ports and high latitudes facilitating occurrences of non-native species. While I encourage in using this general applicability of this observed pattern; these results also suggest that port characteristics such as disturbed physicochemical environments, new structures, structure maintenance should be prioritised whilst monitoring for non-native species which will aid with early detection.

CHAPTER 3

COMMUNITY DEVELOPMENT AND STRUCTURE ON NATURAL AND MAN-MADE SUBSTRATA IN NATURAL AND MAN-MADE ENVIRONMENTS

3.1. Background

Natural coasts around the world have been heavily degraded and replaced by man-made structures such as seawalls, groynes, marinas, jetties and so on (Lam et al. 2009; Airoldi & Bulleri 2011; Scyphers et al. 2015; Cacabelos et al. 2016). Although these man-made structures are mostly built to protect the coastlines from erosion and act as defence structures, such man-made structures do provide novel habitats for marine communities (Burt et al. 2009, 2011; Cacabelos et al. 2016; Heery et al. 2017). These man-made structures are expected to proliferate in the future owing to the migration of humans to the coasts and alteration of coastlines as per human needs (Hinkel et al. 2014; Bulleri & Chapman 2015; Dafforn et al. 2015; Neumann et al. 2015; Dangendorf et al. 2017). The building of continuous coastal defences on the natural coastline can cause habitat loss and habitat fragmentation of natural coastlines having local and regional impacts on marine biodiversity (Airoldi et al. 2008, 2009; Chapman 2012; Scyphers et al. 2015; Perkol-Finkel et al. 2018; Macura et al., 2019). Measures to rectify the negative impacts of the man-made structures by coming up with conservation strategies have only begun relatively recently (Thompson et al. 2002; Airoldi et al. 2005; Chapman & Underwood 2011; Kueffer & Kaiser-Bunbury 2014).

Natural coastal shores are heterogeneous environments with a range of microhabitats providing refuge to many intertidal species from predation and desiccation (Thompson et al., 2002; Waltham & Dafforn, 2018; Bulger et al. 2019). The correlation between heterogeneous habitats and biodiversity has been observed across all ecosystems, be it land such as rainforests or sea such as coral reefs (Simberloff & Von Holle 1999; Tews et al. 2004; Davies et al. 2005; Hansen & Clevenger 2005). This can even be observed at small scales with increased microbiota communities on rough surfaces rather than on smooth surfaces (Lam et al. 2009; (Pister 2009; Cacabelos et al. 2016). Unlike natural habitats, the man-made structures have smooth surfaces, i.e. low structural complexity, with no rockpools or crevices, making it difficult for the species to colonise or find refuge from desiccation, predation or wave action (Chapman & Clynick, 2006; Von Holle, 2011). Therefore, the building of man-made structures

tends to homogenise natural coastlines, having a negative impact on the native marine biodiversity (Mack et al. 2000; Braby & Somero 2006; Brandl et al. 2017; Pastro et al. 2017; Perkol-Finkel et al. 2018). Once coastlines are modified, it is difficult to re-establish diverse communities as there would be competition over limited resources such as food and space (Simberloff & Von Holle 1999; Levine 2000; Bruno et al. 2003; Rius & McQuaid 2009; Branch et al. 2010).

Man-made coastal structures are built using materials such as granite, concrete, plastic, or wood, which are usually not observed in natural coastal habitats (Bulleri & Chapman 2010; Loke & Todd 2016). There has been evidence that some marine organisms are selective of chemical cues provided by substrata (Pawlik 1992; Dobretsov & Wahl 2001; Tamburri et al. 2008). Therefore, species-specific preference for settle on certain substrata (material types) is possible. Experiments using different materials to test for species community comparisons have yielded contradictory results. Some studies indicated similar species richness, but low abundances of species on artificial materials such as ceramic, glass, granite, concrete, steel, aluminium, wood, brick, rubber compared to natural reefs (Anderson & Underwood 1994; Creed & De Paula 2007; Field et al. 2007; Tyrrell & Byers 2007; Loke & Todd 2016; Kennedy et al. 2017; Mallela et al. 2017). Whilst some studies in estuaries showed increased species abundances on artificial structures (tyres, wood, metal) due to additional substrata for the organisms to settlement on (Chapman & Bulleri 2003; Chapman & Clynick 2006; Smith et al. 2014), and still, other studies showed differences in species diversity and abundances as an effect of different habitat type rather than the material type (Burt et al. 2009; Cacabelos et al. 2016). For instance, even when the seawalls along the Sydney coast were built with sandstone to mimic natural reefs, the structures did not support similar communities (Chapman & Bulleri 2003). Therefore, man-made structures on its own cannot replace natural habitats (Bulleri & Chapman 2004; Bulleri & Chapman 2010; Carvalho et al. 2013; Cacabelos et al. 2016). However, eco-engineered man-made structures can act as surrogates for natural habitats.

The orientation of man-made structures is usually vertical and steep, providing reduced settlement opportunity, whilst most natural habitats are horizontal or gently sloping, supporting relatively more species (Chapman & Clynick 2006; Spagnolo et al. 2014; Kennedy et al. 2017). The steep man-made structures act as a barrier for larval dispersal, movement of mobile species, alter recruitment patterns and reduce water flow causing impacts on ecological connectivity (Bulleri & Chapman 2004; Moreira et al. 2006; Rivero et al. 2013 Bishop et al. 2017). This further impacts the gene flow and trophic transfer along coastlines (Branch &

Steffani 2004; Trussell et al. 2004; Burlakova et al. 2012; Inglis & Seaward 2016; Bishop et al. 2017). Thus, low genetic diversity is one of the factors that may be observed amongst species on man-made structures (Fauvelot et al. 2009; Sammarco et al. 2012). Subsequently, some species may develop interspecific and intraspecific relationships amongst the community which are not seen at natural habitats (Chapman 2006, 2013; Tyrrell & Byers 2007; Chapman & Underwood 2009; Quinn et al. 2012). For instance, some invertebrates had a smaller sized body and less reproductive output as a response to increased community density (Moreira et al. 2006).

Recent re-assessments of man-made coastal structures have concluded that it is important to redefine the design features of the structures. Engineering structures with multifunctional use, i.e. for coastal defence as well as providing habitat for marine organisms, have been considered. Addition of rockpools, crevices forming tide pools or even addition of overhangs can promote biodiversity (Bulleri & Chapman, 2010; Chapman & Underwood 2011; Loke & Todd, 2016). For instance, the addition of flowerpots over the vertical seawalls led to an increase in species assemblage diversity by 62%, with 25 species which were not previously found on the seawall (Browne & Chapman 2011). Cost-effective hybrid structures such as revetments, tetra-pods and geo-tubes can be multifunctional, especially in areas where the natural habitats are lost (Moschella et al. 2005; Chapman & Underwood 2011; Browne & Chapman 2014; Firth et al. 2014; Loke et al. 2014). Additionally, precautionary policies regarding the placement of coastal structures had been implemented more towards the beach to protect intertidal marine communities (Dethier et al. 2017).

Man-made habitats such as marinas and ports are usually enclosed areas with limited water/wave action, as well as increased sedimentation rates leading to high turbidity and reduced photosynthesis, thereby degrading the natural habitat and reducing the resident biodiversity (Guerra-García & García-Gómez 2004; Perkol-Finkel & Benayahu 2007; Rivero et al. 2013; Pastro et al. 2017). Levels of disturbance are also thought to vary between man-made and natural habitats (e.g., via strong waves or predation) (Moschella et al. 2005). However, anthropogenic disturbances such as maintenance of man-made structures or over-harvesting of resident species tend to dislodge competitively dominant and settled species, thereby providing bare space for colonisation of opportunistic species (Airoldi et al. 2005; Airoldi & Bulleri 2011; Bracewell et al. 2013; Oricchio et al. 2016). The community structure often varies between different habitats, for example, sessile species composition greatly differed among complex habitats compared to the bare substrate (Burlakova et al. 2012) and

even the microbial communities differed between man-made structures and natural rocky reefs (Tan et al. 2015).

Studies comparing the community composition on natural and man-made structures have observed similar species richness but different relative abundances on both structures (Connell & Glasby 1999; Thompson et al. 2002; Chapman 2003; Bulleri & Chapman 2004; Pister 2009; Carvalho et al. 2013). However, many recent studies have highlighted the two habitats, natural and man-made to support different species assemblages (Moschella et al. 2005; Perkol-Finkel et al. 2006; Clynick et al. 2007; Lam et al. 2009; Bulleri & Chapman 2015; Lai et al. 2018). Whilst some studies have observed the man-made structures to support species that are not generally observed in natural habitats (Goodsell et al. 2007; Browne & Chapman 2011). Man-made structures may act as novel habitat for various benthic communities, especially in sedimentary habitats, providing additional habitat where they support greater species diversity compared to natural habitats (Bulleri & Chapman 2010; Airoldi et al. 2015; Heery et al. 2017). In some instances, species richness was relatively lower at man-made structures than natural habitats (Connell & Glasby 1999; Moschella et al. 2005; Pister 2009; Firth et al. 2013; Aguilera et al. 2014; Munsch et al. 2014). Species richness and effects on ecosystem functioning are dependent on specific functions of species (Chapman 2003; Rius & McQuaid 2006; Stachowicz et al. 2008; Pister 2009; Mineur et al. 2012; Albano & Obenat 2019). Besides, the composition of assemblages is also an important factor as the changes in the diversity of the species (Creed & De Paula 2007; Field et al. 2007).

Ecosystem functions are influenced by 'keystone species' as they strongly affect the energy pathways, and by 'ecosystem engineers' which create or modify habitats. Additionally, species such as sessile organisms that usually facilitate a positive relationship with other species by providing refuge, especially for mobile species and larger predators; are economically significant (Borthagaray & Carranza 2007; Sousa et al. 2009; Green et al. 2013; Martins et al. 2016; O'Shaughnessy et al. 2019). The habitat-forming species or the early recruiters help with the development of a community by providing refuge or acting as a food source. Overgrowth of these initial recruits due to the absence of grazers and plenty of space can have adverse effects on late settlers by blocking the surfaces (Connell 1961; Sousa 1979; Bracewell et al. 2013; Aguilera et al. 2014). However, recognising which species can withstand anthropogenic disturbances and how such disturbance can impact the overall ecosystem structure is essential (Liversage et al. 2014). For instance, habitat-forming sessile species such as ascidians, bivalves, bryozoans, cnidarians, corals, and sponges that are permanently fixed

on substrata may be majorly affected by anthropogenic disturbances that lead to their dislodgment, thereby disrupting the ecosystem structure (Lockwood et al. 2007).

An important change to the community composition is conferred by invasive species (Bulleri et al., 2016). It is universally accepted that bioinvasions are a major threat to marine biodiversity as well as the global economy (Ojaveer et al. 2015; Gestoso et al. 2017; Olenin et al. 2017; Simpson et al. 2017). Invasive species are ubiquitous and can degrade habitats in many ecosystems (Wonham 1999; Pauchard & Shea 2006; Bellard et al. 2016; Bulleri et al. 2016). Consequently, there has been a surge in studies of invasive species all around the world. Frequently, the invasive species have been seen to establish in regions with heavy anthropogenic activities (Thompson et al. 2002; Ruiz et al. 2009; Johnston et al. 2017). Disturbance and maintenance along the coastlines for urbanisation and coastal development are ubiquitous, and provision of non-native species are such sites is typical (Clark & Johnston 2009; Piola et al. 2009; Bulleri & Chapman 2010; Dumont et al. 2011; Rivero et al. 2013). For example, maintenance of breakwaters leads to displacement of dominant space occupiers, mussels and oysters, leading to the growth of opportunistic and invasive biofilms and macroalgae (Airoldi & Bulleri 2011; Ceccherelli et al. 2014).

Ports and bays are sites where ships' ballast water discharge and hull fouling communities may contribute to the introductions of non-native species (Ruiz et al. 1997; Hewitt et al. 2004; Chapman & Underwood 2011; Mineur et al. 2012; Choi et al. 2016; Foster et al. 2016; Olenin et al. 2017). Coastal habitats are vulnerable to invasions due to the changing of natural habitats, local biodiversity and propagule pressure from non-native species (Johnston et al. 2009; Simberloff 2009; Simpson et al. 2017; Epstein & Smale 2018; Riera et al. 2018). Many studies suggest that non-native species are less successful at natural habitats as compared to man-made structures (Chapman & Carlton 1991; Dafforn et al. 2012). There is evidence of non-native species being strongly related to disturbed areas with high turbidity and wave exposure (James & Shears 2016). Man-made structures act as 'stepping stones' for the spread of non-native species and support a high number of non-native species (Dumont et al. 2011; Mineur et al. 2012; Saura et al. 2014; Dong et al. 2016).

Not all non-native species can successfully establish due to unsuitable climatic conditions, diseases, predation and competition by native species through species-specific interactions or invasion resistance by the diverse native community (Elton 1958; Tilman et al. 1994; Mack et al. 2000; Stachowicz et al. 2002; Dumont et al. 2011; Firth et al. 2013;

Henriksson et al. 2016; Leclerc & Viard 2018). The successful non-native species may be highly competitive in terms of their high reproductive/growth rates and phenotypic plasticity, which aids their introduction and establishment success in a new environment (Petes et al. 2008; Piola et al. 2009; MacKie et al. 2012; Fava et al. 2016; Purroy et al. 2019). Once established, the non-native species disperse further from the introductory areas (Tyrrell & Byers 2007; Forrest et al. 2009).

Invasive species can cause changes to community structure and impact ecosystem functioning (Firth et al. 2016), including the loss of native species and a decrease in diversity, thereby leading to a homogenous community (Browne & Chapman 2014; Airoldi et al. 2015; Ferrario et al. 2017). Invasive species, when established in an environment, can co-exist with native species if they have similar ecosystem functions: however, if their functioning is different, it may lead to modified habitats and cascading effects on the other species (Crooks 2002; Trussell et al. 2004; Babarro & Abad 2013; Saura et al. 2014). It is therefore essential to understand the ecological functioning of an invasive species in its new habitat and its relationships with other species (Airoldi & Bulleri 2011; Perkol-Finkel et al. 2012; Zwerschke et al. 2016; Leclerc & Viard 2018; Mayer-pinto et al. 2018). For example, the predatory European green crab (*Carcinus maenas*) in California, established and altered the community structure and reduced the number of native species through predation (Grosholz et al. 2000). Predation by the invasive crab, *Carcinus maenas*, led to the decrease of a grazer, *Littorina littorea*, which in turn resulted in the proliferation of ephemeral algae in rocky reefs (Trussell et al. 2004). Some studies have also highlighted the replacement of native species by non-native species (Geller 1999, Byers 2000; Ojaveer et al. 2002; Rodriguez 2006; Tan et al. 2015).

Spatial, temporal and environmental heterogeneity determine ecological diversity-function relationships (Stachowicz et al. 2008). Ecological succession in community structure helps identify patterns or interactions in abundances and diversity over time (Connell & Slatyer 1977; Loke et al. 2016; Johnston et al. 2017; Chang & Turner 2019). Ecological succession is the study of patterns of colonisation and resilience of species after a disturbance (Connell & Slatyer 1977). In recent times, the two main factors that disturb ecological succession are human activities and climate change (Bishop et al. 2017; Firth et al. 2016). Anthropogenic disturbances causing newly exposed habitats have a significant effect on ecological succession, especially the first succession being highly driven by stochastic processes and colonisation is variable and patchy (Chapman & Underwood 2009; Clark & Johnston 2009; Chapman 2012; Spagnolo et al. 2014). Pioneer species first colonise new barren habitats as they can withstand

extreme conditions - ‘primary autogenic succession’ but are short-lived. Bacteria and biofilms, and other settlers such as diatoms, form an initial layer over the bare substrata. Chemical cues emitted by the initial larval colonists and even the associated substratum are known to influence changes in the recruitment of other species (Pawlik 1992; Dobretsov & Wahl 2001; Tamburri et al. 2008). Over time, new species colonise - ‘secondary succession’ - and may tend to stabilise - ‘climax community’ (Connell & Slatyer 1977; Chang & Turner 2019). The ‘climax community’ is mature and is dominated by a few species (Berlow 1997). In the marine environment, the sequence of recruitment and settlement of species have a strong influence on the diversity as well as the structure of the climax community (Bulleri 2005; Lu & Wu 2007; Becker et al. 2018; Gouezo et al. 2019). Various factors, such as the level of disturbances or prey-predator interaction, can lead to alternative stable states with different community structure (Petraitis & Latham, 1999).

Nevertheless, we cannot assume that similar community structure and sequence of succession observed at natural habitats will be seen on man-made habitats. Another question arises in terms of species status (native vs non-native species), the competitive traits of non-native species could displace native species. This displacement of species can produce changes in community structure found in natural successions (Pandolfi 2008). Thus, comparative studies across a variety of ecosystems can help us to understand the main factors facilitating the succession of both native and non-native species (Chang & Turner 2019). Whilst there is some research done on the succession of species, but no similar studies have been conducted comparing natural and artificial habitats/ substrata in the context of species status.

Studies investigating the community structure, species abundances and diversity as well as the status of the species – native and non-native – with a focus on natural vs man-made structures have been performed all over the world, especially in temperate regions (Connell & Glasby 1999; Connell 2001; Hewitt 2002; Airoldi 2003; Bacchiocchi & Airoldi 2003; Chapman & Bulleri 2003; Airoldi et al. 2005; Bulleri & Airoldi 2005; Wyatt et al. 2005; Airoldi & Beck 2007; Parsons et al. 2016; Mayer-Pinto et al. 2018). The proliferation of built structures along with New Zealand’s (NZ) coastline and an increase of 10% non-native species since 2009 has been outlined by New Zealand's Environmental Reporting Series (Ministry for the Environment & Stats NZ, 2016). However, to the best of my knowledge, no research has been carried out in New Zealand to examine the effects of man-made built structures and natural rocky reefs on marine community composition and species’ abundances over a period of time,

and that also examines preference of native and non-native species in terms of habitat type (Natural reef vs Man-made habitat).

Many previous studies have acknowledged the impacts of man-made structures on community composition and species' abundances, as well as the facilitation of non-native species. Therefore, this chapter attempts to quantify species diversity and community composition at the rocky reef (natural) and marina habitats (built) using slate (natural) and PVC (polyvinylchloride) (man-made) tiles in Wellington Harbour. The successional pathways from the initial bare surface to final community composition have been examined to observe the effects of man-made habitats/substratum for 2 years. This study also analysed the impact of habitat type and substratum type on the recruitment of fouling species with respect to their status; native, non-native and cryptogenic (species which could not be identified or the status could not be determined) and tested if there is a preference by non-native species for a particular habitat or substratum. The variability in the association of native and non-native (positive, i.e. increase in the number of native and non-native species; negative, i.e. increase in non-native abundance with a decrease in the number of native species) may help determine a positive or negative relationship between native and non-native species. The hypotheses investigated in this chapter are: 1) community composition at man-made habitat (3 replicated marinas) is less diverse than at neighbouring natural rocky reefs; 2) community composition on the man-made substratum (PVC) is less diverse than that on a natural substratum (slate), and 3) non-native species are more abundant at the artificial habitats and on artificial substratum relative to natural habitats and substratum.

3.2. Methods

3.2.1. Study sites

Six study sites (3 paired sites) were selected in Wellington Harbour to examine if the marinas (man-made habitats) support similar or different communities to the adjacent natural rocky reefs. The three marina sites were; Chaffers Marina (CM), Evans Bay Marina (EB) and Seaview Marina (SM) and three natural reef sites were; Oriental Bay (OB), Shelly Bay (SB) and Sorrento Bay (SR) (Figure 3.2.1; Table 3.2.1). The three paired sites were; Chaffers Marina – Oriental Bay; Evans Bay Marina – Shell Bay; Seaview Marina – Sorrento Bay which was at ~200 m distance between each marina and reef site.

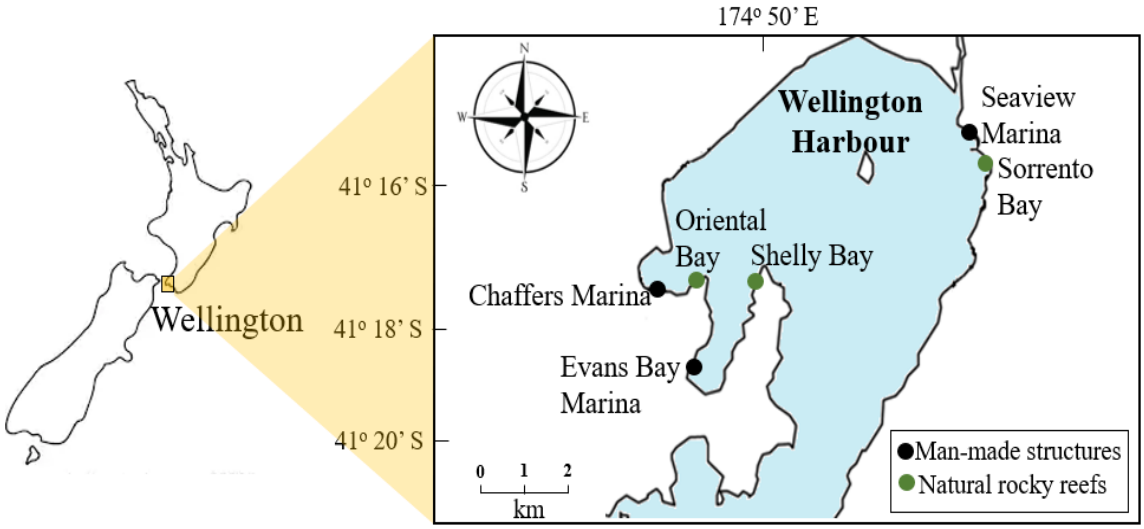


Figure 3.2.1. Map of Wellington Harbour, New Zealand, indicating natural reef and man-made habitats (marinas) as sampling sites for the study.

Table 3.2.1. List of sampling sites with habitat types, codes, latitude and longitudes.

Site	Site code	Habitat	Latitude	Longitude
Chaffers Marina	CM	Marina	S 41°17.194'	E 174°48.165'
Oriental Bay	OB	Reef	S 41°17.377'	E 174°47.340'
Evans Bay Marina	EB	Marina	S 41° 17.983'	E 174°49.028'
Shelly Bay	SB	Reef	S 41°18.100'	E 174°49.049'
Seaview Marina	SM	Marina	S 41°24.765'	E 174°90.299'
Sorrento Bay	SR	Reef	S 41°15.278'	E 174°54.188'

3.2.2. Substratum

To study the fouling community composition on tiles of different substrata (material), PVC as man-made and slate as natural substrata were used. PVC as a man-made material has been previously used in many settlement arrays studies whilst, slate is a natural material and is not chemically treated. Each tile was cut into 0.0225 m^2 (0.15 x 0.15 m) and was 10 mm in thickness. Four holes were drilled at 2 cm from the edge of the tiles in the four corners. The tiles were secured back to back (PVC to slate) with cable ties through the four holes exposing only one side of each tile for settlement, i.e. front view of the tiles (Figure 3.2.2 c & d). The surface of the PVC tiles was lightly scraped with sandpaper to remove the industrial smoothness, to help with species attachment. The slate tile was left untreated because it is naturally slightly rough.

3.2.3. Experimental design

In marinas, wooden wharf pilings were a perfect set-up for the experimental design from which to suspend the settlement tiles, whilst natural reefs had no such set-up. Therefore, different experimental set-ups were designed for the marina (man-made habitat) and reef sites (natural habitat).

a) Marina (Man-made habitat)

At each of the three marina sites, the settlement tiles were hung between two wharf pilings with ropes at ~ 2 m below the sea surface estimated at low tide considering the Mean Low Water Springs (MLWS). Eight sets of PVC and slate paired tiles were tied to a rope with cable ties at equal intervals (Figure 3.2.2 a). In total, 5 such rope set-ups were deployed on 5 different sets of wharf pilings. Eight paired tiles were attached equidistant from each other and were constantly submerged. Hence, for the 2-year study period, 1 marina site had 5 replicate set-ups with 8 paired tiles (1 marina site × 5 replicates × 8 paired tiles = 40 paired tiles at 1 marina site [40 PVC + 40 slate]). At 3 marina sites × 5 replicates × 8 paired tiles = 120 paired tiles [120 PVC + 120 slate].

b) Reef (Natural habitat)

Galvanised steel frames were constructed (1.6 x 0.25 m), from which the tiles were hung across the frames with ropes. The frames were maintained in position underwater with the help of cement-filled tyres used as weights and subsurface buoys to help the frame stay vertical (Figure 3.2.2 b). The frames were placed perpendicular to the coast so that the surfaces of both the tiles are exposed to the waves. Similar to the tile set-up at marina sites, 5 replicates of the frame set-

up were placed at each natural reef site. For the 2-year study period, 1 reef site had 5 replicate set-ups with 8 paired tiles (1 reef site × 5 replicates × 8 paired tiles = 40 paired tiles at 1 reef site [40 PVC + 40 slate]). At 3 reef sites × 5 replicates × 8 paired tiles = 120 paired tiles [120 PVC + 120 slate].

3.2.4. Field sampling and sampling intervals

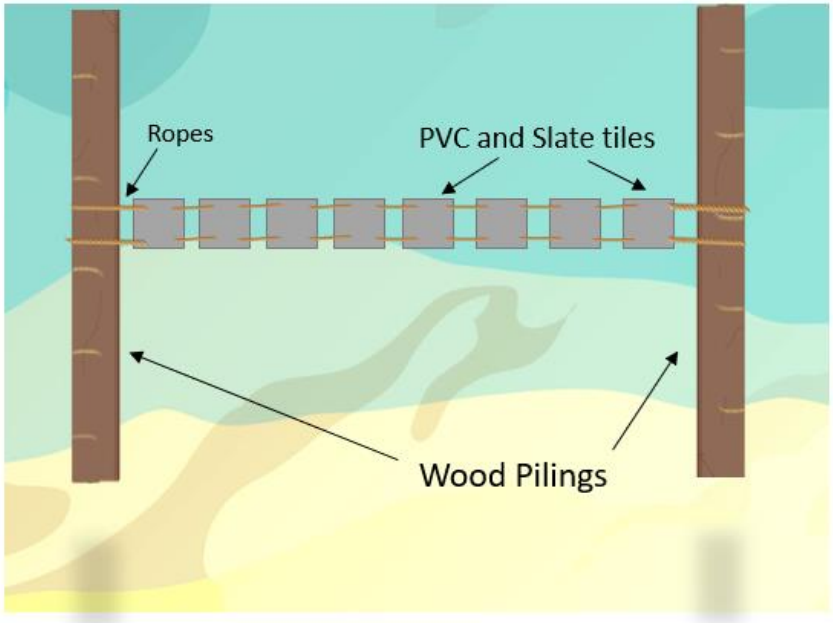
The placement of the set-ups and the sampling (retrieval) of the tiles was carried out by SCUBA divers. Whilst field sampling, the cable ties were cut, and pairs of tiles (PVC and slate) were placed in pre-labelled plastic bags. Once the tiles were retrieved from the water, they were placed in an icebox and then transferred to a freezer (-18 ^{o}C) in the laboratory until they were processed. At every sampling interval (see below), 30 paired tiles (PVC and slate) were collected from the six study sites (marina and reef): in total, 60 tiles (30 PVC + 30 slate) were processed at anyone sampling period. Hence, for 8 sampling intervals, a total of 480 tiles were collected by the end of the 2-year study. The tiles were sampled randomly for every sample interval, for example, at time 1 (Nov 2017) number 6 tiles from all the experimental set-ups were retrieved.

This study was designed to compare the fouling community on PVC and slate substrata from the first time they were deployed in the water (August 2017 - austral winter) to the end of the 2 years (August 2019). Sampling interval after the first deployment in August 2017 was every three months until the final retrieval in August 2019 (Table 3.2.2).

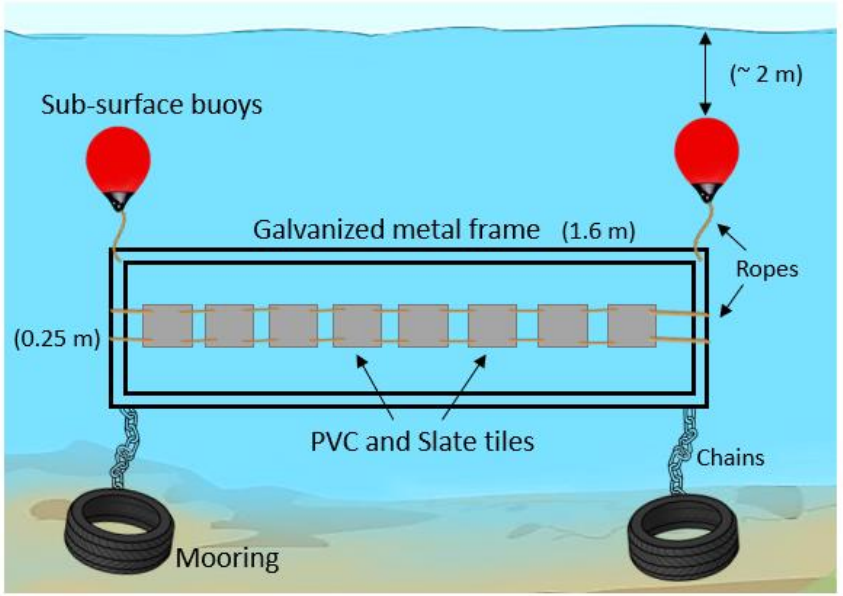
Table 3.2.2. List of sampling intervals, months, seasons and sampling year examined in this study, following set-up and deployment in August 2017.

Sampling interval	Month	Season (Austral)	Sampling year
1	November 2017	Spring	Year 1
2	February 2018	Summer	
3	May 2018	Autumn	
4	August 2018	Winter	
5	November 2018	Spring	Year 2
6	February 2019	Summer	
7	May 2019	Autumn	
8	August 2019	Winter	

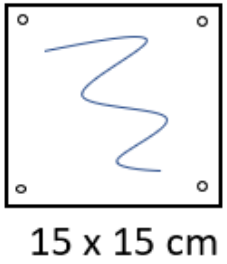
a) Set-up in marinas



b) Set-up at natural reef sites



c) Front view



d) Side view

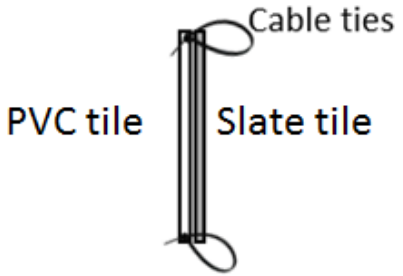


Figure 3.2.2. Set-up of settlement tiles deployed in the a) marinas and at b) natural reef sites; c) front view and d) side view of the PVC and slate substrata.

3.2.5. Tile processing

The fouling community on each tile was thawed and gently patted dry before processing. Subsequently, to have a 2D view of the community on the tiles, high-resolution digital images were taken of the front of the tiles (the side exposed for settlement). At each sampling interval, these images were then analysed using Coral Point Count with Excel extensions (CPCe) to record the community composition over a 2-year study period (Kohler & Gill 2006). A 100-point random grid within 14 × 14 cm was generated (for each tile, a 1 cm border was not included to avoid edge effects). The number of points (100) that overlaid on the image was determined using Lenth's power test as suggested in CPCe manual (Power = 0.998 for 100 points). The species cover at each point was determined for each plate at each time interval for all sites. Similarly, points on the bare space on the tiles were also noted to assess the availability of bare space for settlement through the study period.

Species were identified using field guides for common intertidal and shallow subtidal species of New Zealand, including known non-native species. Species were identified to the lowest possible taxonomic level (most usually to species) and then placed in major systematic groups. The organisms which could not be identified to species were identified to genus or family level and coded as sp. 1 or sp. 2, for example, *Ulva* sp. 1 (see Table 3.3.1).

'Biofilm', herein coded as Biofilm type 1, was classified as a single major group as it is biologically important as an early coloniser, is highly variable in time and space in its exact content and could not be accurately identified to any meaningful taxonomic level. An unknown black-dotted biofilm that was visually different from the clear biofilm (Biofilm type 1) was observed in the initial stages of sampling herein and was labelled 'Biofilm type 2'. An unidentified green moss-like structure (Chlorophyta) was labelled as Green sp. 1; the sheet-like green alga was labelled as '*Ulva lactuca*', the green ribbon-like alga was labelled as '*Ulva* sp. 1', the beige sheet-like tunicate as 'Tunicate sp. 1' and the mustard sheet-like tunicate as 'Tunicate sp. 2'.

3.2.6. Data analyses

a) Preliminary analyses

Data were analysed using the statistical package Plymouth Routines in Multivariate Ecological Research (PRIMER v.6) (Clarke & Gorley 2006). The DIVERSE routine was used to calculate the total number of 'species' occurrences (total species richness) and the total number of 'individuals' as represented by point counts (total individuals); at marina sites (man-made

habitat) on PVC and slate settlement tiles (man-made and natural substrata) as well as for natural reef sites (natural habitat) on PVC and slate settlement tiles. Species accumulation curves were plotted across all 480 samples to determine if the sampling effort was sufficient to discover all likely (expected) taxonomic diversity in Wellington Harbour over 2 years. The metric S_{obs} showed the observed total number of species with the increase in the number of samples (the asymptotic value of the species accumulation curve). The non-parametric estimators used for plots were; Chao1, Jacknife1 and Bootstrap. Chao1 and Jacknife1 estimate richness from single samples (abundance-based)

b) Bare space availability

Multivariate analyses were performed using PRIMER v.6 with permutational multivariate analysis of variance (PERMANOVA) as an add-on package (Anderson et al. 2008). PERMANOVA helps statistically test the differences between two groups and among a group, and the effects of factors on communities using a permutation approach to avoid possible biases and problems associated with regular parametric testing.

Availability of bare space (expressed as a percentage) as a function of habitat and substratum through the tri-monthly sampling periods was tested using permutational multivariate analysis of variance (PERMANOVA). As the units for bare space and species community composition were similar, the bare space data were square-root transformed. The data were square-root transformed based on Bray-Curtis similarity matrices with 9999 permutations of the raw data. PERMANOVA was run with Type III (partial) sums of squares with relevant factors. The main independent factors were substratum (fixed), sample interval (fixed), habitat (fixed) and sites nested within habitat (fixed) and available bare space (point count) was the dependent variable. Factor, sites nested within the habitat, in the PERMANOVA model resulted in no tests. Therefore, a PERMANOVA model with factors habitat, substratum and sample interval were considered. CPCe points for bare space at each sampling time were also plotted on a graph to observe the variations in availability of bare space over time.

c) Fouling community composition

The multivariate analyses based on Bray-Curtis similarity matrices were run after the data were square-root transformed to reduce the effects of abundant species, with 9999 unrestricted permutations of the raw data with Type III sum of squares. A two-dimensional multidimensional scaling (MDS) ordination plot was performed to visualise the similarity in samples for 3 factors; habitat type, substratum and sample intervals (12 months). Additionally,

MDS with the temporal variations displayed as an overlay connecting each sampling interval to visualise the trajectory of change across all 6 sites, respectively. MDS helps visualise the multivariate patterns in fouling community change over time between the habitat types and the substrata. In MDS, samples that are similar cluster together whereas samples which are dissimilar cluster further apart. MDS plot stress values were used to interpret the reliability of the relationships; values < 0.15 = good representation between groups. The stress levels are also affected by the number of samples (Clarke 1993).

The variations in fouling community composition as a function of; habitat type, site (habitat), substratum type and sample interval (given as sampling sequence in the order from the first to the eighth) with their relevant interaction terms were analysed using multi-factorial PERMANOVA. Pairwise PERMANOVA tests were employed to test for the location of the differences (equivalent to standard *post-hoc* tests).

Species contributing to the similarities and dissimilarities between the two groups as a function of Habitat, Substratum and Time were identified using the routine similarity percentages (SIMPER) at a 50% contribution cut-off. The PERMANOVA results were mostly significant ($P < 0.001$), the SIMPER analyses were performed only for major factors (Habitat, Sites, Substratum and Time).

d) Species status (native, non-native and cryptogenic) within the fouling community

The species within the fouling community sampled on the tiles were classified with respect to their status, i.e., native, non-native and cryptogenic species with the help of Word Register of Marine Species (WoRMS). The species whose status could not be identified were classified as a cryptogenic status group. A multivariate PERMANOVA was performed with the species status as the dependent factor whilst habitat, site (habitat), substratum and sample interval as the independent variables. This test helped indicate if the factors of; habitat, site (habitat), substratum and sample interval had any effects on the abundance of native, non-native or cryptogenic species. SIMPER indicated similarity of the presence of species with respect to their status within each factor as well as the dissimilarity between the groups.

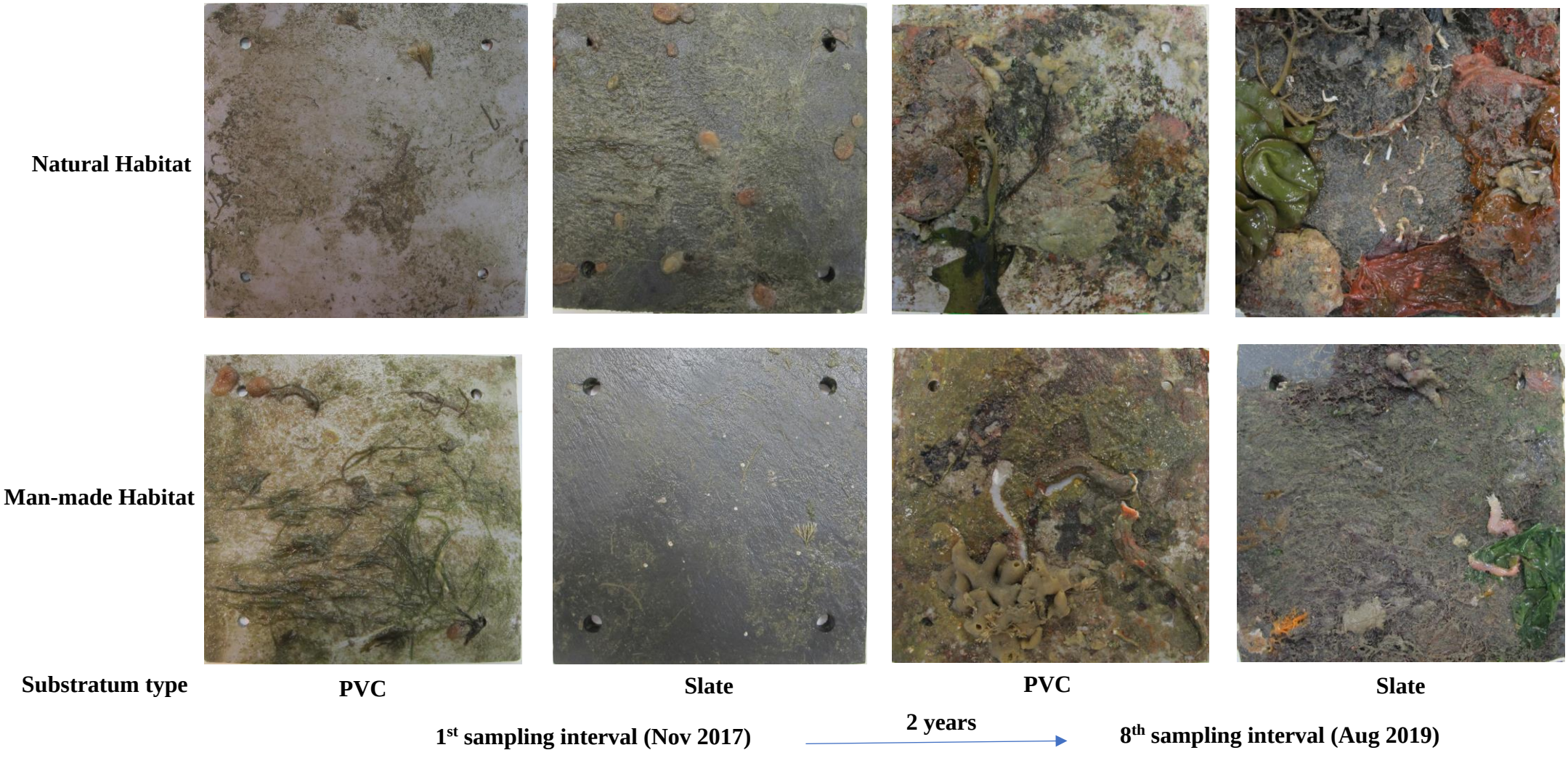


Figure 3.2.3. Representative PVC and slate tiles collected in the study, showing the community growth at first sampling interval (November 2017) and last sampling interval (August 2019)

3.3. Results

3.3.1. Diversity of the fouling community

In total, 47 putative species were identified from 480 experimental tiles. The species were pooled to form 12 major groups; Annelida, Arthropoda, Biofilm, Bryozoa, Chlorophyta, Chordata, Echinodermata, Mollusca, Nemertea, Phaeophyta, Porifera and Rhodophyta (Table 3.3.1).

Table 3.3.1. List of species and major groups recorded at the 6 sampling sites for all 8-time periods in Wellington Harbour, with S = total number of species richness on 480 settlement tiles and N = total number of individuals as represented by point counts.

Habitat type	**Species Status**	**Reef**				**Marina**			
Substratum		**PVC**		**Slate**		**PVC**		**Slate**	
Species / Major group		**S**	**N**	**S**	**N**	**S**	**N**	**S**	**N**
Annelida									
Galeolaria hystrix	Native	7	14	11	14	7	16	6	20
Nereid sp. 1	Cryptogenic	3	3	10	15	3	5	0	0
Serpula vermicularis	Native	0	0	0	0	5	10	41	90
Spirobranchus cariniferus	Native	67	358	79	475	31	77	4	23
Spirorbis spirorbis	Native	28	52	38	80	33	72	20	164
Arthropoda									
Amphibalanus amphitrite	Non-native	1	1	6	7	2	2	42	92
Amphipod sp. 1	Cryptogenic	3	5	3	3	0	0	0	0
Crab sp. 1	Cryptogenic	1	2	2	3	0	0	0	0
Elminius modestus	Non-native	16	60	23	64	3	5	1	1
Isopod sp. 1	Cryptogenic	0	0	0	0	1	1	8	91
Biofilm									
Biofilm type 1	Cryptogenic	96	2608	83	1543	99	2952	3	75
Biofilm type 2	Cryptogenic	6	263	12	517	9	102	0	0
Bryozoa									
Bugula flabellata	Non-native	17	247	13	126	27	132	0	0
Bugula neritina	Non-native	0	0	0	0	4	205	30	466
Bugula stolonifera	Non-native	14	164	9	85	21	171	46	239
Membranipora membranacea	Native	60	803	57	718	33	153	17	111
Rhynchozoon larreyi	Native	4	25	3	23	6	58	23	157
Schizoporella errata	Non-native	17	58	15	65	12	84	44	183
Watersipora subtorquata	Non-native	70	945	59	742	43	230	41	291

Chlorophyta									
Codium fragile	Non-native	3	47	1	7	0	0	4	16
Green sp. 1	Cryptogenic	68	1826	62	1426	61	1662	36	413
Ulva lactuca	Native	11	119	8	53	16	111	2	61
Cladophora	Native	26	196	22	129	43	613	9	17
Ulva sp. 1	Cryptogenic	4	7	10	58	10	94	28	138
Chordata									
Aplidium stellatum	Native	0	0	2	8	4	31	19	181
Asterocarpa humilis	Native	31	313	45	1108	27	425	60	613
Botrylloides leachii	Non-native	1	2	2	5	16	194	4	59
Corella eumyota	Native	6	13	8	18	7	31	16	128
Tunicate sp. 1	Cryptogenic	20	195	20	255	37	340	3	3
Tunicate sp. 2	Cryptogenic	7	145	8	236	6	67	0	0
Tunicate sp. 3	Cryptogenic	0	0	1	7	0	0	0	0
Echinodermata									
Patiriella regularis	Native	0	0	1	1	0	0	35	391
Mollusca									
Anomia trigonopsis	Native	0	0	0	0	4	50	3	5
Mytilus galloprovincialis	Non-native	5	15	3	19	1	2	0	0
Ostrea chilensis	Native	12	83	25	166	40	429	11	25
Perna canaliculus	Native	4	25	3	24	1	1	64	946
Nemertea									
Nemertine sp. 1	Cryptogenic	3	3	10	20	2	12	9	15
Phaeophyta									
Colpomenia peregrina	Non-native	7	16	7	87	2	6	66	1400
Ralfsia verrucosa	Native	91	1444	66	508	60	560	1	1
Undaria pinnatifida	Non-native	1	6	6	118	3	46	56	800
Porifera									
Clathrina sp. 1	Cryptogenic	24	382	29	355	21	197	0	0
Cliona sp. 1	Cryptogenic	1	1	2	10	1	1	67	799
Rhodophyta									
Apophlaea lyallii	Native	1	9	0	0	1	2	7	18
Bangia atropurpurea	Non-native	39	345	34	315	73	1094	9	60
Coralline algae	Native	13	41	11	24	21	138	0	0
Gigartina circumcincta	Native	4	9	10	80	8	57	2	14
Rhodymenia dichotoma	Non-native	0	0	2	7	0	0	0	0

3.3.2. Species accumulation

Species accumulation curves across all 480 samples for the two-year study period indicated a rapid initial increase in species count and then stabilised (Figure 3.3.1). Species count estimators (Chao1, Jacknife1, Bootstrap) did not vary much from the observed species count (S_{obs}). Within the first 100 samples, the accumulation of new species had flattened off, such that ≥90% of all species had been recorded. However, the results indicated that approximately 400 samples were required to observe all the species sampled (i.e., to reach the asymptotic value of each curve at approx. 50 species). Overall, these results support the contention that the sampling effort was adequate and sufficient to reasonably represent the diversity of the fouling community in Wellington Harbour.

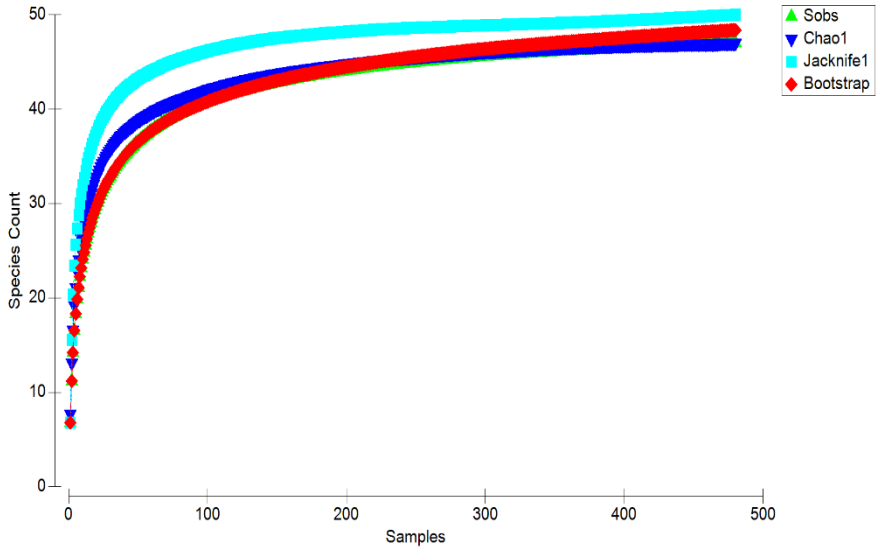


Figure 3.3.1. Species accumulation curves for observed species (S_{obs}) and for non-parametric estimators of species count richness (Chao1, Jacknife1, Bootstrap).

3.3.3. Bare space availability

The multivariate PERMANOVA showed no significant differences in the availability of bare space considering the interaction of all factors; Habitat, Substratum and Time (Habitat × Substratum × Time; $P = 0.48$). However, the bare space availability significantly differed with the Habitat × Time interaction ($P < 0.05$). The availability of bare space differed as a function of Habitat, Substratum and Time, respectively ($P < 0.001$) (Table 3.3.2).

Pairwise tests for main factors indicated significantly ($P < 0.001$) more available bare space at the marina (73.78%) than reef habitats (72.48%). In terms of substratum, Slate vs PVC indicated a significant difference with significantly ($P < 0.001$) more available bare space on the slate (78.49%) than PVC (72.15%) (Table 3.3.3). The factor, habitat × sample interval

indicated significant results ($P < 0.05$) for sample interval 2, 3 and 7 (Table 3.3.3), with relatively higher bare space availability at reef sites for time 2 and 7, whilst the bare space availability was higher at marina sites for time 3.

Table 3.3.2. Results for PERMANOVA to determine the availability of bare space as a function of habitat, substratum and sample interval with their interactions.

Source	**df**	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**
HABITAT × SUBSTRATUM × SAMPLE INTERVAL					
Habitat	1	8403.9	8403.9	20.168	**0.0001**
Substratum	1	34121	34121	81.885	**0.0001**
Time	7	9759.7	1394.2	3.3459	**0.0007**
Habitat × Substratum	1	312.97	312.97	0.75108	0.4094
Habitat × Sample interval	7	8135.1	1162.2	2.789	**0.0037**
Substratum × Sample interval	7	2871.4	410.2	0.98441	0.4456
Habitat × Substratum × Sample interval	7	2768.4	395.48	0.94909	0.4778
Residuals	448	1.8668E5	416.7		
Total	479	2.6641E5			

Table 3.3.3. Results of pairwise PERMANOVA test for bare space as a function of habitat type, substratum type and habitat × sample interval. Significance marked in bold ($P < 0.05$).

Groups	**t**	***P* (perm)**	**Avg. similarities**		
			Reef	**Marina**	**Reef × Marina**
Habitat (Reef vs Marina)	4.49	**0.0001**	72.48	73.78	72.10
Substratum (PVC vs Slate)	9.05	**0.0001**	**PVC**	**Slate**	**PVC × Slate**
			72.15	78.49	69.91
Habitat × Sample interval			**Reef**	**Marina**	**Reef ×Marina**
Time 1	1.666	0.084	69.55	72.43	67.99
Time 2	2.557	**0.011**	73.42	73.20	73.75
Time 3	4.058	**0.001**	72.54	74.03	58.99
Time 4	0.889	0.423	75.12	72.83	74.51
Time 5	0.924	0.385	80.88	73.11	76.70
Time 6	1.258	0.162	66.24	80.81	70.91
Time 7	2.602	**0.007**	78.10	77.39	73.30
Time 8	0.793	0.483	79.72	74.78	77.23

Figure 3.3.2 indicates the temporal variation in available bare space observed in this study. The tiles at the time of deployment (Time 0) were barren, i.e. 100% bare space availability with nearly 64% bare space availability within 3 months. Settlement of species led to variations in bare space availability over time, indicating rapid settlement within 3 months (Time 1). Throughout the study, there was always~20% available bare space for settlement and species cover did not reach its limit (0% bare space). However, a clear trend of an increasing number of species indicated the variations in recruitment and settlement of fouling community over time, with rapid settlement within the first 3 months (Time 1) of deployment of the bare tiles (PVC and slate).

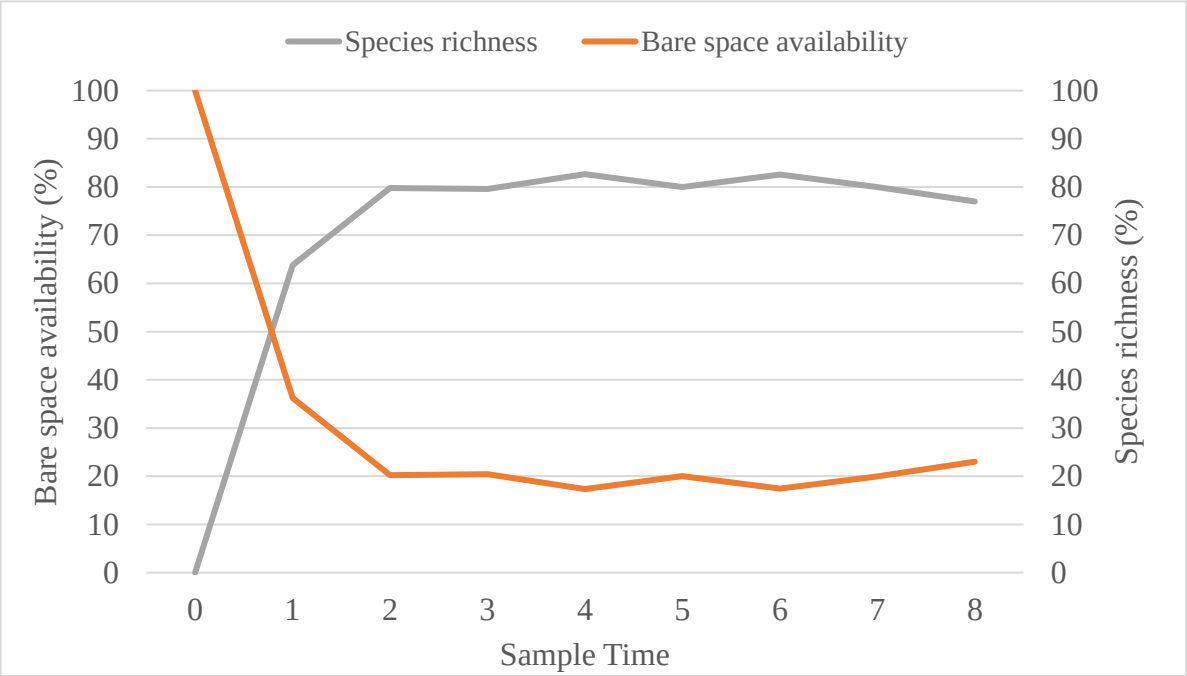


Figure 3.3.2. Temporal variation of average bare space availability (%) and species richness (%) by point counts (100-point grid) for the 2-year study (irrespective to habitat type and substratum type).

3.3.4. Fouling community ordination

Two-dimensional MDS ordination plots to see if the communities varied as a function of habitat type, substratum and time showed a cluster of points in the centre with no distinct separation between habitat type, substratum and sampling time. However, the high-stress level of the plot (2D Stress: 0.28) indicated that the 2-D plot could not represent well the multidimensional nature of the data set (Figure 3.3.3 a, b & c). Examination of the 3-D plot revealed a stress level of 0.20, which is the generally accepted upper limit for such a plot (Clarke 1993). The 3-D plots based on habitat type (marina vs reef) and substratum type (PVC vs slate), showed evidence of segregation in the communities for each group, but both the groups clustered in the centre. In terms of sampling intervals, the communities showed some evidence of distinct clusters for each sampling interval, although there was still a level of cluster overlap (Figure 3.3.3 c).

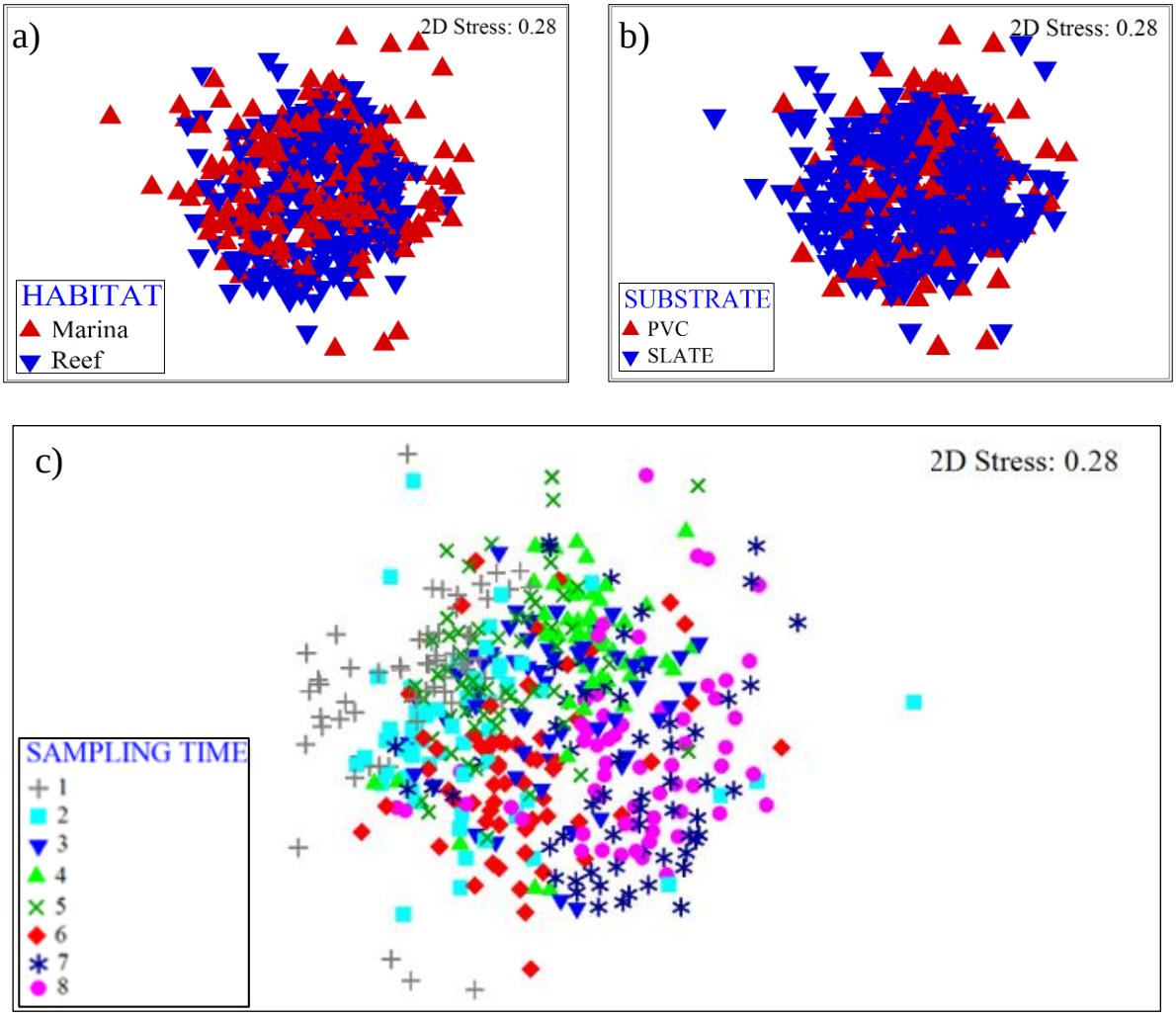


Figure 3.3.3. Two-dimensional MDS plot based on community composition between a) habitat type (marina and reef) b) substratum type (PVC and slate) and c) sampling interval (1-8).

The dataset was averaged for each sampling interval (1-8), and substratum type (PVC and slate) for each study site. MDS plots were generated for each site (6 sites) to examine the change in community composition over time. The paired tiles (PVC and slate) for each sampling time tended to group (Figure 3.3.4) with the clear transitions between sampling times (time intervals 1-8), indicating that the fouling communities changed continuously between consecutive sampling times. As expected, all six site-specific plots showed a trajectory of change, from the initial colonisation community (sample interval 1) through to the final community (sample interval 8).

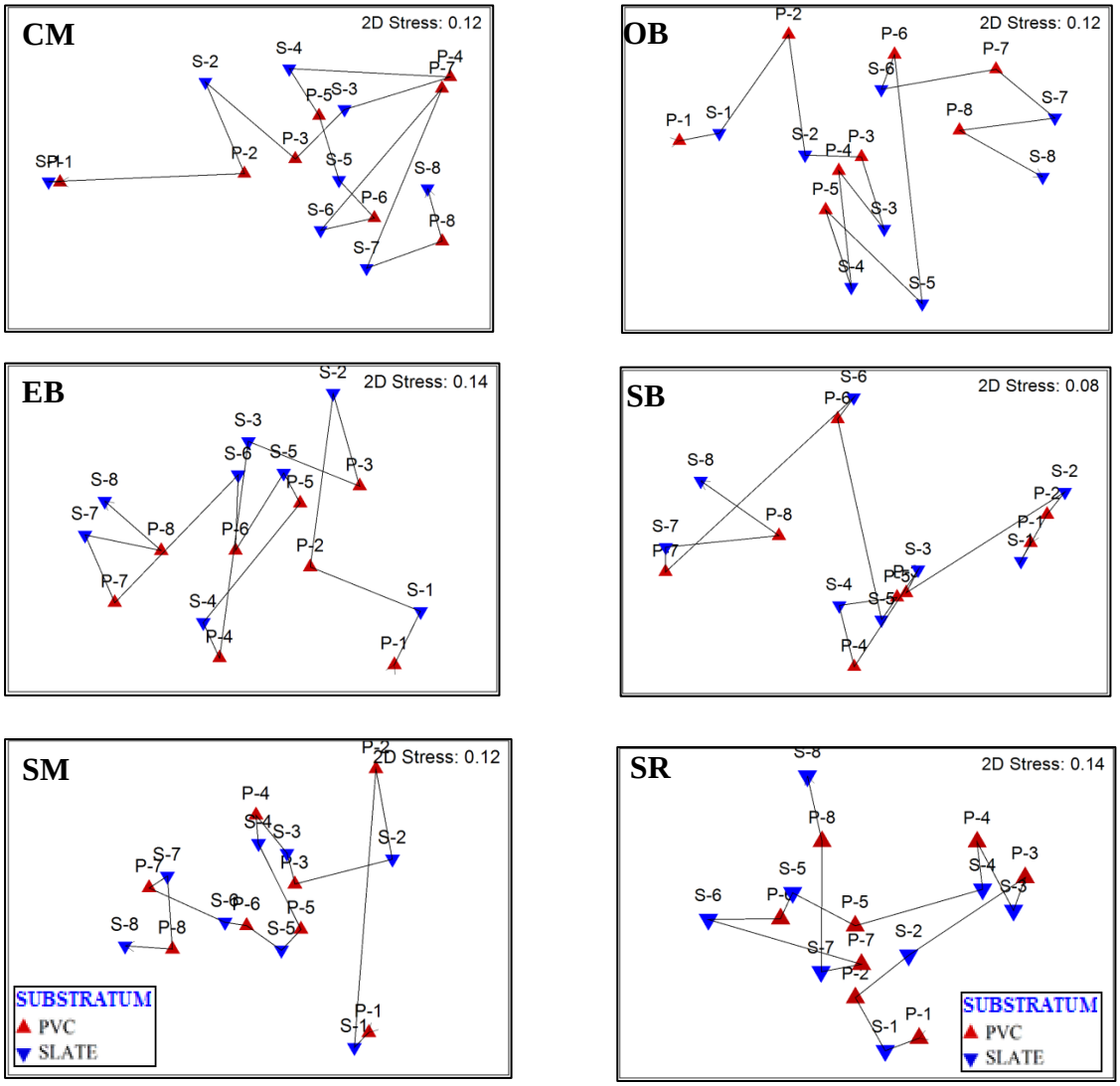


Figure 3.3.4. MDS ordination of temporal variation of the fouling community on three marina sites (CM= Chaffers marina, EB= Evans Bay marina, SM= Seaview marina) and three reef sites (OB= Oriental Bay, SB= Shelly Bay, SR= Sorrento Bay). Sample labelling: P = PVC substratum and S = Slate substratum; numbers denoted sampling intervals: 1= November 2017, 2= February 2018, 3= May 2018, 4= August 2018, 5= November 2018, 6= February 2018, 7= May 2018 and 8= August 2018.

3.3.5. Variations in the fouling community composition as a function of habitat, site (habitat), substratum and sample intervals

Multivariate PERMANOVA of the fouling community composition revealed that all terms were statistically significant ($P < 0.05$) and that most were highly significant ($P < 0.001$) (Table 3.3.4).

Table 3.3.4. Permutational ANOVA (PERMANOVA) analysis used to determine differences in community composition between factors: habitat type (2 levels), site (habitat) (6 levels), substratum type (2 levels) and sampling intervals (8 levels), Significant value in bold ($P < 0.05$).

Source of variation	**df**	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**
Habitat	1	53993	53993	37.112	**0.0001**
Substratum	1	25917	25917	17.814	**0.0001**
Sample interval	7	2.69E+05	38385	26.384	**0.0001**
Sites (Habitat)	4	1.15E+05	28668	19.705	**0.0001**
Habitat × Substratum	1	6990.7	6990.7	4.805	**0.0001**
Habitat × Sample interval	7	56417	8059.6	5.5397	**0.0001**
Substratum × Sample interval	7	22258	3179.7	2.1856	**0.0001**
Sites (Habitat) × Substratum	4	8925.2	2231.3	1.5337	**0.0173**
Sites (Habitat) × Sample interval	28	1.77E+05	6331.1	4.3517	**0.0001**
Habitat × Substratum × Sample interval	7	17342	2477.4	1.7028	**0.0005**
Sites (Habitat) × Substratum × Sample interval	28	57669	2059.6	1.4157	**0.0001**
Residuals	384	5.59E+05	1454.9		
Total	479	1.37E+06			

i. Habitat type

The pairwise PERMANOVA revealed that the reef sites exhibited slightly more within-group community similarity (29.35%) than the marina sites (26.12%) and that this difference was significant ($P < 0.001$) (Table 3.3.5). At both the habitat types, the same suite of species was observed. However, the difference in abundances of species explained the dissimilarity between habitat type (Table 3.3.6 & Table 3.3.7). For instance, overall, Biofilm type 1 and Green sp. 1 were the dominant contributors for average similarity and dissimilarity between habitat type. A subset of 7 species for marina and reef habitats explained most patterns of

similarity and dissimilarity; Biofilm type 1, Green sp. 1, *Ralfsia verrucosa, Bangia atropurpurea, Watersipora subtorquata, Asterocarpa humilis* and *Membranipora membranacea* (Table 3.3.7).

ii. Substratum type

The pairwise PERMANOVA revealed that the PVC substratum exhibited more within-group community similarity (29.89%) than the slate substratum (23.80%) and that this difference was significant ($P < 0.001$) (Table 3.3.5). Similar to habitats, a similar suite of species was observed. However, the differences in abundances of species explained the dissimilarity between substratum type (Table 3.3.6 & Table 3.3.7). Biofilm type 1 and Green sp. 1 were the main contributors among PVC vs slate substratum similarity and between PVC vs slate substratum dissimilarity. A subset of 7 species for PVC and slate substratum explained the most patterns of similarity and dissimilarity; Biofilm type 1, Green sp. 1, *Ralfsia verrucosa, Bangia atropurpurea, Watersipora subtorquata, Asterocarpa humilis* and *Membranipora membranacea* (Table 3.3.7).

Table 3.3.5. Results of pairwise PERMANOVA test performed on fouling communities as a function of habitat and substratum with the average similarities between groups.

Groups	**t**	***P* (perm)**	**Unique perms**	**Average similarity (%)**		
Habitats Marina vs Reef	6.09	**0.0001**	9940	**Marina** (26.12)	**Reef** (29.35)	**Marina x Reef** (24.55)
Substratum PVC vs Slate	4.22	**0.0001**	9921	**PVC** (29.89)	**Slate** (23.80)	**PVC x Slate** (25.43)

Table 3.3.6. SIMPER results for major species contributing to the average similarity between habitat type and substratum type.

Marina = Average similarity: 26.12				**Reef = Average similarity: 29.35**			
Species	**Avg. Abund.**	**Contrib %**	**Cum. %**	**Species**	**Avg. Abund**	**Contrib%**	**Cum.%**
Biofilm type 1	2.93	27.33	27.33	Biofilm type 1	3.11	27.49	27.49
Green sp. 1	2.27	17.55	44.88	*Ralfsia verrucosa*	2.04	16.23	43.71
Bangia atropurpurea	1.88	14.19	59.07	Green sp. 1	2.35	15.58	59.29
Ostrea chilensis	1.27	6.63	65.7	*Watersipora subtorquata*	1.69	9.95	69.24
Ralfsia verrucosa	1.01	5.11	70.81	*Spirobranchus cariniferus*	1.22	8.62	77.86
Tunicate sp. 1	1.05	4.97	75.78	*Membranipora membranacea*	1.39	6.79	84.65
Cladophora	1	4.42	80.2	*Asterocarpa humilis*	1.16	4.11	88.77
Watersipora subtorquata	0.68	3.2	83.41	*Bangia atropurpurea*	0.76	2.5	91.27
Membranipora membranacea	0.64	2.77	86.17				
Asterocarpa humilis	0.8	2.45	88.63				
Spirorbis spirorbis	0.44	2.23	90.86				
PVC = Average similarity: 29.89				**Slate = Average similarity: 25.43**			
Species	**Avg. Abund.**	**Contrib %**	**Cum. %**	**Species**	**Avg. Abund**	**Contrib%**	**Cum.%**
Biofilm type 1	3.87	37.78	37.78	Biofilm type 1	2.17	20.02	20.02
Green sp. 1	2.44	15.63	53.41	Green sp. 1	2.19	18.91	38.93
Ralfsia verrucosa	1.98	13.58	66.99	*Ralfsia verrucosa*	1.07	7.32	46.25
Bangia atropurpurea	1.44	7.19	74.18	*Bangia atropurpurea*	1.2	7.16	53.41
Watersipora subtorquata	1.29	6.13	80.31	*Spirobranchus cariniferus*	0.91	6.9	60.31
Membranipora membranacea	0.99	3.67	83.98	*Watersipora subtorquata*	1.09	6.32	66.63
Spirobranchus cariniferus	0.73	3.25	87.23	*Membranipora membranacea*	1.05	6.01	72.65
Cladophora	0.84	2.76	89.99	*Asterocarpa humilis*	1.21	5.52	78.16
Asterocarpa humilis	0.75	1.91	91.90	*Ostrea chilensis*	1.05	5.27	83.44
				Tunicate sp. 1	0.94	4.26	87.69
				Spirorbis spirorbis	0.46	2.97	90.66

Table 3.3.7. Results for SIMPER analysis. Average similarities within groups and average dissimilarities in fouling communities between habitat type and substratum type.

	Marina & Reef = Average dissimilarity = 74.45				**PVC & Slate = Average dissimilarity = 74.57**			
Species	**Marina Avg. Abund.**	**Reef Avg. Abund.**	**Contrib %**	**Cum. %**	**PVC Avg. Abund.**	**Slate Avg. Abund.**	**Contrib %**	**Cum. %**
Biofilm type 1	2.93	3.11	11.16	11.16	3.87	2.17	11.96	11.96
Green sp. 1	2.27	2.35	10.68	21.84	2.44	2.19	10.82	22.79
Ralfsia verrucosa	1.01	2.04	7.25	29.09	1.98	1.07	7.15	29.94
Bangia atropurpurea	1.88	0.76	6.83	35.92	1.44	1.2	6.57	36.51
Watersipora subtorquata	0.68	1.69	6.01	41.93	1.29	1.09	5.77	42.28
Asterocarpa humilis	0.8	1.16	5.61	47.54	0.75	1.21	5.65	47.93
Membranipora membranacea	0.64	1.39	5.38	52.93	0.99	1.05	5.28	53.21
Ostrea chilensis	1.27	0.37	4.72	57.64	0.59	1.05	4.59	57.8
Cladophora	1	0.46	4.39	62.03	0.84	0.62	4.4	62.2
Tunicate sp. 1	1.05	0.5	4.33	66.37	0.61	0.94	4.29	66.49
Spirobranchus cariniferus	0.42	1.22	4.19	70.55	0.73	0.91	3.93	70.42
Clathrina sp.	0.45	0.69	3.42	73.97	0.59	0.56	3.44	73.85
Bugula stolonifera	0.62	0.25	2.75	76.72	0.38	0.49	2.74	76.59
Bugula flabellata	0.44	0.35	2.35	79.07	0.43	0.36	2.37	78.95
Spirorbis spirorbis	0.44	0.36	2.16	81.23	0.34	0.46	2.19	81.15
Biofilm type 2	0.15	0.47	2.14	83.37	0.26	0.36	2.13	83.28
Coralline algae	0.41	0.15	1.74	85.11	0.28	0.27	1.74	85.02
Ulva lactuca	0.35	0.19	1.69	86.8	0.25	0.29	1.7	86.72
Schizoporella errata	0.27	0.24	1.49	88.29	0.24	0.27	1.5	88.22
Tunicate sp. 2	0.18	0.28	1.42	89.71	0.19	0.26	1.43	89.65
Botrylloides leachii	0.35	0.02	1.15	90.86	0.2	0.17	1.14	90.79

iii. Habitat × Substratum

Fouling community composition as a function of habitat and substratum ($P < 0.001$) exhibited relatively more within-group similarity on PVC than on slate at both marina and reef habitats (pairwise PERMANOVA tests; Table 3.3.8).

Table 3.3.8. Results of pairwise PERMANOVA test performed on fouling communities as a function of the interaction between habitat × substratum with the average similarities between groups.

Groups	**t**	***P* (perm)**	**Unique perms**	**Average similarity (%)**		
Habitat x Substratum						
Marina PVC vs Slate	3.65	**0.0001**	9930	**PVC** (30.04)	**Slate** (24.49)	**PVC x Slate** (24.99)
Reef PVC vs Slate	2.97	**0.0001**	9953	**PVC** (33.18)	**Slate** (26.66)	**PVC x Slate** (28.79)

In summary, the fouling community composition as a function of habitat and substratum and their interactions indicated statistically significant results (PERMANOVA; $P < 0.001$). Pairwise PERMANOVA indicated relatively more within-group community similarity at reef sites than at marina sites and on PVC substratum than on slate substratum. However, when comparing the fouling community composition between substrata at each habitat, PVC substratum had more within-group similarity than that on slate substratum at both reef and marina habitats. SIMPER results also revealed a similar suite of 2 species contributing to > 50% within-group similarity and 7 species > 50% between-group dissimilarity [Habitat (Marina vs Reef); Substratum (PVC vs Slate)] in the relative abundance of the community.

iv. Sample interval

The fouling community composition differed significantly between sample intervals ($P < 0.001$). As expected, Time 1 (41.19%) had relatively fewer species contributing to its within-group similarity, with an increase in fouling community species diversity over time resulting in a decrease in within-group similarity over time (Table 3.3.9). However, most of the between-group community dissimilarity was explained by the slight differences in abundances of the observed species.

SIMPER analysis showed that Biofilm type 1 and Green sp. 1 were the first recruits that appeared on the tiles (they were present within 3 months, by Time 1) suggesting these two

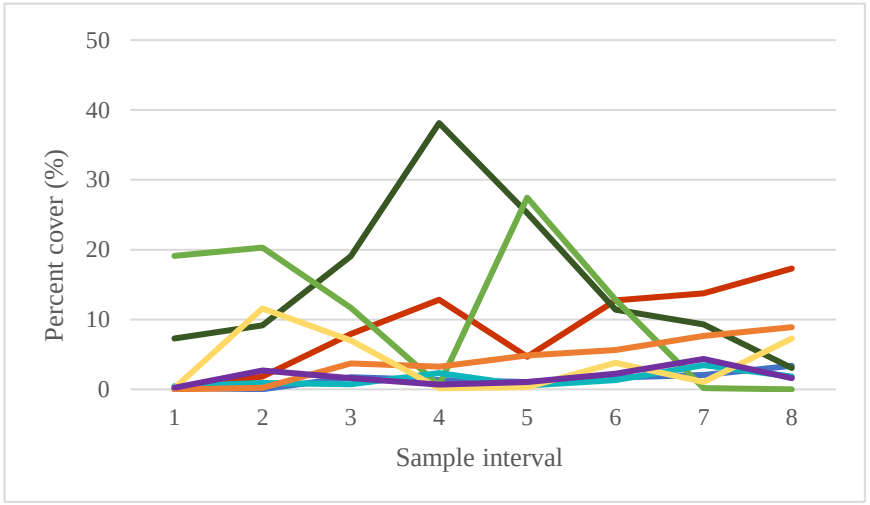
species to be opportunistic species which rapidly dominated much of the available bare space. Biofilm type 1 and Green sp. 1 also consistently contributed the most to the within-group community similarity and between-group community dissimilarities for all sample intervals. Biofilm type 1 increased with time (Time 1; Biofilm type 1 = 29.97%) and was the highest at Time 4 (60.08%) and decreased thereafter, suggesting Biofilm type 1 may be an ephemeral species, i.e. short-lived species. Additionally, Green sp. 1 showed a bimodal trend, with a decrease at Time 4, which marks the austral winter, suggesting that abundance of Green sp. 1 may be seasonally dependent (Figure 3.3.5). As observed, the dominance of Biofilm type 1 and Green sp. 1 changed over time and was replaced by the dominance of the red alga, *Bangia atropurpurea* at Time 8, i.e. the end of the 2-year study. Other contributors to top-ranked abundance included *Asterocarpa humilis, Membranipora membranacea, Ostrea chilensis, Ralfsia verrucosa* and *Watersipora subtorquata.* Increase in the abundance of these aforementioned species was gradual with no interaction observed between these species, suggesting varied patterns of succession for each species (Table 3.3.9).

The interaction factor, Habitat × Sample interval, the community composition indicated significant ($P < 0.005$) results between habitat type (marina vs reef) for all sampling intervals. The community composition for the interaction factor Substratum × Sample interval showed significant results ($P < 0.05$) each sample interval except for time 1 ($P = 0.54$) (Table A4). When comparing the temporal variation of the top 8 species between habitat type and substratum type (SIMPER, Figure 3.3.5), the species showed a similar overall trend of percentage cover. The species between habitat type (marina vs reef) indicated a relatively high abundance of; native tunicate *Asterocarpa humilis,* cryptogenic Biofilm type 1, native bryozoan *Membranipora membranacea,* native crustose brown seaweed *Ralfsia verrucosa* and non-native bryozoa *Watersipora subtorquata* in reef habitat than at marina habitat. Whilst, non-native red alga *Bangia atropurpurea,* native oyster *Ostrea chilensis,* cryptogenic Tunicate sp. 1 and cryptogenic *Ulva* sp. 1 had relatively high abundances at marina habitat than at reef habitat.

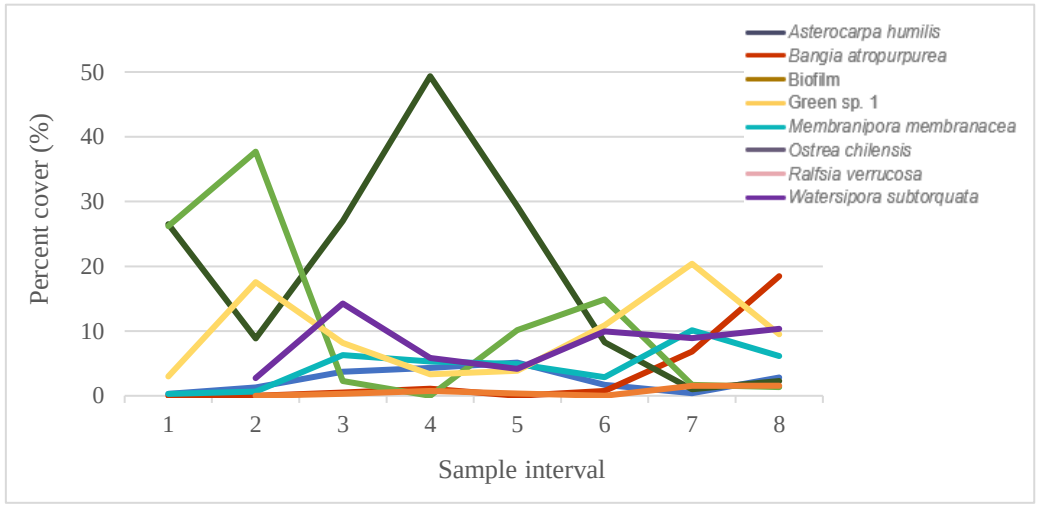
Table 3.3.9. SIMPER results for 10 major consistent species contributing to the average similarity within each sampling interval. A = Avg. Abundance, C% = Per cent Contribution.

	Time 1		**Time 2**		**Time 3**		**Time 4**		**Time 5**		**Time 6**		**Time 7**		**Time 8**	
Avg. similarity	**41.19%**		**37.81%**		**32.49%**		**39.48%**		**36.47%**		**31.69%**		**26.17%**		**28.28%**	
Species	**A**	**C%**	**A**	**C%**	**A**	**C%**	**A**	**C%**	**A**	**C%**	**A**	**C%**	**A**	**C%**	**A**	**C%**
Asterocarpa humilis	0.23	0.49	0.52	0.74	1.26	4.21	1.4	3.78	1.25	4.3	0.91	2.77	0.77	2.14	1.51	5.57
Bangia atropurpurea	0.1	0.06	0.45	0.54	1.00	4.82	1.53	7.11	0.83	2.29	1.42	7.19	2.22	18.42	3.02	29.9
Biofilm type 1	3.34	29.97	2.04	13.3	3.77	35.47	6.13	60.08	4.09	41.11	1.97	14.63	1.68	7.54	1.15	4.37
Green sp. 1	3.84	44.23	4.76	43.96	1.86	8.96	0.37	0.24	3.55	27.14	2.83	21.64	0.72	1.28	0.59	0.79
Membranipora membranacea	0.34	0.78	0.59	1.23	1.37	4.37	1.12	5.23	1.1	2.87	0.84	3.27	1.59	11.95	1.21	5.92
Ostrea chilensis	-	-	0.12	0.11	0.77	2.4	0.83	2.73	1.07	3.36	0.9	2.26	1.32	7.39	1.52	7.89
Ralfsia verrucosa	0.77	2.41	2.62	22.37	1.65	11.66	0.69	1.75	0.68	2.14	1.88	10.8	1.96	13.92	1.94	13.65
Watersipora subtorquata	0.09	0.11	0.99	4.08	1.75	8.92	1.09	3.67	0.92	3.3	1.49	8.46	1.7	11.91	1.46	7.47

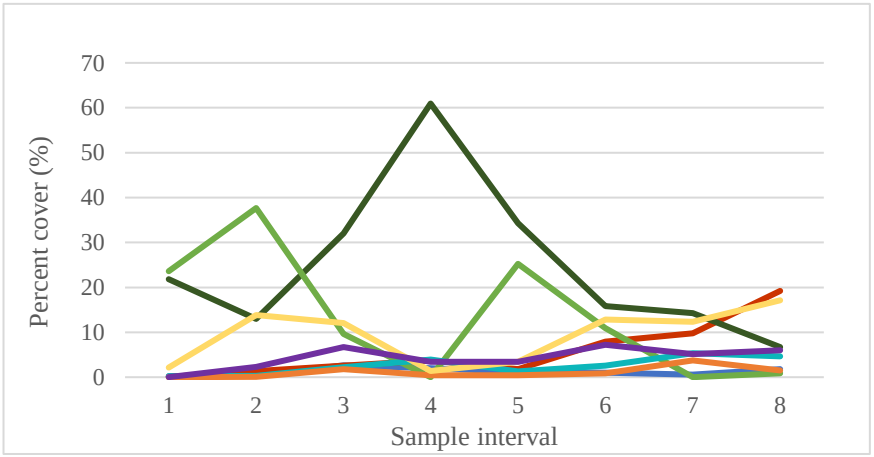
a) Man-made habitat



b) Natural habitat



c) Man-made substratum



d) Natural substratum

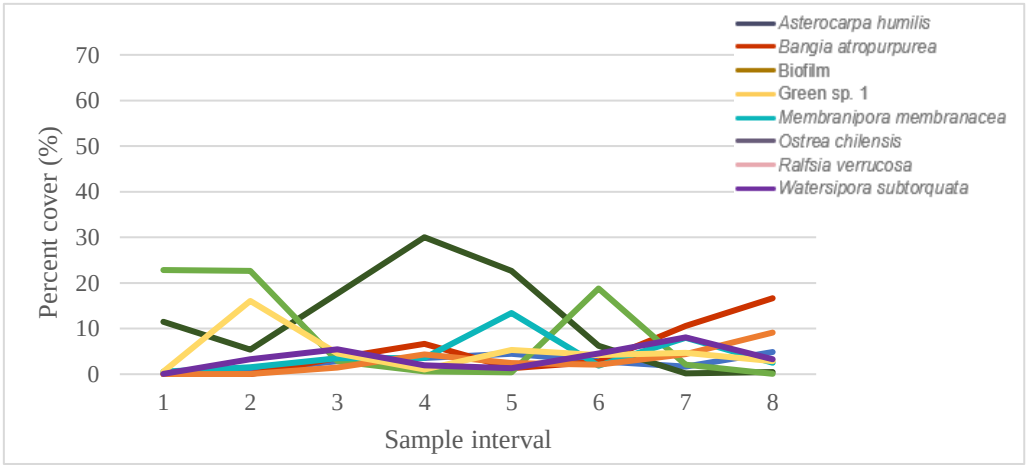


Figure 3.3.5. The percent cover (SIMPER) of top 8 major consistent species contributing to within-group similarity for each sample interval indicating variations over time at a) man-made habitat b) natural habitat c) man-made substratum and d) natural substratum

3.3.6. Species status (native, non-native and cryptogenic) within the fouling community

a) Species status and their occurrences

The 47 putative species were classed according to their status as native, non-native and cryptogenic. There were 19 native species, 12 non-natives and 16 cryptogenic species (Table 3.3.1).

b) Species status as a function of habitat, site, substratum and sample interval

Multivariate PERMANOVA for the species status revealed that all main factors were statistically significant ($P < 0.001$), with significant interaction between Habitat × Sample interval and Site (Habitat) × Sample interval ($P < 0.001$), indicating variations in the species status between habitat type/site (habitat) over time. Other interaction terms were not significant (Table 3.3.10).

Table 3.3.10. Permutational ANOVA (PERMANOVA) analysis used to determine differences in the status of the species between factors: habitat type (2 levels), site (habitat) (6 levels), substratum type (2 levels) and sampling time (8 levels), Significant value in bold ($P < 0.05$).

Source	**df**	**SS**	**MS**	**Pseudo-*F***	***P* (perm)**	**Unique perms**
Habitat	1	2759.6	2759.6	8.1738	**0.0003**	9966
Substratum	1	4920	4920	14.573	**0.0001**	9961
Time	7	43896	6270.9	18.574	**0.0001**	9914
Site (Habitat)	4	20889	5222.2	15.468	**0.0001**	9942
Habitat × Substratum	1	807.32	807.32	2.3913	0.0911	9952
Habitat × Time	7	19211	2744.5	8.1291	**0.0001**	9913
Substratum × Time	7	4158.6	594.08	1.7597	**0.04**	9918
Site (Habitat) × Substratum	4	2302.6	575.65	1.7051	0.089	9931
Site (Habitat) × Time	28	53135	1897.7	5.6208	**0.0001**	9871
Habitat × Substratum × Time	7	2238.2	319.74	0.94705	0.5121	9925
Site (Habitat) × Substratum × Time	28	11276	402.72	1.1928	0.164	9828
Residuals	384	1.30E+05	337.61			
Total	479	2.95E+05				

i. Habitat type

Numbers of occurrences as a function of the status of the species - native, non-native and cryptogenic- were similar as a function of time at reef and marina habitats (Figure 3.3.6). However, PERMANOVA revealed a significant difference ($P < 0.001$) between the reef and marina habitats, but the within-group similarity was very similar (Reef = 70.09%; Marina = 69.01%; Table 3.3.11). SIMPER analysis further revealed that the cryptogenic species contributed most to similarity at both reef (47.44%) and marina sites (47.33%) followed by native species (Reef = 37.15%; Marina = 31.70%). The non-native species were abundant significantly ($P < 0.05$; Table 3.3.12) at marina sites (20.97%) than reef sites (15.41%). The cryptogenic species contributed most to the between-group dissimilarity (Table 3.3.13 a).

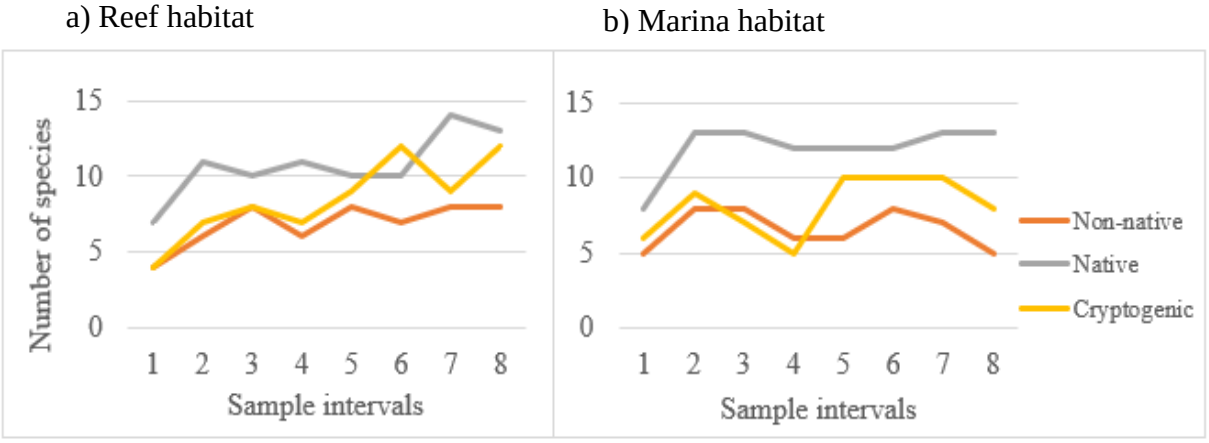


Figure 3.3.6. Temporal change in the number of species with respect to species status (native, non-native and cryptogenic) as a function of habitat type (Reef vs Marina)

Table 3.3.11. Results of pairwise PERMANOVA test performed on species status as a function of habitat type and substratum type with the average similarities between groups.

Groups	**t**	***P* (perm)**	**Avg. similarities**		
			Reef	**Marina**	**Reef × Marina**
Habitat (Reef vs Marina)	2.88	**0.0004**	70.09	69.01	69.29
Substratum (PVC vs Slate)	3.83	**0.0001**	**PVC**	**Slate**	**PVC × Slate**
			71.53	67.86	69.14

Table 3.3.12. Results of pairwise PERMANOVA test performed for non-native species as a function of habitat type and substratum type.

Groups	t	*P* (perm)	Unique perms
Habitat (Reef vs Marina)	1.53	**0.03**	9923
Substratum (PVC vs Slate)	0.88	0.56	9924

ii. Substratum type

The number of native, non-native and cryptogenic species as a function of time on PVC and slate substrata were similar (Figure 3.3.7). However, PERMANOVA revealed a significant difference ($P < 0.001$) between PVC and slate substrata, with PVC exhibiting greater within-group similarity (71.53%) than the slate substratum (67.86%) (Table 3.3.11). SIMPER analyses revealed that cryptogenic species followed by native species contributed most to the within-group similarities and between-group dissimilarities for both substrata. (Table 3.3.13 b). The non-native species observed to contribute more on slate substratum than PVC; however, their difference was not significant (Table 3.3.12).

a) Slate substratum b) PVC substratum

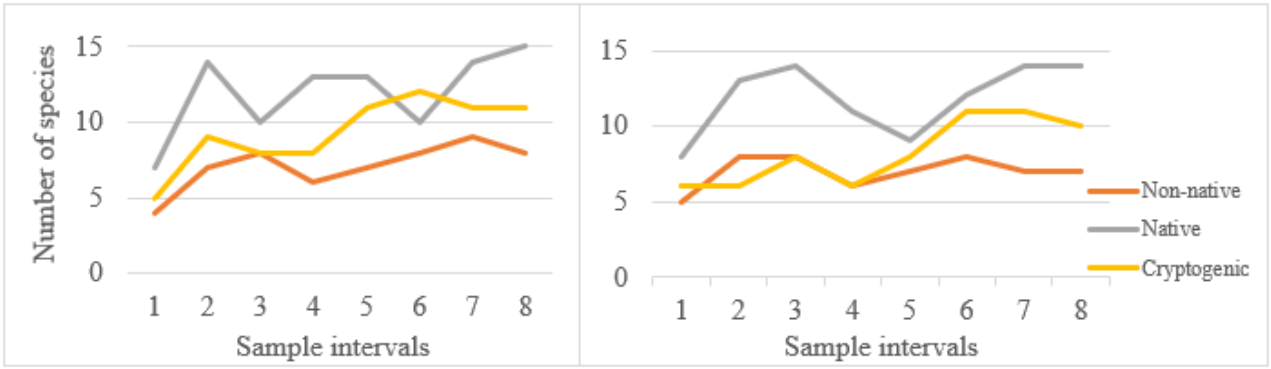


Figure 3.3.7. Temporal change in the number of species with respect to species status (native, non-native and cryptogenic) as a function of substratum type (PVC vs Slate)

Table 3.3.13. SIMPER results for species status contributing to the average within-group similarity and dissimilarity between a) habitat type (Reef vs Marina and b) substratum type (PVC vs Slate).

a)

Marina: Average similarity = 69.01%				**Reef: Average similarity = 70.09%**				**Habitat (Marina vs Reef) Average dissimilarity = 30.71%**				
Species Status	**Avg. Abund.**	**Contrib %**	**Cum. %**	**Species Status**	**Avg. Abund.**	**Contrib %**	**Cum.%**	**Species Status**	**Avg. Abund. Marina**	**Avg. Abund. Reef**	**Contrib %**	**Cum. %**
Cryptogenic	5.69	62.09	62.09	Cryptogenic	5.96	76.27	76.27	Cryptogenic	5.69	5.96	34.50	34.50
Native	4.27	29.64	91.73	Native	4.87	20.65	96.92	Native	4.27	4.87	32.91	67.40
Non-native	3.28	8.27	100	Non-native	2.95	3.08	100	Non-native	3.28	2.95	32.60	100

b)

PVC: Average similarity = 71.53%				**Slate: Average similarity = 67.86%**				**Substratum (PVC vs Slate) Average dissimilarity = 30.86%**				
Species Status	**Avg. Abund.**	**Contrib %**	**Cum. %**	**Species Status**	**Avg. Abund.**	**Contrib %**	**Cum. %**	**Species Status**	**Avg. Abund. Slate**	**Avg. Abund. PVC**	**Contrib %**	**Cum. %**
Cryptogenic	6.40	5.80	50.80	Cryptogenic	5.23	44.28	44.28	Cryptogenic	5.25	6.40	35.31	35.31
Native	4.59	31.57	82.37	Native	4.55	37.24	81.53	Native	4.55	4.59	32.41	67.72
Non-native	3.23	17.63	100	Non-native	3.00	18.47	100	Non-native	3.00	3.23	32.28	100

iii. Sample interval

The PERMANOVA tests revealed that species status - native, non-native and cryptogenic species - exhibited significant variation ($P < 0.001$) between sample intervals irrespective of the effects of habitats or substratum, with >50% within-group species status similarity for all sample intervals. SIMPER analysis of species status at each sample interval revealed that cryptogenic species were the most abundant group contributing to within-group similarity, followed by native species (Table 3.3.14). However, with time, the cryptogenic species decreased with an increase in the abundance of native and non-native species. This trend was also observed for species status as a function of sample interval at both habitat type and substratum type (Table 3.3.15).

Table 3.3.14. Major species status contributing to the average similarity within each sampling interval. A = Avg. Abundance, C% = Per cent Contribution.

	Time 1		**Time 2**		**Time 3**		**Time 4**	
Average similarity	**73.57%**		**70.56%**		**69.60%**		**70.86%**	
Species Status	**A**	**C%**	**A**	**C%**	**A**	**C%**	**A**	**C%**
Cryptogenic	6.16	66.45	5.82	46.60	5.44	40.13	6.91	52.66
Native	3.71	31.75	4.50	36.43	4.86	34.37	4.30	28.03
Non-native	0.58	1.80	2.98	16.47	3.93	25.50	3.39	19.31
	Time 5		**Time 6**		**Time 7**		**Time 8**	
Average similarity	**71.04%**		**62.62%**		**67.33%**		**67.31%**	
Species Status	**A**	**C%**	**A**	**C%**	**A**	**C%**	**A**	**C%**
Cryptogenic	6.47	56.32	6.66	51.39	5.06	36.40	4.11	26.97
Native	4.11	29.21	4.37	29.02	4.97	37.29	5.72	43.15
Non-native	2.40	14.47	3.21	19.59	3.99	26.31	4.45	29.88

Table 3.3.15. The temporal variation of species status (percent contribution) as per SIMPER results for habitat type (reef vs marina) and substratum type (slate vs PVC).

Habitat type × Sample interval								
Reef habitat								
Sampling interval	1	2	3	4	5	6	7	8
Cryptogenic	66.73	51.13	31.05	53.82	49.12	59.29	31.66	28.22
Native	32.63	40.42	44.3	30.7	38.8	25.11	44.25	33.89
Non-native	0.63	8.46	24.65	15.47	12.08	15.6	24.1	37.89
Marina habitat								
Sampling interval	1	2	3	4	5	6	7	8
Cryptogenic	65.22	39.25	48.57	51.19	62.49	43.67	40.82	24.99
Native	31.25	30.77	26.25	25.64	21.19	32.88	31.17	52.6
Non-native	3.54	29.97	25.17	23.18	16.31	23.45	28.01	22.41
Substratum type× Sample interval								
Slate substratum								
Sampling interval	1	2	3	4	5	6	7	8
Cryptogenic	65.81	41.17	34.78	46.53	48.45	54.95	35.21	25.18
Native	32.34	44.1	35.76	31.66	36.09	28.31	36.8	46.03
Non-native	1.85	14.73	29.46	21.81	15.46	16.74	27.99	28.79
PVC substratum								
Sampling interval	1	2	3	4	5	6	7	8
Cryptogenic	67.48	52.09	46.04	58.81	64.52	47.65	37.58	28.97
Native	30.88	29.33	32.57	24.47	22.4	29.63	37.93	40.24
Non-native	1.65	18.58	21.39	16.73	13.09	22.72	24.5	30.79

3.3.7. Regression between the native and non-native species as a function of the sample interval

The relationships of native and non-native species number were strongly positive, with significant positive relationships for all 8 sample intervals at both habitat type (r^2 = 0.58, r = 0.76, P < 0.001) and substratum type (r^2 = 0.58, r = 0.76, P < 0.001) (Figure 3.3.8). These results suggest that; an increase in the number of native species led to an increase in the number of non-native species over time.

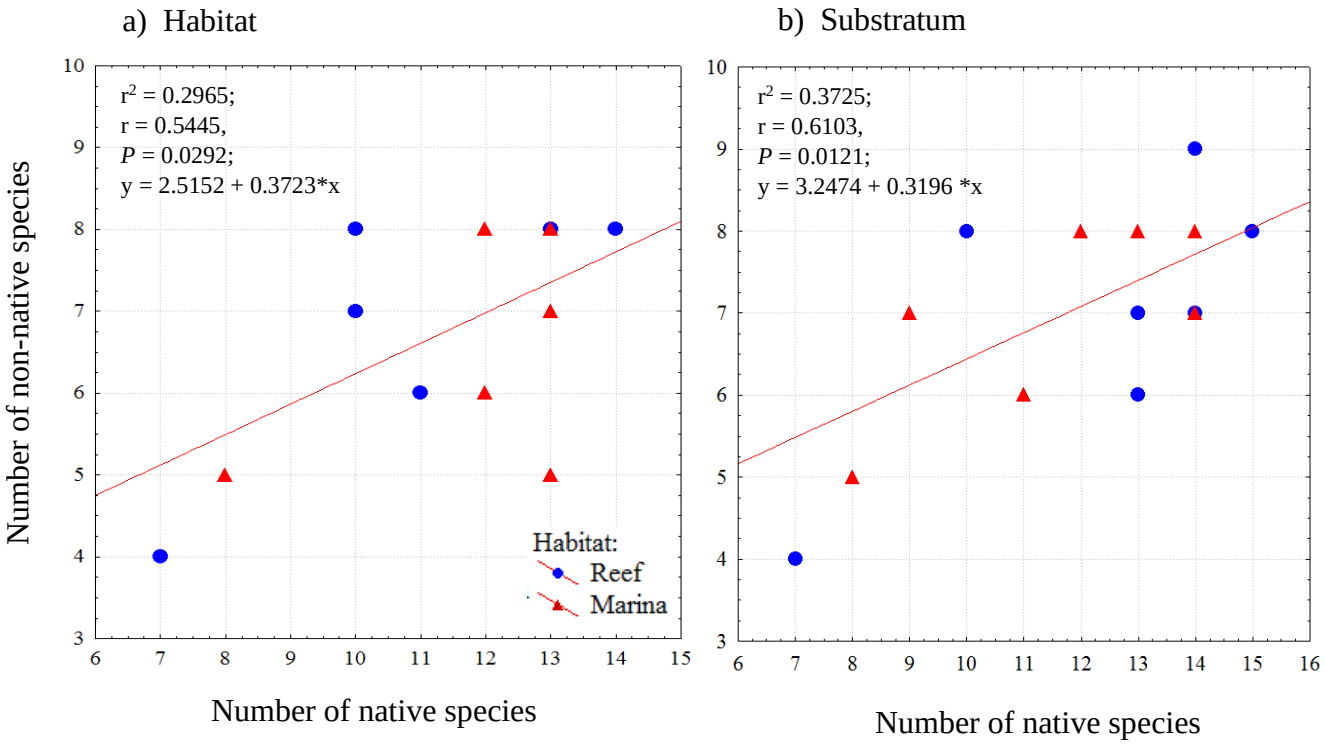


Figure 3.3.8. Correlation of number of native and non-native species as a function of time at a) habitat type (Reef vs Marina); b) substratum type (Slate vs PVC).

3.4. Discussion

Humans have contributed significantly to the modification of the marine environment and the corresponding impacts of these modifications on the associated marine assemblages (Airoldi & Beck 2007; Firth et al. 2016; Ruiz et al. 2009). This study aimed to examine the effect of natural and man-made built habitats (Reef vs Marina) and substrata (Slate vs PVC) on a fouling community. The settlement tiles (Slate & PVC) were deployed at 3 reef sites and 3 marina sites over two years, with tri-monthly sampling. To my knowledge, this study is the first to examine and compare fouling community and species status (native, non-native, cryptogenic) using an experimental setup of slate and PVC tiles at reef and marina habitats which are analogous to natural and man-made habitats or structures in New Zealand. I observed a total of 47 species on 480 tiles, consistent with species number observed in other studies concerning artificial structures (Glasby 1999; Connell & Glasby 1999; Bacchiocchi & Airoldi 2003; Firth et al. 2013). The majority of the species identified were observed to have settled by ~6 months of the study period.

3.4.1. Availability of bare space

In this study, the bare space availability varied significantly between habitat type; however, the differences were too small to be of ecological importance. Considering the substratum type, the bare space availability significantly varied between PVC and slate tiles with relatively more available bare space on a slate tile. However, the temporal variations in the availability of bare space between substratum type were similar. The temporal and spatial changes indicate the rate of change of bare space availability varied with temporal changes in the development of species community. The rapid settlement of species covered~64% of the tile within 3 months of immersion of the bare tiles (100% bare space). However, the percentage cover of species did not reach 100%, indicating the availability of bare space for future settlements.

3.4.2. Fouling community composition as a function of habitat type and substratum type

Species number was observed to be similar between habitats (Reef vs Marina) and substrata (Slate vs PVC). Upon further analysis, the species abundances (i.e., not presence/absence) and per cent contributions to the group similarity differed between both habitat type and substratum type resulting in significant differences. These results are consistent with studies comparing natural rocky reefs and seawalls as artificial structures that observed similar species taxa between both habitats, even if community structure and abundances were different (Chapman 2003; Bulleri et al. 2005; Albano & Obenat 2019). These authors speculated the differences in

assemblages to intrinsic features of the substrates at both habitats and physical attributes such as wave-exposure. Previous studies using settlement plates have shown differences in community composition at the initial stages, but over time the community became more similar (Anderson & Underwood 1994; Andersson et al. 2009). This highly depends on the seasons of submersion of settlement tiles and the recruitment or settlement time of the species (Anderson & Underwood 1994). Submersion time is an essential factor in any community structure comparison study. Submersion time coinciding with reproductive periods of species can lead to high larval settlement due to the availability of free space (Anderson & Underwood 1994; Andersson et al. 2009; Smith et al. 2014).

Upon further analysing the species composition between substratum-type and habitat-type, respectively, at each sample time, a similar suite of species colonised the Slate and PVC tiles at Reef and Marina habitats but with slightly differing abundances. These results suggest that differences between Reef vs Marina habitat and Slate vs PVC substratum, although statistically significant, maybe due to small-scale temporal and spatial differences in the recruitment patterns of each species (Chang & Turner, 2019). Ultimately, in this study, these small-scale differences that most likely reflect stochastic processes, give rise to similar patterns of ecological succession between both habitat type and substrata type in Wellington Harbour. Whilst the statistical analyses revealed highly significant differences in community composition (based on differences in abundance, not in species presence) between habitats and substrata, the importance of these highly significant differences from an ecological point of view is still not clear. The man-made habitat (marina) and substratum (PVC) do not promote or degrade species richness and community composition, although many other studies have shown this to be the case. Therefore, indicating that relative to adjacent natural reefs (~200 m), i.e. local spatial scale, marinas do not degrade species richness. However, this might not be the case in terms of broader scale effect.

This study also revealed similar multi-species succession trajectories between habitat type and substratum type. For example, the transition of Biofilm type 1, which was the dominant species led to the dominance of red algae, *Bangia atropurpurea* and other encrusting species by the end of the 2-year study. Within 3 months of immersion, the initially bare settlement tiles (PVC vs Slate)~64% of all observed species were found amongst the initial colonisers (Biofilm type 1 and Green sp. 1). Early settlers are also known to modify a habitat, which may make it habitable for later recruiting species (Connell 1972; Morand & Briand 1996; Dang & Lovell 2000; Lewis et al. 2003; Salta et al. 2013; Lotze et al. 2020). This finding

is consistent with earlier observations that new, barren, surfaces are more prone to be colonised by rapidly growing opportunistic species (Sousa 1979; Fletcher & Callow 1992; Dafforn et al. 2012; Tan et al. 2015). In this study, Biofilm type 1 readily settled on both PVC and slate substratum; however, the percent contribution to the within-group similarity by Biofilm type 1 was 38% on PVC substratum whereas 20% on the slate substratum. This difference, however, did not impact the community composition or succession patterns.

Biofilm type 1 was the major space occupant, at least initially until it reached a peak of abundance (cover on the tiles) at about 1 year into the 2-year study, before declining dramatically in abundance after that. The other colonists observed in the study were encrusting species such as *Ostrea chilensis*, *Asterocarpa humilis*, *Ralfsia verrucosa*, *Watersipora subtorquata* and *Membranipora membranacea* which have slow growth rates and occupancy of the available space (Chapman 2012). However, it is not clear in this study if the Biofilm Type 1 facilitated the establishment of other species. Besides, the recruitment and community development may be largely dependent on local recruitment, reproduction and growth rates which are likely to vary with time, available space and nutrients (Smith et al. 2014). Presumably, the reproduction time of a given species with available bare space for settlement led to the settlement of the other species. Whether the species composition would change given a longer time for colonisation or whether the red algae, *Bangia atropurpurea* observed represents as 'climax state' remains unknown.

Grazers are known to influence the species distribution, abundance and diversity of algal species (Williams et al. 2013). Grazers are dependent on space availability and predation intensity (Williams et al. 2000). The grazers were not quantified in this study which may have provided more information about the algal succession and similarities in other species succession patterns. The other factor impacting patterns of colonisation are physical factors such as environmental stress, disturbance, availability of resources, space and functional characteristics like recruitment, competition, growth, dispersal and reproduction rate of a species (Sousa 1985; Menge et al. 1986; Benedetti-Cecchi 2000; Petes et al. 2007). A study conducted on a larger scale comparing intertidal species composition and biogeographic patterns between New Zealand and New South Wales, Australia, found relatively similar species composition and contribution of major taxa due to similarity in various other patterns such as temperature and latitude that regulate the communities in these areas (Schiel et al. 2019). Hence, determining the changes in physical and biological processes at specific habitats at a given time may also explain the variations in species diversity and species composition

(Tilman et al. 1994). Unfortunately, environmental data for this study could not be processed due to failure in calibrations; however, this is one factor to be considered for future research. Wellington Harbour is one of the largest natural harbours in the Southern Hemisphere and is heavily modified by port development, indicating that it is a 'disturbed' environment. Therefore, dispersal of species from artificial structures to nearby habitats, thereby altering the developing community may be a cause-effect of disturbance (Sousa 1979; Chapman 2012).

3.4.3. Species status – native, non-native and cryptogenic species

Analyses of multi-species community composition (described above) provide a powerful approach by which to identify how and perhaps why built environment when compared to the natural environment influences biological diversity. Another approach, using the species status, i.e., native, non-native, cryptogenic allows for a more definitive test of if and how native and non-native biodiversity make use of natural (reef) and man-made environments in coastal regions.

Artificial structures may provide habitats for certain species that are not found on natural rocky reefs because of their low predation rates and increased availability of bare space (Bulleri & Airoldi 2005). The native, non-native and cryptogenic species significantly differed between Reef vs Marina habitats and between PVC vs Slate substrata. The cryptogenic species were the dominant species status between habitat type and substrata type. For non-native species, the species were relatively abundant at marina sites. This confirms my hypothesis that non-native species are more abundant than native species at the man-made habitats (marina) relative to natural habitats. These results coincide with many other studies where a high number of non-native species are observed at artificial habitats (Connell 2001; Bacchiocchi & Airoldi 2003; Airoldi et al. 2005; Bulleri & Airoldi 2005; Airoldi & Beck 2007; Glasby et al. 2007; Perkol-Finkel et al. 2012). However, the non-native species were abundant on PVC substratum; however, the difference of non-native species between PVC vs Slate substrata was not significant.

The number of native and non-native species were positive and strong correlated for each time at both habitat type and substratum type. However, a previous comparative study of different substratum types indicated that the non-native tunicates increased in abundance on artificial substrates, with an associated decline in other native species (Tyrrell & Byers, 2007). Non-native species are generally seen as a threat to the native species richness. However, if a habitat is conducive to native species with sufficient resources and space, it also provides an

opportunity for non-native species (Davis 2003). Therefore, the quality of a habitat determines the settlement of species irrespective to the species status (Sax 2002; Stohlgren et al. 2003). These results are in accordance with the ecological theory stating effective 'biotic acceptance hypothesis' (Stohlgren 2003, 2006). The 'biotic acceptance hypothesis' defined as the establishment and coexistence of introduced species despite the presence and abundance of native species (Stohlgren et al. 2006). Another ecological theory to consider for this study is the 'empty niche' hypothesis where the ecosystem is not saturated with native species, and the non-native species occupy the vacant niches and available resources (Elton 1958; Stohlgren et al. 2003). However, co-existence of native and non-native species in a habitat further raises need to analyse for 'invasional meltdown'. Invasion meltdown' hypothesis is the presence of non-native species in a habitat facilitates the invasion of other species, increasing their likelihood of survival and ecological impact (Simberloff & Von Holle 1999). That being said, there is a need for a comprehensive study to observe if we see the same positive relationship between native and non-native species at a large spatial and temporal scale.

In summary, these results suggest that the differences between Reef vs Marina habitat and Slate vs PVC substratum, although statistically significant, maybe due to small-scale temporal and spatial differences in the recruitment patterns of each species (Chang & Turner 2019). These small-scale differences that most likely reflect stochastic processes give rise to similar patterns of ecological succession between both habitat type and substratum type in Wellington Harbour. The present study also highlighted the importance of species status-native, non-native and cryptogenic with different habitat types and substratum types. Although the native species were predominant, the non-native species were relatively abundant on PVC tiles and marina sites. These results indicate relatively more preference of non-native species towards man-made substratum and habitats. Besides, the native and non-native species positively correlated, indicating co-existence of the same. Given these observations, future studies should focus more on basic knowledge of the life-history traits and functioning of the species at various trophic levels, which will give a better understanding of species-specific interactions. Longer duration of experimental study will aid with acquiring complex community to have an overall knowledge of the species composition and interactions.

This study from a management point of view informs that anthropogenic alterations of natural habitats can lead to the destruction of natural habitats. Empty niches and disturbed habitats are a haven for non-native species (Airoldi et al. 2000; Guerra-García et al. 2004; Erlandsson et al. 2006; Oricchio et al. 2016; Pastro et al. 2017). It is evident from this study

that non-native species prefer man-made habitats and substratum. Maintenance of structures or dredge along the coast can lead to the removal of intertidal species exposing it to the settlement of non-native species (Airoldi et al. 2005; Airoldi & Bulleri 2011; Bracewell et al. 2013; Oricchio et al. 2016). Building new port infrastructures along the coast also provides additional habitats which are relatively more preferred by non-native species than native species, i.e. non-native more in abundance (Bulleri & Chapman 2010; Dumont et al. 2011; Rivero et al. 2013). Hardening the coastlines will degrade the quality of the habitat by obstructing the water flow bringing in nutrients thereby causing competition between native and non-native species for resources (Clark & Johnston 2009; Piola et al. 2009).

Additionally, the vertical orientation of substrata provides relatively less surface area to colonise compared to natural reefs. Even though this study showed co-existence of native and non-native species, there is a chance of provision of other non-native species by existing non-native species. This study highlights the need for a conservation strategy to manage natural habitats along the Wellington Harbour coastline. With the increasing modification of natural habitats to artificial habitats, there is a need to have a comprehensive understanding of the novel design of structures that can facilitate more native/local species and maintain native biodiversity (Chapman 2012; Dafforn et al. 2015a, 2015b; O'Shaughnessy et al. 2019). Eco-engineering of artificial structures is still at an experimental stage and may vary at different habitats. Future studies considering this study as a baseline work in Wellington Harbour should focus on different potential designs that can enhance the native biodiversity, reduces the non-native abundance and provide beneficial ecosystem services.

CHAPTER 4

DO NATIVE *M. GALLOPROVINCIALIS* LINEAGE, AND ITS NON-NATIVE *M. GALLOPROVINCIALIS* LINEAGE CONGENER DIFFER IN REPRODUCTIVE RESPONSE TO MAN-MADE HABITATS?

4.1. Introduction

4.1.1. Importance of habitat type

Modified coastal environments have recently raised many ecological concerns, new challenges and opportunities for an improved understanding of the management of marine biodiversity in the modern world (Firth et al. 2016). The heterogeneous natural habitats inhabit more diverse and complex species, providing refuge from biotic and abiotic stressors (Moschella et al. 2005; Moreira et al. 2006; Chapman & Underwood 2011; Firth et al. 2013; Firth et al. 2014; Loke et al. 2014; Aguilera et al. 2014; Oliver et al. 2015; Firth et al. 2016; Loke & Todd 2016). Unlike natural habitats, the man-made habitats have very different physical characteristics such as the smooth surface textures, artificial materials (e.g. cement, plastic, etc.) and vertical orientation (Perkol-Finkel et al. 2006; Dafforn et al. 2012; Perkol-Finkel et al. 2012; Spagnolo et al. 2014; Cacabelos et al. 2016; Brzozowska et al. 2017; Johnston et al. 2017). The different habitat structures have a significant impact on the environment as well as the ecological functioning of the species (Glasby & Connell 2001; Bulleri & Chapman 2004, 2010; Bulleri 2005; Tyrrell & Byers 2007; Chapman 2012; Tan et al. 2015; Megina et al. 2016).

Numerous studies have investigated the impacts of man-made habitats and substrata on the population and community structure (Bulleri 2005; Airoldi et al. 2005; Bulleri & Airoldi 2005; Wyatt et al. 2005; Airoldi & Beck 2007; Parsons et al. 2016; Mayer-Pinto et al. 2018). However, we still know very little about the effects of the man-made structures on the energy output, i.e., fitness of a species. For instance, Moreira et al. (2006) reported smaller sized limpet *Siphonaria denticulata* on seawalls compared to natural rocky reefs leading to reduced reproductive output. Similarly, Martins et al. (2016) reported smaller sized and low densities of barnacle *Chthamalus stellatus* on man-made structures compared to natural rocky reefs.

At a local scale, the physiological processes of a species are directly or indirectly affected by environment factors temperature, food quality/quantity, wave exposure and water quality (Green et al. 2011; Rivero et al. 2013; Bagley et al. 2015; Bishop et al. 2017; Heery et

al. 2017). In case of port and marinas as man-made habitats, semi-enclosed habitats have restricted water flow, reduced nutrient availability, increase water temperatures, contaminated, turbid waters which may have an adverse effect on the physiological processes of a species (Johnston & Keough 2002; Piola & Johnston 2008; Vaselli et al. 2008; Piola et al. 2009). The differences in environmental conditions also influence the growth, survival and reproduction of a species. Furthermore, the inter and intraspecific interactions in a community also influence the larval dispersal, recruitment, reproduction, growth, predation, competition and co-existence (Airoldi et al. 2005; Bulleri 2006; Perkol-Finkel et al. 2006; Burt et al. 2009; Quinn et al. 2012; Munari 2013; Firth et al. 2014; Bishop et al. 2017; Mayer-Pinto et al. 2018); and are therefore important factors to study the performance of a species on the man-made structures.

4.1.2. Impacts of man-made structures on bioinvasions

Bioinvasions are an increasing threat to biodiversity worldwide, especially to native biodiversity (Ruiz et al. 1999; Glasby et al. 2007; Hewitt & Campbell 2007; MacKie et al. 2012; Thomsen et al. 2014; Ojaveer et al. 2015; Cook et al. 2016; Gestoso et al. 2017; Olenin et al. 2017; Wells 2018; Albano & Obenat 2019). There have been previous studies indicating the man-made habitats to favour low density of native species and the successful invasion of non-native species (Ruiz et al. 2000; Byers 2002; Glasby et al. 2007; Bulleri & Chapman 2010; Airoldi & Bulleri 2011; Airoldi et al. 2015; Marraffini & Geller 2015; Johnston et al. 2017). Several studies have also indicated that the invasive species have a competitive edge over the native species as they have relatively high reproductive rate, high survival rate, fast growth and phenotypic plasticity (Dafforn 2017; Johnston et al. 2017; Simpson et al. 2017; Epstein & Smale 2018; Riera et al. 2018). Ultimately, non-native species may perform better at an invaded area than at their native regions (e.g., Parker et al. 2013). Several other studies have raised concerns regarding hybridisation and introgression between native and non-native species (Seehausen 2004; Wonham 2004; Roman & Darling 2007; Fauvelot et al. 2009; Pickett & David 2018); leading to genetic homogeneity in a community.

However, not all non-native species cause negative impacts, and some non-native species tend to naturalise, i.e. they become established without causing any major impact on the environment (Simberloff & Von Holle 1999; Mack et al. 2000; Branch & Nina Steffani 2004). Such naturalised species tend to co-exist with the native species in an environment with plenty of food and space without replacing them (Rius & McQuaid 2006; Zardi et al. 2008; Nicastro et al. 2010; Dafforn et al. 2012; Ojaveer & Kotta 2015; Zwerschke et al. 2016; Reise et al. 2017). For example, Ruiz et al. (1999) showed that of the 196-non-native species studied

in the Chesapeake Bay (Atlantic coast of the USA), 6% of the species had some measurable negative impact. Therefore, indicating that invasive species may promote biodiversity. Another example is that of a study in Chile which reported competition between the non-native tunicate *Pyura praeputialis* and native primary space occupiers. These tunicates formed massive mats along the coast, creating a new habitat for 116 invertebrates and algae, whereas the adjacent natural (non-invaded) coast had just 66 species (Castilla et al. 2004). A recent meta-analysis by Katsanevakis et al. (2014) reported that out of 63 non-native species, about 35% species had a positive impact by increasing the diversity of other species. Therefore, non-native species do not always have a negative effect on an invaded system, and understanding why this is the case may be challenging. It is harder still to predict *a priori* what the outcome of an invasion maybe.

4.1.3. Study species

Mussels are dominant space occupiers on hard substrata, colonising the entire middle region of the intertidal zone (Paine 1966; Capelle et al. 2016; Hetherington et al. 2019). Mussels are also ecosystem engineers and play an important role in promoting other species by forming biogenic reefs and because they are a food source for predators (Crooks 2002; Borthagaray & Carranza 2007; Sousa et al. 2009; Bertolini et al. 2017). The genus *Mytilus* (common blue mussels) is widely distributed, having an anti-tropical distribution around the world (Hilbish et al. 2000). The genus contains numerous species, but its taxonomy and systematics are still unresolved in many parts of the world. The widely distributed smooth-shelled *Mytilus edulis* species complex has three distinct lineages, *Mytilus edulis* (Linnaeus 1758), *Mytilus galloprovincialis* (Lamarck 1819) and *Mytilus trossulus* (Gould 1850), all of which are of Northern hemisphere origin.

Evolutionary evidence suggests allopatric speciation of *Mytilus* spp., with *M. trossulus* being the oldest of the three Northern hemisphere origin *Mytilus* spp. which first originated in North Pacific (Vermeij 1991). According to genomic and mitochondrial DNA analysis, *M. edulis* and *M. galloprovincialis* are closely related whilst *M. trossulus* is most distinct (Geller 1999; Hilbish et al. 2000). About 3.5 M ybp (years before present), first range expansion of *M. trossulus* into the North Atlantic via the Bering Strait gave rise to *M. edulis* (Cunningham & Collins, 1994; Vermeij, 1991). By ~ 2 M ybp, sea-level changes led to spread of north Atlantic *M. edulis* to Mediterranean Sea (Vermeij 1991). However, persistent sea-level fluctuations led to the separation between the North Atlantic *M. edulis* hindering the gene flow, which led to Mediterranean Sea *M. galloprovincialis* (Barsotti & Meluzzi 1968; Riginos & Cunningham 2005). These different lines of evidence show how natural range expansion (and associated

invasion pressure) has led to hybridisation and introgression between the genetically similar *Mytilus* spp. (Seehausen 2004; Wonham 2004; Pickett & David 2018; Gardner et al. 2020). The second wave of range expansion of North Pacific *M. trossulus* during the Pleistocene or Holocene period gave rise to *M. trossulus* on the Atlantic coast of North America. These two lineages varied genetically and showed a difference in physiological tolerance (e.g. salinity) (Gardner & Thompson 2001; Braby & Somero, 2006). Further, RFLP assays and DNA sequencing by various researchers confirmed *M. trossulus*, *M. edulis* and *M. galloprovincialis* of the Northern hemisphere origins (Levinton & Koehn 1976; Gardner & Skibinski 1991; Toro 1998; Hilbish et al. 2000; Gérard et al. 2008).

Grant & Cherry (1985) were the first to point out that the blue mussels in South Africa are not native and are the invasive Northern hemisphere origin *M. galloprovincialis* by examining the shell morphometric and genetic variations. This study was of much importance regarding the taxonomy of blue mussels in the Southern hemisphere. Following that, McDonald et al. (1991) identified two groups of Southern hemisphere mussels, a South America groups (Chile, Argentina, the Falkland Islands and the Kerguelen Islands) which had more *M. edulis*-like alleles and, an Australasian group including Australia and New Zealand that had more *M. galloprovincialis* - like alleles. This has been further confirmed by Borsa et al. (2007), Pickett & David (2018) and Malachowicz & Wenne (2019). Additionally, Hilbish et al. (2000) and Gérard et al. (2008), both suggested two Southern hemisphere invasion events via the North Atlantic Ocean, with first expansion ~ 1.2 M ybp in South America, i.e. Chile (*Mytilus chilensis*), Argentina (*Mytilus platensis*), the Falkland Islands (*Mytilus platensis*) and Kerguelen Islands (*Mytilus desolationis*) and a second recent expansion ~ 0.7 M ybp in the Australasian group i.e. Australia (*Mytilus planulatus)* and New Zealand (*Mytilus aoteanus*) (Gardner et al. 2020) . The nomenclature for these blue mussel sub-species in the Southern hemisphere has been controversial, with historical samples (i.e., pre-human arrival) being classified and described with the help of fossil and morphological data (e.g. Gardner 2004).

Recent evidence regarding the 'cryptic dispersal' of *M. galloprovincialis* has suggested both natural, and human mediation range expansion; together with adaptation and hybridisation events has led to the absence of distinct differences between Southern and Northern hemisphere haplotypes (Hilbish et al. 2000; Gérard et al. 2008; Westfall & Gardner 2010; Pickett & David 2018). Considering all these evolutionary evidences of *Mytilus* spp. range expansion and molecular studies relating to taxonomy, it is evident that Australasian mussels are most similar to Northern hemisphere *M. galloprovincialis* but are, however, native to Southern hemisphere.

Fossil evidence indicates the presence of some form of *M. galloprovincialis* in the Southern hemisphere before human arrival, but which may have been displaced by, or are co-occurring with, accidentally introduced Northern hemisphere *M. galloprovincialis* in some regions (McDonald et al. 1991; Westfall & Gardner 2013). In New Zealand, concerns about hybridisation and introgression of Southern and Northern hemisphere lineages were expressed because the invading mussel may displace the Southern hemisphere lineage *M. aoteanus* (Gardner et al. 2016; Zbawicka et al. 2019). There are still many ongoing studies (e.g. SNPs-based work) relating to the taxonomy of the aforementioned species especially the Northern vs Southern hemisphere *M. galloprovincialis* lineages and insights into hybridisation and introgression between the invasive and native mussel (Gardner et al., 2016; Gardner et al. 2020).

Mytilus galloprovincialis is one of the world's most successful invading species, being ranked in the Top 100 (Lowe et al. 2000). *Mytilus galloprovincialis*, the Mediterranean mussel, has spread from its native Mediterranean coastline to numerous locations in the world except for Antarctica, including but not limited to the Pacific coast of Canada, the California coast (Wonham 1999; Anderson & Thompson 2002), Hong Kong (Lee & Morton 1985), Japan (Wilkins et al. 1983), Australia and New Zealand (reviewed by Daguin & Borsa 2000; Pickett & David 2018), and Chile (Borsa et al. 2012; Oyarzún et al. 2016). *M. galloprovincialis* is cultivated as one of the most important commercial species all over the world; however, in New Zealand, this species is a pest on native green shell mussel, *Perna perna*, aquaculture farms (Forrest & Atalah 2017).

The impacts of *M. galloprovincialis* on various native species and its congeners have been studied extensively throughout the years. Previous studies in South Africa have reported displacement of native species due to the dominance of invasive *M. galloprovincialis* (Griffiths et al. 1992; Branch & Steffani 2004). Whilst, Bownes & McQuaid 2006, reported co-existence but with niche separation for the native *Perna perna* and non-native *M. galloprovincialis* in the south coast of South Africa. Competition for habitat and hybridisation between *M. galloprovincialis* and resident dominant *M. trossulus* were observed on the Pacific coast of North America and Canada (Wonham 2004; Dutton & Hofmann 2008; Shields et al. 2008, 2010). The *M. galloprovincialis* is a strong competitor, possess traits which help them acclimatise to fluctuating water temperatures due to metabolic adjustments, heat shock protein expression, high fecundity, rapid growth rate and resistance to desiccation (Hockey & Van Erkom Schurink 1992; Erlandsson et al. 2006; Anestis et al. 2007; Shinen & Morgan 2009).

Subsequently, mussels observed at such varied environments experience differences in physiological processes (Bayne & Thompson 1970). The mussels have strategies to overcome the variable environments, by maximizing the growth, reproduction and survival processes (Bayne & Thompson 1970; Hockey & Van Erkom Schurink 1992). Therefore, there might be differences in life-history traits such as reproduction timing (lifecycles), feeding or growth in different habitats (for example, natural vs man-made habitats).

In New Zealand, the impacts of the non-native Northern hemisphere *M. galloprovincialis* lineage on the native Southern hemisphere *M. galloprovincialis* lineage is not yet known. This is especially the case in the context of how man-made habitats influence the invasion success of Northern hemisphere lineage (henceforth, NH*Mg*) vs Southern hemisphere lineage (henceforth, SH*Mg*) mussels. For co-occurring mussel lineages (native vs non-native) where interspecific competition is taking place, differences in the energy utilised for reproduction, growth and byssus thread production for attachment may explain the outcome of competitive interactions (e.g., Gosling 1992; Steffani & Branch 2003). Therefore, examining the energy invested in reproductive output (e.g. gonadosomatic index - GSI) at natural vs man-made habitats may be a pivotal way to understand the mussel's comparative physiological processes. GSI is measured by quantifying the gonad weight with respect to body/soma weight (Hickman 1979; Devlaming et al. 1982; Santos et al. 2011). The gonadosomatic index (GSI) is an important metric to study the magnitude of gametogenic events and seasonal patterns in gonad development. It has been used by Gardner & Skibinski (1990) to study the fecundity and temporal variations in *Mytilus* spp. (*M. edulis*, *M. galloprovincialis* and their hybrids in southwest England). Their results showed *M. galloprovincialis* to have greater mean fecundity compared to congener *M. edulis*. Therefore, in New Zealand, it is interesting to observe two congener species that co-occur, one of which is the non-native NH*Mg* lineage, and the closely related, native SH*Mg* lineage.

The objective of the present study is to measure and compare the reproductive output (GSI) of the two lineages to observe if reproductive output contributes to their differences in performance (presumptive fitness) at reef vs marina sites, which are analogous to natural habitats and man-made habitats. Firstly, I hypothesised that both the blue mussel lineages (NH*Mg* and SH*Mg*) would have bigger shells on natural reefs compared to marinas. Due to the close evolutionary affinities between the non-native, NH*Mg* and native, SH*Mg* (McDonald et al. 1991; Hilbish et al. 2000; Gérard et al. 2008; Westfall & Gardner 2010; Pickett & David 2018); I hypothesised that both the blue mussel lineages would have similar reproductive

patterns (i.e., timing and magnitude of spawning events). I further hypothesised that the mussels at the natural reef sites have a relatively higher reproductive output (GSI) than those at marina sites. Lastly, hypothesised that the non-native NH*Mg* would have higher reproductive output at marina sites (man-made) compared to rocky reefs (natural).

4.2. Methods

4.2.1. Study site

The study was carried out in Wellington Harbour (41°16'45.5"S, 174°52'02.3"E) which is an enclosed bay on the southernmost tip of New Zealand's North Island (Figure 4.2.1). The Harbour is one of the largest natural harbours in the Southern hemisphere, whilst most of it is heavily modified for urban and port development, some of it is still intact. Hutt River on the eastern side of the Harbour is the only source of freshwater into the catchment. Wellington Harbour serves as a significant international commercial shipping port and is one of the busiest ports in New Zealand. Hence, sites around Wellington harbour were selected to compare gonadosomatic index (GSI) as an indicator for the reproductive effort by SH*Mg* (native) and NH*Mg* (non-native) blue mussels on the reef (natural) and marina (man-made) habitats. Westfall (2011) indicated the presence of SH*Mg*, NH*Mg* and *M. edulis/M. galloprovincialis* (NH*Mg/Me*) hybrids at different proportions at different sites in Wellington Harbour.

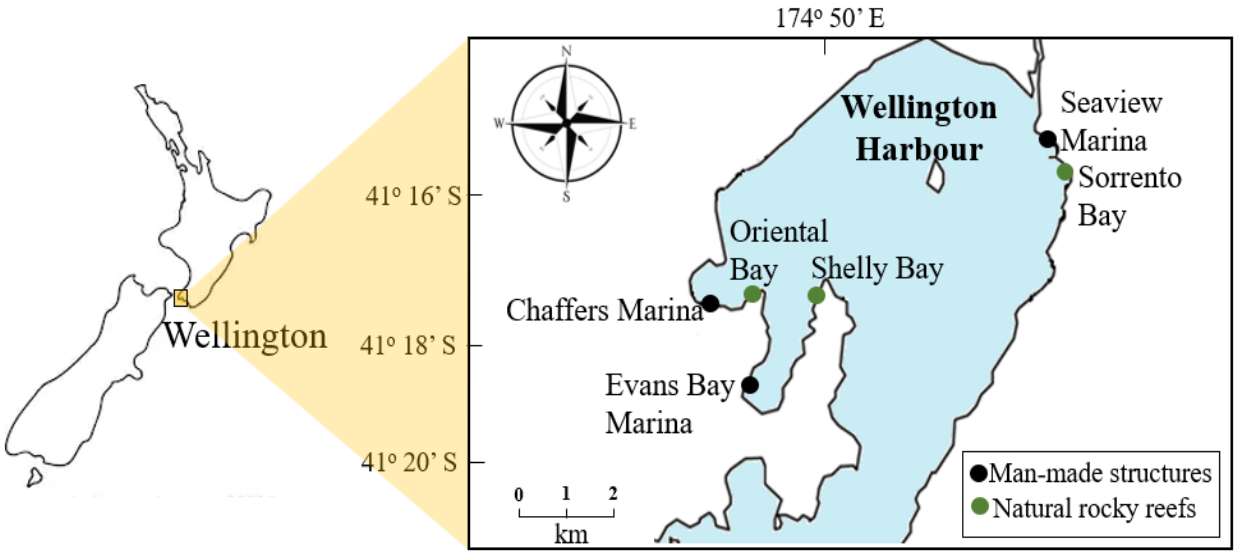


Figure 4.2.1. Map of Wellington Harbour, New Zealand. Points denoting marinas as man-made structure sites (black) and natural rocky reefs as natural sites (green) for this study.

In my study, three paired sites (natural vs man-made) were chosen around the harbour: Oriental Bay (OB; natural) and Chaffers Marina (CM; man-made), Shelly Bay (SB; natural) and Evans Bay Marina (EB; man-made) and Sorrento Bay (SR; natural) and Seaview Marina (SM; man-made). Paired sites (natural vs man-made) were selected at a distance of ~ 200 m to examine the monthly GSI of NH*Mg* and SH*Mg* in the marinas and at adjacent reef habitats. All sites had extensive coverage of blue mussels present through the sampling period.

4.2.2. Field sampling

Westfall (2011) identified 8 SH*Mg*, 1 NH*Mg* and 1 NH*Mg/Me* (hybrid) with 20 unknowns out of the 30 blue mussels collected in Wellington Harbour from her study. Therefore, at each site, random collections of 40 blue mussels were carried out (irrespective of their sex) to provide what was expected to be large enough lineage-specific sample sizes per site. Mussel size was > 2 cm shell length to ensure that only sexually mature individuals, for which a GSI could be calculated, were sampled. The mussels were collected from the intertidal zone at each site during low tide (similar tidal elevations) every month for a year from June 2017 to May 2018 (40 mussels × 12 months × 6 sites; N_{total} = 2880). The mussels on natural sites were collected from rocky reefs and for marina sites, the mussels were collected from wharves, artificial structures or ripraps. Immediately after collection, the mussels were placed in pre-labelled bags and frozen (-18 ^{o}C) until processing. Environmental variables such as pH, dissolved oxygen (DO, mg.l^{-1}), salinity (PSU), turbidity (NTU) and chlorophyll (µg.l^{-1}) were measured at each site for each month. The pH, DO, and salinity measurements were taken with a handheld YSI Meter (PRO-Series, YSI) and turbidity as well as chlorophyll with a handheld fluorometer/turbidimeter (Aquafluor™, Turner Designs). Unfortunately, the data for turbidity and chlorophyll was not accurate even after cross-referencing with CTD data for the same. Therefore, environmental data were not included in this study.

4.2.3. Shell length

The weight of soma and gonad tissue increases as a function of shell length (Suchanek 1981). Therefore, after removal of all the flesh, each mussel was numbered. The shell length (distance from the anterior to the posterior side of the shell), height (distance from dorsal to ventral side)

and width (maximum distance between closed valves) of the mussel shell (Gardner 2004) were measured using a vernier calliper (± 0.01 cm) (Figure 4.2.2).

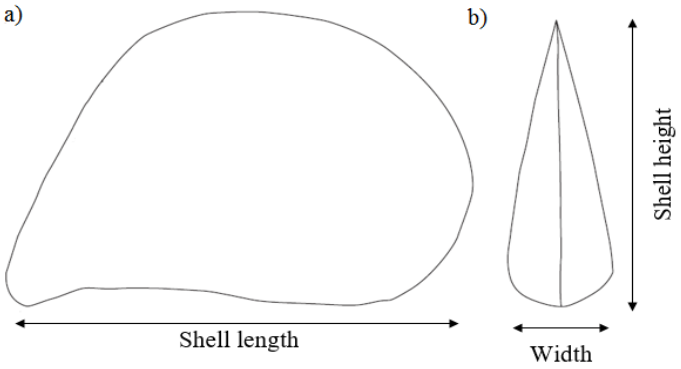


Figure 4.2.2. Illustration representing the measurements taken for shell length, height and width; a) frontal view; b) lateral view. Image sourced and modified from Gardner

4.2.4. Laboratory analysis

After defrosting,~30 mg of mantle tissue was extracted from each mussel for DNA extraction (details below). Subsequently, the soma and gonad of each mussel were dissected and weighed separately (0.001 g) after 24 h at 60 ^{o}C to determine their dry weights. The gonadosomatic index (GSI = gonad mass/body mass × 100%) was calculated for each mussel to qualitatively determine the energy investment in gametogenesis as a function of total body weight, and also the timing of spawning events as indicated by a decrease in GSI values from one month to the next (Seed & Suchanek 1992).

4.2.5. Lineage identification

a) DNA extraction

The DNA extraction was performed from the mantle tissue using Tissue Genomic DNA kits (Geneaid) following the manufacturer's recommendations. DNA concentrations were measured using a Nano-Photometer™ NP 80 (Implen, Germany) before the concentrations were standardised to a 50 ng/µl stock concentration with double distilled water to prepare a final volume of 20 µl.

b) PCR

The 16s rRNA RFLP assay (Westfall et al., 2010) was used to distinguish the lineage of SH*Mg* (native), NH*Mg* (non-native) and NH*Mg/Me* (hybrids). The primers 16sAR/16sBR (1 µl each), 12.5 µl MyTaq Remix, 8.5 µl double distilled water and 2 µl template DNA (100 ng) were used to amplify the 16sRNA gene in a 25 µl total solution. PCR was carried out in an Eppendorf

Thermocycler (Master cycler ep groups S). Amplification conditions applied were 3 min at 95 ^{o}C, 30 cycles at 95 ^{o}C for 30 s, 30 cycles at 52 ^{o}C for 30 s, 30 cycles at 72 ^{o}C for 45 s and final extension of 3 min at 72 ^{o}C.

c) DNA Digest

A double restriction endonuclease digest was performed on the PCR product using 1 µl each of the *Eco*RV and *Nhe*I enzymes, 1 µl loading buffer, 2 µl red buffer, 5 µl distilled water and 10 µl PCR product that was incubated in the Thermocycler at 37 ^{o}C for 15 min. The enzymes *Eco*RV and *Nhe*I distinguish SH*Mg* (native) and NH*Mg* (non-native) (Westfall et al. 2010). The enzyme *Spe*I enzyme used by Westfall & Gardner (2010) to distinguish the blue mussels was not used in this study because after testing a few mussels with *Eco*RV and *Nhe*I enzymes, SH*Mg* and NH*Mg* were successfully determined.

d) Gel Electrophoresis

DNA concentrations (5 µl) were run on a 2% agarose gel with an Easy Ladder 1 (band size range: 100 to 2000 bp) to help with fragment sizing. The gel was run at 100 volts for 30 to 40 mins. The gel was viewed under ultraviolet, and pictures were recorded using an imaging system (UVITEC, Essential V6, Cambridge, UK). The resulting bands were observed for each sample and referenced against the Easy Ladder 1 and fragment profiles of NH*Mg* at 537 bp whilst SH*Mg* at 370 and 167 bp and NH*Me*/*Mg* (hybrid) at 370, 85 and 82 bp (Westfall et al. 2010).

4.2.6. Statistical analyses

Lineage distributions between reef and marina habitats were analysed using a contingency test (R×C). Statistical tests were performed using the STATISTICA v.7 (Stat Soft Inc.) software package. Normality testing using the Kolmogorov-Smirnov (K-S) test (shell length: d = 0.05, $P < 0.01$; GSI: d = 0.04, $P < 0.01$) revealed that both variables were not normally distributed, whilst examination of quantile-quantile plots (Q-Q plots) showed that the data were approximately normally distributed, although some heteroscedasticity was observed. Because the violations of assumptions of normality were small in both cases, and because the parametric analysis is generally robust to such small-medium deviations, the data were not transformed.

a) Shell length

Variation in shell length was analysed using a two-way ANOVA (analysis of variance) as a function of habitat type and lineage and their interactions ($P < 0.05$). Paired *t*-tests were

employed to test the hypothesis that shell length differs as a function of habitat type irrespective of lineage and with regard to the lineage regardless of habitat type, respectively. Cohen's '*d*' effect size 'r' of shell length was tested for lineages (NH*Mg* vs SH*Mg*) and habitat type (reef vs marina). Cohen's '*d*' evaluates the size of an effect of the test statistic (observed *P*-value) because a significant effect does not necessarily mean a large effect. The evaluation relies on standard deviations instead of standard errors. Cohen's '*d*' measures the size of the mean difference in terms of the standard deviation. The magnitude interpretations of the Cohen's *d* value are; < 0.30 is small effect size, 0.50 is moderate effect size, and > 0.80 is a large effect size (Cohen 1992).

$$\text{Cohen's } d = M_1 - M_2 / s_{pooled}$$
$$\text{where } s_{pooled} = \sqrt{[(s_1^2 + s_2^2) / 2]}$$
$$r_{YI} = d / \sqrt{(d^2 + 4)}$$

where; d = Cohen value, r = effect-size, M_1 = Mean of group 1, M_2 = Mean of group 2, σ_1 = Standard deviation of group 1, σ_2 = Standard deviation of group 2.

b) Gonadosomatic index (GSI)

Correlation and regression analyses were conducted to determine the relationship between GSI (%) and shell length (cm) of SH*Mg* and NH*Mg* between the reef and marina habitats. Because larger (presumptive older) individuals have greater gamete production than smaller mussels (Rodhouse et al. 1986), it is important to establish that any difference in GSI between the lineages results from the genotypic background rather than a bias in the collection of larger versus smaller mussels. The regressions between GSI vs shell length were plotted with 95% confidence intervals; R^2 and *P* values were calculated for each association. The significance of these tests was set at $P < 0.05$.

Analysis of covariance (ANCOVA) was performed, with shell length as co-variate, habitat-type, lineage and month as the independent variables and GSI as the dependent variable. GSI were analysed using a three-way factorial ANCOVA as a function of; the effects of the interaction of the factors; month, habitat type and lineage were analysed. The significance level was set at $P < 0.05$ with $P < 0.001$, indicating high significance Paired *t*-tests were also employed to test the hypothesis that GSI values differ as a function of habitat type irrespective of lineage and for lineage regardless of habitat type, respectively. Lineage-specific GSI was also tested in each habitat using a paired *t*-test. Cohen's '*d*' effect-size 'r' was calculated for GSI for the habitat type (reef vs marina) to test the effect size of the significant results.

4.3. Results

Of the 2880 mussels, the 16s mitochondrial rDNA RFLP assay was able to identify a total of 1884 SH*Mg* (native), 656 NH*Mg* (non-native) and 273 NH*Me/Mg* hybrids from the monthly reef (natural) and marina (man-made) habitat collections (i.e., 2813 of 2880 mussels or 97.7% of all individuals). However, the RFLP assay failed to identify the lineage for 67 mussels which were removed from further analyses. As *M. edulis*/*M. galloprovincialis* hybrids are of Northern hemisphere origin (i.e., they are invasive in New Zealand), they were assigned as Northern hemisphere non-native lineage (NH*Mg*). Subsequently, 1884 SH*Mg* and 929 NH*Mg* (2:1, native: non-native) individuals were tested in this study.

Based on the RFLP assay results, testing revealed a non-significant difference in NH*Mg* and SH*Mg* distributions between the reef and marina habitats (χ^2 = 0.003, df = 1, *P* = 0.96). Both the habitats were dominated by native SH*Mg* compared to NH*Mg* (Reef: SH*Mg* = 66.74%, NH*Mg* = 33.26%; Marina: SH*Mg* = 66.57%, NH*Mg* = 33.43%; Figure 4.3.1).

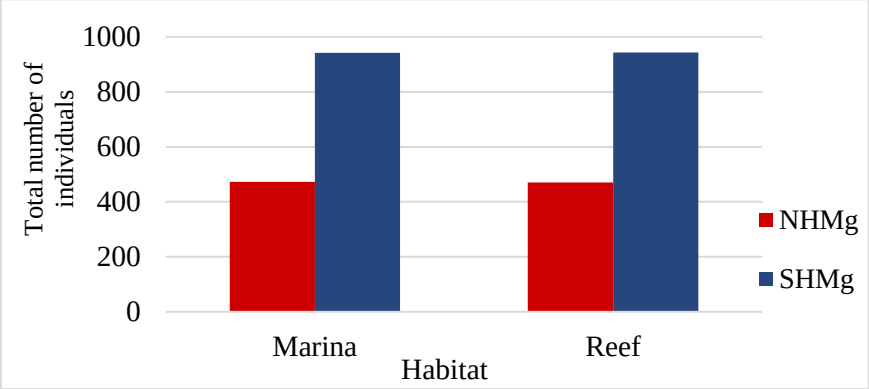


Figure 4.3.1. Total number of Northern hemisphere (NH*Mg*- non-native) and Southern hemisphere (SH*Mg*- native) *Mytilus galloprovincialis* at the marina and reef habitats.

4.3.1. Shell length

The shell length of the mussels ranged from 2.5 - 8.30 cm with a mean shell length of 5.23 cm ± 0.85 irrespective of habitat type and lineage. Two-way ANOVA revealed that shell length differed significantly between habitat type (*P* = 0.008), but not between lineage (*P* = 0.19) and no interaction effect between Habitat × Lineage was detected (*P* = 0.26) (Table 4.3.1). Paired *t*-tests of shell length as a function of habitat type revealed a significant difference (*t*-value = -2.40, df = 2812, *P* < 0.05; Table 4.3.2) with larger mean shells occurring at marina (5.27 cm ± 0.9) than at reef (5.20 cm ± 0.8) habitats. However, such small differences in shell length (to the level of tenths of a millimetre) are not likely to have any biological significance. These results were supported by Cohen's *d* value (habitat type: *d* = 0.09, r = 0.046) which states that

the effect size of shell length between habitat type is trivial (Table 4.3.2). A paired *t*-test of shell length as a function of lineage indicated no significant difference in shell length between NH*Mg* and SH*Mg* lineage (*t*-value = 1.30, df = 2812, *P* = 0.19; Table 4.3.2).

Table 4.3.1. Two-way ANOVA for shell length (cm) as a function of habitat type and lineage (significance = $P < 0.05$, marked in bold).

Source of variation	df	MS	F	*P*
Habitat type	1	5.00	6.94	**0.008**
Lineage	1	1.19	1.65	0.19
Habitat type x Lineage	1	0.90	1.25	0.26
Error	2810	0.72		

(df = degree of freedom, MS = mean square, F = F-statistic, *P* = *P*-value)

Table 4.3.2. Paired *t*-tests for shell length (SL) as a function of habitat type and lineage (significance = $P < 0.05$, marked in bold). Cohen's *d* effect size 'r' of shell length for habitat type (reef vs marina) and lineage (NH*Mg* vs SH*Mg*).

Variable		Mean SL (cm) ± SD	*t*- value	*P*	Cohen's *d*	Effect-size 'r'
Habitat type	Marina	5.28 ± 0.90	-2.40	**0.02**	0.093	0.046
	Reef	5.20 ± 0.80				
Lineage	NH*Mg*	5.20 ± 0.87	1.30	0.19	0.058	0.029
	SH*Mg*	5.25 ± 0.84				

SD = Standard deviation, *t*-value = t-statistic

4.3.2. Regression - GSI as a function of shell length for the NH*Mg* and SH*Mg* lineages

At reef sites, no significant effect ($R^2 = 0.0009$, $P = 0.35$) was observed between shell length and GSI of NH*Mg* and SH*Mg*, but there was a significant weak relation ($R^2 = 0.01$, $P < 0.0001$) at marina sites for both lineages where shell length coincided with GSI (Table 4.3.3).

Table 4.3.3. Results for regression for Gonadosomatic index (GSI %) as a function of shell length for NH*Mg* and SH*Mg* at the marina and reef habitats (significance = $P < 0.05$, marked in bold).

Habitat type	R^2	R	*P*	y
Reef	< 0.001	0.03	0.35	13.9451 + 1.1855*x
Marina	0.011	0.12	**< 0.0001**	13.9451 + 1.1855*x

4.3.3. GSI as a function of habitat type and lineage

GSI values of SH*Mg* (native) at reef sites ranged from 0 - 51.3% and at the marina sites from 0 - 60.6%. GSI values of NH*Mg* (non-native) ranged from 0 - 50.8% and 0 - 57.6% at marina sites. Three-way ANCOVA testing for GSI as a function of the month (sample intervals), lineage and habitat type with shell length as co-variate showed no significant interaction (Table 4.3.4). However, significant results were observed for factors; month, habitat type and their interaction (Month × Habitat type; $P < 0.001$). Furthermore, Tukey HSD *post hoc* test indicated statistically higher GSI values of mussels at reef than at marina sites (Marina: 20.20% ± 10.03; Reef: 22.80% ± 8.84).

Cohen's d test ($d = 0.275$, r = 136) showed a trivial effect of the significance of GSI between habitat type (Table 4.3.5). The GSI values as a function of Habitat type × Month indicated significant results only for the months, July ($d = 0.426$, moderate effect), November ($d = 809$, large effect) and December ($d = 667$, large effect) (Table 4.3.5). The GSI values of mussels were relatively higher at reef (natural) habitat than at marina (man-made) habitat (Table 4.3.5). Therefore, indicating relatively larger spawning activity in marinas, especially during November followed by quick gametogenesis in December compared to reproductive activity in reef habitat (Figure 4.3.3).

Table 4.3.4. Results of ANCOVA for GSI values and shell length (cm; Co-variate) as a function of Month × Lineage × Habitat type (significance = $P < 0.05$; marked in bold).

Source of variation	df	MS	F	*P*
Month × Lineage × Habitat type				
Shell length	1	6492.501	85.5688	**< 0.0001**
Month	11	2809.963	37.0343	**< 0.0001**
Lineage	1	13.699	0.1805	0.67
Habitat type	1	4228.210	55.7263	**< 0.0001**
Month × Lineage	11	92.633	1.2209	0.27
Month × Habitat type	11	339.841	4.4790	**< 0.0001**
Lineage × Habitat type	1	11.594	0.1528	0.69
Month × Lineage × Habitat type	11	44.818	0.5907	0.84
Error	2765	75.875		

(df = degree of freedom, MS = mean square, F = *F*-statistic, *P* = *P*-value)

Table 4.3.5. Tukey HSD *post hoc* tests for GSI values as a function of significant factors as per ANCOVA, i.e. habitat type and month (significance $P < 0.05$, marked in bold). Cohen's *d* effect size of GSI for habitat type (reef vs marina) for significant effects.

Variable		GSI values (%) ± SD	MS	df	*P*	Cohen's *d*	Effect-size 'r'
Habitat type	Marina	20.20 ± 10.03	78.194	2766	< **0.0001**	0.275	0.136
	Reef	22.80 ± 8.84					
Month x Habitat type (Natural vs Man-made)	June		78.194	2766	0.926		
	July				**0.011**	0.426	0.208
	August				0.136		
	September				1.00		
	October				0.617		
	November				**0.00001**	0.809	0.375
	December				**0.00007**	0.667	0.316
	January				0.467		
	February				0.99		
	March				1.00		
	April				0.99		
	May				0.54		

SD = Standard deviation, *t*-value = t-statistic

Overall, the GSI cycles of both mussel lineages at the reef and marina sites were qualitatively very similar (Figure 4.3.2). At reef habitats, the GSI values were highest during the start of the austral winter (June) for both species (SH*Mg* = 28.82% ± 7.28, NH*Mg* = 29.08% ± 6.32) indicating gametogenesis had occurred earlier. GSI values decreased dramatically in August (end of winter) reaching their lowest values (SH*Mg* = 18.76% ± 6.93, NH*Mg* = 18.18% ± 7.04) (Figure 4.3.2 a), suggesting spawning activity. This was followed by an increase in GSI values during September-October (gametogenesis), and again a drop in GSI values (spawning) during austral spring (October-November), especially in November (SH*Mg* = 19.39% ± 10.27, NH*Mg* = 20.55% ± 8.72). A gradual recovery period (increase in GSI values – gametogenesis) from December to May (Summer-Autumn) then followed (Table 4.3.6).

At the marina sites, the highest GSI values (SH*Mg* = 27.33% ± 11.47, NH*Mg* = 25.40% ± 11.56) were observed in June (Figure 4.3.2 b), suggesting that gametogenesis occurred from May-June (austral autumn and early winter), or perhaps earlier. A sudden drop in GSI values

in August (SH*Mg* = 14.51% ± 8.54, NH*Mg* = 15.51% ± 6.88) indicated a spawning period. The GSI values were lowest in November (SH*Mg* = 12.88% ± 8.27, NH*Mg* = 11.24% ± 8.98), and the gametes seemed to be spawned out (Table 4.3.6). Two spawning events were observed from June-August (austral winter) and October-November (spring) for NH*Mg* and SH*Mg* on both the habitats.

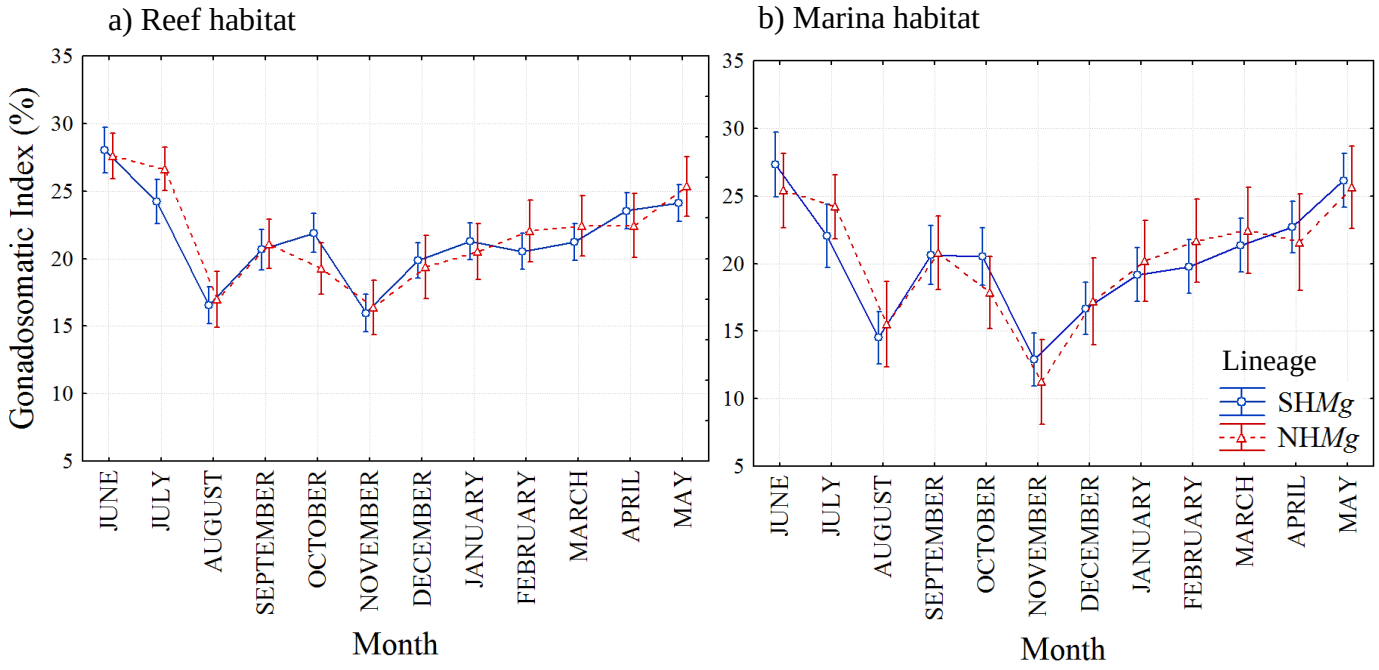


Figure 4.3.2. Monthly variations of the GSI values of SH*Mg* (blue) and NH*Mg* (red) lineages at a) marina and b) reef habitats in Wellington Harbour from June 2017-May 2018.

Table 4.3.6. Monthly variations in Gonadosomatic Index (%) ± standard deviation (SD) of SH*Mg* and NH*Mg* at reef and marina habitats during June 2017-May 2018.

	Reef habitat		Marina habitat	
Month	NH*Mg* ± SD	SH*Mg* ± SD	NH*Mg* ± SD	SH*Mg* ± SD
June	29.08 ± 6.32	28.82 ± 7.28	25.40 ± 11.56	27.33 ± 11.47
July	28.98 ± 10.64	26.48 ± 10.74	24.22 ± 11.29	22.05 ± 10.88
August	18.18 ± 7.04	18.76 ± 6.93	15.51 ± 6.88	14.51 ± 8.54
September	21.33 ± 6.15	20.69 ± 5.96	20.80 ± 8.67	20.64 ± 9.87
October	20.87 ± 7.69	23.29 ± 7.37	17.84 ± 7.94	20.50 ± 9.45
November	20.55 ± 8.72	19.39 ± 10.27	11.24 ± 8.98	12.88 ± 8.27
December	22.17 ± 9.84	22.87 ± 8.48	17.21 ± 9.08	16.66 ± 9.03

January	20.90 ± 6.88	23.37 ± 7.69	20.18 ± 7.41	19.18 ± 7.87
February	22.56 ± 11.57	21.21 ± 10.50	21.68 ± 7.58	19.77 ± 8.47
March	22.42 ± 5.58	21.12 ± 6.29	22.45 ± 8.71	21.36 ± 7.93
April	23.22 ± 6.95	24.46 ± 6.06	21.58 ± 8.99	22.69 ± 9.07
May	24.99 ± 10.39	22.26 ± 11.31	25.64 ± 11.78	26.15 ± 10.59

4.4. Discussion

4.4.1. Background

With the proliferation of man-made structures along the world's coast, there are many chances for a non-native species to establish and spread (Simberloff & Von Holle 1999; Bulleri & Airoldi 2005; Bulleri et al. 2006; Tyrrell & Byers 2007; Dafforn et al. 2009, 2012; Airoldi & Bulleri 2011; Perkol-Finkel et al. 2012; Theuerkauf et al. 2018). This is especially the case for Northern hemisphere *M. galloprovincialis,* which is known as one of the aggressive invaders, with competitive traits such as high growth, high reproduction rate and phenotypic plasticity that help them acclimatise to many environments (Dafforn 2017; Johnston et al. 2017; Simpson et al. 2017; Epstein & Smale 2018; Riera et al. 2018). Having said that, *M. galloprovincialis* is highly used in shellfish industries for its economic value all around the world as it has successfully invaded most of the regions worldwide (Wonham 1999; Daguin & Borsa, 2000; Hilbish et al. 2000; Anderson & Thompson 2002; Borsa et al. 2012; Oyarzún et al. 2016; Pickett & David 2018). Northern hemisphere *M. galloprovincialis* lineage has invaded ~0.7 M ybp in NZ and has observed to have spread in most of the regions, marinas, ports or natural rocky reefs (Gardner et al. 2020). These blue mussels form biogenic reefs providing refuge to various other species but competing for food and space could be a negative impact on the native habitat-forming species (Crooks 2002; Castilla et al. 2004; Borthagaray & Carranza 2007; Sousa et al. 2009; Bertolini et al. 2017). The congeneric comparisons help to determine the attributes of invasions, to examine the performance of non-native species compared to native species and to determine if they outcompete native congeners. This chapter aimed to investigate the reproductive output (measured as GSI) of NH*Mg* and SH*Mg* on natural rocky reefs and marina sites as analogous to natural and man-made habitats. Patterns of abundances, shell length and GSI of the two lineages were tested for a year at natural reef and marina sites.

4.4.2. Abundances

In this study, the NH*Mg* and SH*Mg* co-occur on both natural and man-made habitats as also previously seen in Wellington Harbour (Westfall 2011; Gardner & Westfall 2012). The two

lineages, NH*Mg* and SH*Mg*, were distinguished using 16s RNA RFLP assay developed by Westfall & Gardner (2010). When considering the reproduction rate in displacing native lineage with non-native lineage, competitive traits and abundances of native species also play an important role to decide the success of non-native species. The native SH*Mg* lineage was most abundant at both natural and man-made habitats throughout the one year of the study period. It has been widely reported that non-native species prefer man-made structures/ habitats and native habitats to promote more native species and local communities (Chapman & Bulleri 2003; Glasby et al. 2007; Airoldi et al. 2015; Marraffini & Geller 2015; Gestoso et al. 2017; Johnston et al. 2017; Simpson et al. 2017). However, in this case, there was no preference for habitats observed by NH*Mg*, but it is observed to be very well established. As seen in NW Spain, the larvae of *M. galloprovincialis* settled on various kinds of available substrata (Caceres Martinez et al. 1994). Native lineage SH*Mg* was still the dominant space occupier at both habitat types and is not yet seen to be displaced by non-native NH*Mg* lineage.

4.4.3. Shell length as a function of habitat type and lineage

The shell length of the blue mussels was examined in this study to observe if any differences exist in the shell lengths of NH*Mg* and SH*Mg* at natural reef sites or marina sites. Previous studies have reported smaller sized limpets (Moreira et al. 2006) and barnacles (Martins et al. 2016) on man-made structures compared to natural reefs. The shell length of the mussels collected in this study ranged from 25 to 83 mm. The *M. galloprovincialis* observed in eastern Pacific, California was an average shell length of 60.7 mm (Dutton & Hofmann 2008) whilst in Chile ranged from 32 to 70 mm (Díaz et al. 2019). In this study, the shell length of the two lineages collected at random from reef and marina sites were relatively similar with an average length of 52.0 mm ± 8.7 for NH*Mg*, and 52.5 mm ± 8.4 for SH*Mg*. Therefore, the average shell length of the mussels collected was within a standard shell length range. The shell length showed statistically significant differences between habitats (Reef vs Marina) irrespective of the lineage; however, the difference was small and probably without any ecological significance.

Generally, an increase in reproductive output, i.e. gamete production in a mussel is directly comparable to the age or size of the mussels. Reproductive output is calculated by gonad weight divided by total body weight (i.e., gonad + soma). Older or larger mussels are expected to have higher gamete production (Gardner & Skibinski 1990; Seed & Suchanek 1992). In this study, NH*Mg* and SH*Mg* had a mean shell length of 52.0 mm ± 8.7 and 52.5 mm ± 8.4, respectively, and a mean GSI value of 22.07% ± 9.61 and 21.24% ± 9.5, respectively.

M. galloprovincialis studied in Chile had an average shell length ~55.0 mm with GSI of ~28.9% (Díaz et al. 2019) therefore, a common range of size and reproductive output range was seen in this study for both *M. galloprovincialis* lineages. Furthermore, there was no relationship observed between shell length and GSI for both NH*Mg* and SH*Mg* at reef sites whilst, a significant but very weak relation was observed between shell length and GSI at marina sites. It is important to note that the different habitat types (Reef vs Marina) did not have any distinct impact on the relationship of shell length to GSI for NH*Mg* and SH*Mg*. Therefore, I reject the hypothesis that the shell lengths of both lineages are greater at natural reef sites than at marina sites. This suggests but does not prove that growth rates of the two lineages are not significantly different at both habitat types. However, a study in Chile, comparing gonad weight in similar sized (~70 mm) native *Mytilus chilensis* and non-native *M. galloprovincialis* showed relatively higher gonad weight for native *M. chilensis* due to the physical characteristics of the two blue mussels (Díaz et al. 2019).

4.4.4. GSI as a function of habitat type and lineage

Comparing the reproductive effort between two congeneric species helps to determine their response to different habitat types (Thompson 1984). At exposed sites (natural rocky reefs), where there is plenty of food supply, *M. galloprovincialis* is observed to grow faster with increased soma and gonad production than at sheltered sites (marinas), although, stronger waves at exposed areas lead to energy investment for production of byssus threads for attachment (Steffani & Branch 2003). There is evidence of different reproductive effort between different populations, even at a local scale (Bayne et al. 1983). For instance, food quality, food availability, tidal level and sediment type influence growth and reproduction (Honkoop and Beukema 1997; Beukema et al. 2002). Elsewhere, a study comparing the reproductive output of limpets on seawalls vs natural reefs observed relatively small-sized limpets leading to low reproductive output by limpets on seawalls (Moreira et al. 2006). However, in my study, the reproductive output (GSI) as a function of habitat type showed significant differences (Marina = 20.20% ± 10.03, Reef = 22.80% ± 8.84), therefore accepting the hypothesis that reproductive output of both lineages is relatively higher at natural reef than at marina sites, but the differences in GSI values are very small. The ecological significance of such small differences in GSI values is yet to be determined. This study observed no significant effect of GSI values between lineages

GSI values as a function of the interaction effect of habitat type ×lineage did not show significant differences. Therefore, the lineages (NH*Mg* and SH*Mg*) did not show differences

in reproductive output at each habitat type, i.e. reef (natural) and marina (man-made) habitats, respectively. Thus, I reject my hypothesis that NH*Mg* has a greater reproductive output at marina sites than at natural reef sites, as both the lineages had relatively higher GSI values at reef sites than marina sites. The reproductive output of the mussels is a function of the partitioning of energy between somatic growth and reproduction and also acts as a physiological stress response (Cáceres-Martínez & Figueras 1998; Seed & Suchanek 1992; Okaniwa et al. 2010). In the case of environmental stress like temperature variation, low food availability, desiccation, predation, and wave exposure, mussels may invest relatively more energy in defence against the stress than in reproduction (e.g., Gosling 1992; Steffani & Branch 2003). In this study, the co-occurring NH*Mg* and SH*Mg* were sampled within environments with not very distinct variations in temperature and food availability (Gardner, pers. comm., unpublished data), which might be the reason for the similar reproductive output by the two lineages at both habitats (Reef vs Marina).

The GSI values as a function of the interaction of factors, month × habitat type indicated significance during the months – July, November and December. The GSI values were relatively higher at reef sites than at marina sites. Subsequently, these results indicate that the mussels irrespective to the lineages had a quicker first spawning response in July and a larger spawning activity during November was observed in the marina sites compared to reef sites. However, the reason for larger spawning activity by the mussels in the marina could be speculated because of the slightly warmer temperatures in enclosed marina conditions. However, there are no environmental data to support this speculation.

4.4.5. Reproductive cycle

Temporal variations in reproductive output is a likely result of gamete production (gametogenesis) and gamete loss (mostly spawning, but may also be resorption) (Seed & Suchanek 1992; Cáceres-Martínez & Figueras 1998). In this study, temporal variations (monthly) in GSI values showed significant difference as a function of habitat type (Reef vs Marina) but not as a function of lineage (NH*Mg* vs SH*Mg*). However, the reproductive patterns for both lineages (NH*Mg* vs SH*Mg*) showed a similar timing of gametogenesis and spawning at both Reef vs Marina habitats. Previous studies of mussel reproductive output have reported differences in spawning periods between other *Mytilus* spp. (Gardner & Skibinski 1990; Secor et al. 2001; Toro et al. 2002). In this study, two spawning events were observed with two periods of gonad build-up (gametogenesis) observed during summer and spring. In this study, gametogenesis took place in early winter (June) and with spawning during late winter (August),

followed by a quick gonad condition recovery in spring (October), and a second spawning during late spring (November). These events were recorded by observing the conspicuous peaks and drops in GSI values. These observations also indicate the influence of temperature on the gonad cycle of the mussels (Seed & Suchanek 1992; Cáceres-Martínez & Figueras 1998) as well as food availability during May leading to gametogenesis (Lachowicz 2005). For instance, Okaniwa et al. (2010) reported that the gametogenesis in *M. galloprovincialis* in Japan coincided with an increase in chlorophyll-a concentration as well as low sea and air temperature.

The spawning events of NH*Mg* and SH*Mg* lineages coincided with rising water temperatures as has been previously reported for other *Mytilus* spp. (Seed & Suchanek 1992; Carrington 2002; Okaniwa et al. 2010). Warmer temperatures were observed to influence gametogenesis, but lower temperatures stimulated spawning (Ceccherelli & Rossi 1984; Oyarzún et al. 2011). Such spawning periods were also observed in *M. galloprovincialis* in South Africa (Zardi et al. 2007) and NW Spain (Cáceres-Martínez & Figueras 1998) during late spring and summer. However, *M. galloprovincialis* in Pacific coast (Curiel-Ramirez & Caceres-Martinez 2004) and *M. edulis* and *M. galloprovincialis* in southwestern England (Secor et al. 2001) has previously shown a single spawning event from autumn to early spring. *M. galloprovincialis* in South Africa showed two spawning periods, during summer and winter (Schurink & Griffiths 1991). Gardner & Skibinski (1990) reported prolonged reproductive cycles and multiple spawning events in *M. edulis*/ *M. galloprovincialis* hybrids.

The NH*Mg* and SH*Mg* lineages show similar responses in terms of reproduction timing and output in Wellington Harbour, during this study period. Even though, in this study, difference by sex of the mussels in the GSI was not addressed. A study in southern New Zealand on gonad indices of blues mussels, irrespective to their lineages, i.e. NH*Mg* and SH*Mg* indicated synchronous trend between male and female blue mussels (Smart et al 2020). Similar spawning, i.e. release gametes at the same time may facilitate hybridisation between the two lineages, and further studies should concentrate on observing if there are chances of backcrossing and future impacts on the native SH*Mg* lineage (Gardner & Skibinski 1990; Secor et al. 2001). Many studies have referred to the importance of spawning periods of closely related species to examine the scope of hybridisation (Gardner & Skibinski 1990, Seed 1992; Seed & Suchanek 1992; Wonham 2004; Westfall & Gardner 2013; Oyarzún et al. 2016), especially where they co-exist (McDonald et al. 1991; Seed 1992; Elliott et al. 2008; Brannock et al. 2009).

Hybridisation and repeated backcrossing with the parental species can risk the extinction of the native species (Fitzpatrick et al. 2010; Harrison 2012). Subsequently, the concern of hybridisation was also reported by Westfall & Gardner (2013), they reported that continuous invasion, hybridisation and introgression preferring the non-native NH*Mg* lineage could extirpate the native SH*Mg* lineage. There is evidence of high rates of hybridisation between native and non-native *Mytilus trossulus* and *Mytilus galloprovincialis*, respectively, with low introgression in Japan (Brannock et al. 2009) and California, USA (Saarman & Pogson 2015), whilst a higher rate of introgression in Australia and NZ (Westfall & Gardner 2013). In the North Atlantic, hybridisation between *M. edulis* and *M. galloprovincialis* had led to asymmetric introgression favouring *M. galloprovincialis* alleles (Gardner & Skibinski 1988; Bierne et al. 2002). In the north-eastern Pacific, low rates of hybridisation and limited introgression were observed between *M. galloprovincialis* and *M. trossulus* favouring larger sized *M. galloprovincialis* alleles (Anderson et al. 2002; Wonham 2004).

In summary, this study concluded that the co-occurring non-native, NH*Mg* and native, SH*Mg* lineages have no preference towards natural reefs or man-made habitats for their ecological functioning. This is because the reproductive output (GSI) and shell length were nearly similar between the two lineages at both the habitats. NH*Mg* and SH*Mg* lineages also showed similar reproductive patterns at both habitats for the 1-year study period. Two spawning events (late winter and late spring) with a major and a quick gametogenesis period observed. Future work comparing the performance of congeners should focus on the effects of highly varying environmental conditions on natural and man-made structures.

4.4.6. Management implications

It is challenging to predict invasion occurrences and success through accidental human mediation and to avoid the continuous invasions of NH*Mg* lineage. Therefore, it is crucial to undertake management applications and strategies focussing on hull cleaning and ballast water exchange (Schwindt et al. 2014). A baseline study is required to identify the non-native *M. galloprovincialis* lineage and then to examine what impacts they have on the native communities, especially the co-existence of NH*Mg* and SH*Mg* over time (e.g., Gardner et al. 2016). However, with the ongoing addition of coastal structures, stepping stone invasions are ubiquitous (e.g., Apte et al. 2000) and once established, eradication is nearly impossible (Mack et al. 2000). *M. galloprovincialis* is an aggressive invader, with external fertilisation and the production of millions of larvae with a long-lived pelagic state it is impossible to stop its spread.

The competitive traits of *M. galloprovincialis*, i.e. fast growth, tolerance to stress, high reproduction and immunity to disease is essential in terms of aquaculture/ shellfish farming (Branch & Steffani 2004) and ironically is also important in terms of invasions.

In this study, it is evident that NH*Mg* and SH*Mg* respond similarly, in terms of their reproductive patterns. Furthermore, the lack of ecological differences – GSI, shell length, etc. – reflect the very close evolutionary history of NH*Mg* and SH*Mg* and raises a question about how important it is to invest in the management of NH*Mg*. From a manager's perspective, it may not be important to invest in the management of NH*Mg* instead focus on different problems such as the high-risk invasive species. This study has highlighted that native, and non-native *M. galloprovincialis* have similar biological characteristics; therefore, eradication of non-native Northern *M. galloprovincialis* lineage may not be necessary.

CHAPTER 5

GENERAL DISCUSSION

5.1. Background

The number of biological invasions has increased over the decades, and invasions are now ubiquitous (Firth et al. 2016; Olenin et al. 2016; Johnston et al. 2017). There is evidence of ports and harbours, increasing opportunities for non-native species to settle and proliferate (Zbawicka et al. 2019). This thesis aimed to investigate the marine man-made environments, their impacts on the marine biodiversity regarding species status and the factors facilitating the non-native species. In this thesis, the community composition and species status (native, non-native and cryptogenic) between natural and man-made habitats were analysed. Chapter 1 presented basic information on habitat type and effects of man-made structures in the coastal environment and in relation to bioinvasions. Data Chapter 2 focussed on the national scale baseline port surveys (Australian and New Zealand port surveys) and examined the factors port type and latitudinal groups for the community composition and species status. The local-scale study (Wellington Harbour) was conducted using settlement tile arrays (PVC and slate tiles) in the reef and marina habitats (Chapter 3). The data was applied for comparative assessment of the community composition, ecological succession of species and frequencies of species status between the habitat types and substratum types. Lastly, in Chapter 4, the reproductive output (GSI, presumptive fitness) of the congener blue mussel lineages (non-native, NH*Mg* and native SH*Mg*) was analysed at the natural reef and man-made marina habitats. By comparing the GSI results between the habitat type, the reproductive cycles (spawning and gametogenesis), and the reproductive output, between the lineages, were constructed. In the present chapter, the main conclusions from the previous chapters are summarised. Additionally, the limitations, future research and management suggestions are discussed.

5.2. Chapter synthesis

In chapter 2, the two national-scale baseline port surveys; Australian port survey (APS) and New Zealand port surveys (NZPS) assessed the community composition and species status as a function of surveyed ports, port type (major vs minor) and latitudinal groups. Results for **APS** showed that the community composition significantly varied as a function of the surveyed port. However, despite the higher frequencies of native species across all surveyed ports, there was

no specific pattern in surveyed ports observed for community composition. The community composition and species status significant results for the factor port type with relatively abundant non-native species observed at major ports compared to minor ports. For latitudinal groups, the community structure and species status showed a significant relationship with an increase in non-native species with the increase in latitudes. For NZPS, results indicated significance for community composition and species status as a function of surveyed ports. There was a significant relationship observed for community composition as a function of latitudes with high significance observed between low (35^{o}S) and high latitudes (40, 45 ^{o}S). Hence, the results for both the dataset indicated grouping of ports located at proximity, i.e., having common species. The natural dispersal of species or domestic marine traffic may be the pathways for the spread of species at regional scales (Coutts & Taylor 2004; Floerl et al. 2004; Floerl & Inglis 2005).

The findings of the dataset analyses highlight several on-going challenges such as major commercial ports being hotspots for marine invasions and the role of shipping as the main pathway for introductions at multiple spatial scales (Bishop et al. 2017). Thereby spread of species through regional transport connecting ports for domestic trade or recreational activities. However, the influence of human-mediated transfer of species may be of less importance for marine species which have typically 3-5 weeks of larval stage (for example, molluscs, polychaetes) (Shanks 2009). Therefore, the dispersal rates of the species might be an important factor to consider the propagule pressure at regional and local scales. The species observed at both APS and NZPS are benthic species such as tunicates, barnacles, mussels, crabs, bryozoans and polychaetes, which typically need a hard substratum to adhere. Nevertheless, for species such as bryozoans and ascidians, with 2-10 hours of larval could disperse long distances; however, it can reduce their chances of survival, reduced growth rates or smaller sized adults (Marshall et al. 2003; Burgess et al. 2012). The influence of anthropogenic activities results in alteration of connectivity in marine systems (Bishop et al. 2017) and a major challenge to identify the factors characterizing the bioinvasions at multiple spatial scales. This study, however, highlights that the responses in Australia are very different from those in New Zealand, which suggests that responses are regional or country-specific and not global.

In **Chapter 3**, the marine biological community composition and species' abundances regarding species status were compared between man-made, and natural habitats/substrata, respectively. The field tests were undertaken in Wellington Harbour using settlement tile arrays (PVC vs slate). The aim was to determine differences in the overall species assemblage and

species status between habitat type (natural reef vs man-made habitat) and substratum type (PVC vs slate tile). Rapid colonisation of species was observed within 3 months of submersion, with nearly 64% cover of the bare tiles. The two-year study was not enough to observe the climax community. A total of 47 putative species were observed on the tiles in this two-year study; which is nearly 1/4th of the number of species seen in Wellington Harbour sampled for New Zealand port survey (Chapter 2 B).

The ecological succession observed on both habitat type and substratum type showed a similar pattern of recruitment and post-settlement processes. The community structure may be influenced to a greater extent by stochastic recruitment (Chang & Turner 2019). The species explaining most of the variation among and between habitat types and substratum types were; cryptogenic Biofilm type 1, Green sp. 1, native crustose brown seaweed, *Ralfsia verrucosa,* non-native red alga *Bangia atropurpurea,* non-native bryozoan *Watersipora subtorquata,* native tunicate *Asterocarpa humilis* and native bryozoan *Membranipora membranacea.* These species are typically seen fouling on ships hulls or marina infrastructures (Connell 2001; Wood & Probert 2013). For example, the of the larval life span of bryozoan species may range from one to a few weeks (Gordon 1977); however, in the case of sea squirts *Asterocarpa humilis*, their natural dispersal is very limited. The marina and reef sites were at ~ 200 m distance from each other; therefore, their natural dispersal is possible. The community composition showed significant results as a function of habitat type and substratum type. The differences in biological communities between man-made (marina; PVC) and natural (reef; slate) habitats/tiles are explained by abundance differences, not by species differences. The cryptogenic species were abundant at both habitat type and substratum type. The non-native species were relatively abundant at marina sites; however, did not show preference to the two substratum types. This study acknowledges the on-going problem of the role of man-made structures as more suitable habitats for non-native species. The species dispersal rate plays an important role in the spread of species from marina sites to neighbouring natural habitats. These results suggest that Wellington Harbour is a well-mixed site, and control of invasive species cannot be easily achieved.

The aim of chapter 5 was to examine whether the reproductive out (GSI) of the native (SH*Mg*) and non-native (NH*Mg*) lineages of the blue mussel, *Mytilus galloprovincialis*, differed between natural (reef) and man-made (marina) habitats. To analyse the reproductive performance, the temporal variation in the reproductive output (GSI) of the NH*Mg* and SH*Mg* were measured for 1 year in Wellington Harbour. The shell length of the two mussel lineages,

when compared between natural and man-made habitats, showed a significant difference, but the difference was trivial (~ 0.5 mm). The GSI of the mussels indicated significant between habitat type and sample intervals and not for lineage × sample interval, indicating similar GSI values between native SH*Mg* and non-native NH*Mg*. The GSI values were relatively greater at reef sites, thus, indicating increased spawning activity in the marina sites. These results were portrayed in the reproduction patterns of both lineages, with NH*Mg* and SH*Mg* showing similar timing of gametogenesis and spawning at both the reef and marina sites. The temporal variation of GSI showed with two spawning events (August and November). The mussels (NH*Mg* and SH*Mg*) had a large spawning event in November in the marina sites. This presumably could be because of warmer temperatures in the semi-enclosed marina conditions. The results suggest that the ecologically similar response of NH*Mg* and SH*Mg* (GSI: NH*Mg* = SH*Mg*) could be due to their close evolutionary affinities.

Overall, this study highlights that the most species observed were native species suggesting that the local species pools are still important for overall diversity than the introductions, even in the highly modified habitats. Additionally, many cryptogenic species were observed across all the chapters; molecular approach to taxonomy and frequent surveillance programmes - to detect the cryptic introductions should be considered. At the local scale (Chapter 3 and 4), the reef sites are performing differently from the marina sites, with relatively higher non-native species in the marinas and better spawning activity by native and non-native species in the marinas.

5.3. Statistical vs Biological significance

The results of my study raise several questions with regards to statistical significance and biological relevance. Under a 95% confidence interval, the denoted *P*-values exhibit statistical significance; however, under stricter parameters (i.e. 99% CI), statistical significance is refuted. This calls into question the biological impacts being described in these tests and the magnitude of these impacts with regards to the animal's physiology.

To process large sample size data, statistical software is convenient to conclude results. Statistical significance is important to detect differences between treatments; however, assessing biological relevance should be of primary importance. Hence, both the statistical significance and biological relevance are important to evaluate a dataset. That is why, even if the results are statistically significant, the differences are small enough to consider them as not biologically important (Lovell 2013). Cohen's *d* test is an effect size index that evaluates the

size of an effect in a study. It is a standardised measure of the impact of a statistically significant intervention (independent variable). Cohen's *d* equals the difference in the means divided by the average of the standard deviations (Cohen 1992). This test can be used to accompany *t*-test or ANOVA to examine the strength of the significant results. Cohen (1992) indicated an effect size of about 0.25 was "small", about 0.5 was "medium", and about 0.8 was "large".

5.4. Limitations of the monitoring study

Large scale monitoring datasets (APS and NZPS) are formed by quantifying single occurrences of species on a single date; however, factors at local scales such as environmental conditions, nutrient supply, pollution, habitat complexity and physical disturbances can lead to variations in species assemblages. For instance, Underwood & Murphy (2008) found a seasonal latitudinal increase in species richness from north to south in winter but not in summer. Therefore, a complete census of available species in an area is impossible due to seasonal variations. Surveying and re-surveying sites to have better knowledge are not cost-efficient and are very timing consuming (Bishop & Hutchings 2011).

Current surveillance programmes are conducted with preliminary taxonomic identification based on morphology instead of molecular techniques. Very few taxonomic experts and scientists have the training to identify congeneric native and non-native species, which results in the number of cryptic invasions not being identified (Ponchon et al. 2013). Consequently, the accuracy of identification of the native and non-native species is questionable. Such inadequacies in surveillance and monitoring programmes can hinder the process of well-developed biosecurity and management approaches to restrict invasions (Peters et al. 2017). In recent years, a variety of DNA based (molecular) techniques have been developed to derive information about organisms (Pochon et al. 2017). These molecular techniques can be used to identify species, especially non-native species (Zaiko et al. 2018). Several countries – USA, Canada, Australia and New Zealand have already adopted molecular genetic techniques to survey and early detection of non-native species and support management decisions.

For settlement tile study (Chapter 3), the settlement tile arrays justified the community composition and identifying impacts of habitats for 2 years. However, it should be kept in mind that the growth on PVC and slate tiles might be a representation of natural reef or marina habitats but not an exact copy. The study period of 2 years was not enough to observe a stable or climax state of the community, as there was always 20% bare space observed on the tiles.

With respect to environmental factors, it is important to have accurate measurements in the study areas. The variability of growth between habitats and substrata could have explained with the environmental data. Unfortunately, due to calibration difficulties, environmental data could not be included in my study. Similarly, for Chapter 4, the fact that NH*Mg* and SH*Mg* reproductive activity – gametogenesis and spawning could have been influenced by environmental conditions. The environmental data could have explained the differences in GSI values between reef and marina sites.

5.5. Management implications

Australia and New Zealand have established some of the world's strongest biosecurity and management measures, i.e. comprehensive pre-border, at-border and post-border management responses (Hewitt & Campbell 2007; Commonwealth of Australia 2013; Ojaveer et al. 2015). However, this study has highlighted the need for regulations that address the problem of regional or local spread of non-native species. Ports, harbours and other coastal structures play a role in facilitating non-native species by providing suitable habitats and substratum, which is evident in this study. The macrofouling species observed in the study such as the bryozoans, ascidians, arthropods, settle on readily available substrata irrespective to the substratum type. Non-native species are often *r*-selected strategists, i.e., fast-growing opportunist species, and the availability of bare space can be enough to facilitate their settlement and establishment. Maintenance of coastal structures, construction of new structures and marine traffic close to intertidal habitats should be managed appropriately as displacement of native assemblages due to these activities may provide opportunities for the invaders to settle on vacant surfaces (Clark and Johnston 2009; Airoldi and Bulleri 2011; Hedge and Johnston 2012). Maintenance of structures can be employed at suitable timings considering the spawning periods of species. For instance, many species do no show reproductive activities in winter, thereby encouraging the timing of a controlled maintenance approach (Hopkins and Forrest 2010).

Many eco-engineering approaches related to multifunctional designs of coastal structures have now been investigated such as the cost-effective approaches - designing coastal structures more similar to natural rocky reefs by building structures on a gentler slope (Department of Environment and Climate Change 2009). Also, increasing the surface area for the settlement of native species or restoring local biodiversity to restrict the establishment of non-native species (Sella and Perkol-Finkel 2015). However, there is a need to have a full understanding of the functional properties of the man-made structures. Different characteristics

of man-made structures such as size, substratum material, construction design and orientation may alter the fouling community structure. The community structure in this study did not differ between natural and man-made substratum materials, though the size of the substrata and orientation was similar between habitat type. Eco-engineering and it is potential to reduce invasions are still at an experimental stage, and the designing of appropriate structures will largely depend on coastal attributes. Therefore, coastal structures need to be monitored for longer timescales and at different habitats since varying physicochemical conditions may have different impacts on species and their functioning.

The number of bioinvasions has increased over the decades, and invasions are now ubiquitous. Eradicating every invaded species will be an expensive and more so impossible task (Ruiz et al. 2000, 2009; Hewitt et al. 2004; Forrest & Hopkins 2013). Much of the conservation management work to date has focussed on prevention of new invasions followed by eradication of non-native species (Melbourne et al. 2007; Hewitt et al. 2009; Cook et al. 2016). However, there is still no stopping the invasion pressure. Some researchers think that the introduction of non-native species can improve the stocks of declining native species, also the economically valuable species and benefit the economy, e.g. shellfish production industries (Leppäkoski et al. 2002; Schlaepfer et al. 2011; Cook et al. 2016). It is evident from the decade worth of studies that it is difficult to get to grips with invasions and their unpredictable consequences to the environment. The importance of bioinvasions varies on a case by case basis, as in some instances they can improve the functional diversity and can also pose a threat to the native species and their environment (Leppäkoski 2002; Glasby et al. 2007; Gallardo & Aldridge 2013; Thomsen et al. 2014; Corriero et al. 2016; Gestoso et al. 2017; Riera et al. 2018). An ongoing increase in human population and demand for resources will put pressure on the marine environment, thereby altering ecosystem services. Better integrative ecological theories providing new knowledge to stakeholders and managers can help to deliver effective management approaches.

5.6. Future work

Based on my results, it is clear that non-native species are abundant in major commercial shipping ports with a high frequency of international marine traffic. This study also supports the growing evidence that non-native species are generally more abundant in man-made habitats (e.g. ports, harbours, marinas) compared to natural reefs. It is undisputed that large-scale surveys and monitoring can be costly. Still, frequent monitoring of major ports receiving high volumes of marine traffic can aid with early detection and eradication measures.

The next step is to examine the environmental conditions (biotic and abiotic) that determine the invasions and proliferation of non-native species (not included in my study). The settlement tile array study indicated ecological succession patterns for 2 years; however, if the community reached its climax state (stable state) is still not known. Therefore, future studies with relatively long immersion periods for settlement tiles may be an effective monitoring approach and could detect the climax state of a community on both habitat/substratum types. It is important to improve the knowledge about life-history traits of a species - to understand the propagule lifespan, dispersal rate and recruitment timing. Lastly, manual identification of species has its major drawback, as stated in the 'Limitation section' above. It is advisable to find cost-effective ways such as molecular tools to identify species which are already providing accurate detection of non-native species (Westfall and Gardner 2010).

5.7. Conclusion

This study found that the fouling community composition on the natural reef and at man-made marina habitats was similar, although relative abundances of species differed. The results suggest that Wellington Harbour is well-mixed site and with natural sites being adjacent (~ 200 m) to marina sites; the dispersal of species from one site to another is highly possible. However, the differences in abundances at each habitat could probably be due to environmental conditions and community dynamics in the habitat. This study forms a baseline of the community composition of the modified habitats in an already modified busy harbour (Wellington harbour). Further, the congener *M. galloprovincialis* native and non-native lineages lack ecological differences – GSI, shell length, etc. at reef and marina sites may be due to the very close evolutionary history of NH*Mg* and SH*Mg*. Additionally, it would be worthwhile to assess other biotic and abiotic factors such as grazing, predation, salinity, temperature, water flow and light to explain the differences in community composition between habitat type. Analyses of baseline surveys examined potential predictors for the distribution of non-native species and indicated major ports as hotpots for invaders as well as point of transfer. Combination of the number of major ports at high latitudes increases invasion pressure. Consequently, the transfer of marine traffic from major to minor ports risks domestic transfers. Globalisation and urban sprawl are expected to increase in future with requirements for more man-made coastal infrastructure such as ports, harbours and marinas. These findings suggest that most vulnerable habitats, such as the major ports should be prioritised and frequently monitored for non-native species for early detection.

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Appendix

Table A1. SIMPER analysis: average similarity in the status of species as a function of the surveyed port.

Abbot Point Average similarity: 65.04			**Adelaide Average similarity: 74.02**		**Albany Average similarity: 64.69**		**Bunbury Average similarity: 56.51**		**Burnie Average similarity: 68.56**	
Species	Abund	C%	Abund	C%	Abund	C%	Abund	C%	Abund	C%
Native	3.7	85.65	2.47	46.7	1.26	47.98	1.03	54.03	3.33	84.72
Non-native	0.86	13.76	1.78	36.84	1.18	47.62	0.84	45.3	0.82	13.7
Cryptogenic	0.21	0.58	1.02	16.46	0.37	4.41	0.12	0.66	0.33	1.59
Devonport Average similarity: 68.00			**Geelong Average similarity: 85.75**		**Esperance Average similarity: 64.91**		**Geraldton Average similarity: 82.48**		**Gladstone Average similarity: 77.62**	
Species	Abund	C%	Abund	C%	Abund	C%	Abund	C%	Abund	C%
Native	2.12	81.69	2.17	43.31	2.17	94.46	1.28	99.87	2.17	83.11
Non-native	0.73	17.28	2.23	40.86	0.41	5.16	0.11	0.13	0.68	16.89
Cryptogenic	0.18	1.03	0.92	15.83	0.12	0.38	0	0	0	0
Eden Average similarity: 71.56			**Fremantle Average similarity: 69.84**		**Hay Point Average similarity: 71.34**		**Launceston Average similarity: 84.50**		**Mourilyan Average similarity: 67.12**	
Species	Abund	C%	Abund	C%	Abund	C%	Abund	C%	Abund	C%
Native	2.44	52.79	2.26	59.34	3.38	89.98	4.3	61.97	2.87	79.12
Non-native	1.09	20.55	0.79	13.74	0.3	1.95	1.41	18.13	0.57	6.94
Cryptogenic	1.12	26.66	0.96	26.91	0.64	8.07	1.47	19.9	0.7	13.93
Hastings Average similarity: 85.03			**Hobart Average similarity: 87.28**		**Lady Barron Average similarity: 59.92**		**Lucinda Average similarity: 52.43**		**Mackay Average similarity: 72.99**	

Species	Abund	C%	Abund	C%	Abund	C%	Abund	C%	Abund	C%
Native	2.64	76.82	3.05	41.82	1.39	78.67	2.4	65.92	3.44	82
Non-native	1.12	23.18	3.11	40.39	0.85	20.47	0.96	29.58	0.97	15.83
Cryptogenic	0	0	1.54	17.8	0.2	0.86	0.43	4.49	0.35	2.17
Melbourne Average similarity: 67.94			**Newcastle Average similarity: 68.68**		**Port Hedland Average similarity: 73.23**		**Port Lincoln Average similarity: 66.55**		**Portland Average similarity: 79.11**	
Species	Abund	C%	Abund	C%	Abund	C%	Abund	C%	Abund	C%
Native	1.38	41.23	2.35	63.92	2.8	92.67	1.94	93.43	2.49	70.35
Non-native	1.27	37.88	1.06	18.82	0.43	4.85	0.41	6.42	1.23	28.96
Cryptogenic	0.74	20.89	0.81	17.26	0.3	2.48	0.07	0.14	0.23	0.69
Townsville Average similarity: 57.72			**Weipa Average similarity: 61.01**							
Species	Abund	C%	Abund	C%						
Native	2.64	82.38	2.02	84.65						
Non-native	0.79	11.84	0.36	3.98						
Cryptogenic	0.51	5.78	0.5	11.36						

C% = percent contribution

Table A2. Species identified in the 27 port surveys around Australia and species status – native, non-native and cryptogenic species.

Species	Phyla	Species status
Acanthochitona bednalli	Mollusca	Native
Acanthochitona granostriata	Mollusca	Native
Acanthochitona kimberi	Mollusca	Native
Acanthochitona pilsbryi	Mollusca	Native
Acanthochitona retrojecta	Mollusca	Native
Acanthochitona sueurii	Mollusca	Native
Acanthodesia cf. savartii	Bryozoa	Cryptogenic
Acanthophora cf. muscoides	Rhodophyta	Native
Acanthophora dendroides	Rhodophyta	Native
Acanthophora muscoides	Rhodophyta	Native
Acanthophora spicifera	Rhodophyta	Native
Acanthopleura gaimardi	Mollusca	Native
Acasta cf. dofleini	Arthropoda	Native
Acasta dofleini	Arthropoda	Native
Acasta pectinipes	Arthropoda	Native
Achaeus lacertosus	Arthropoda	Native
Achelia assimilis	Arthropoda	Native
Achelia shepherdi	Arthropoda	Native
Aclophoropsis festiva	Mollusca	Native
Acrocarpia paniculata	Ochrophyta	Native
Acrosorium uncinatum	Rhodophyta	Native
Acrosorium venulosum	Rhodophyta	Native
Actaea cf. ruppelli	Arthropoda	Native
Actaea peronii	Arthropoda	Native
Actaeodes hirsutissimus	Arthropoda	Native
Actinia cf. tenebrosa	Cnidaria	Native
Actinia tenebrosa	Cnidaria	Native
Actinocucumis cf. typica	Echinodermata	Native
Aetea anguina	Bryozoa	Cryptogenic
Aglaophenia cf. parvula	Hydroid	Native
Aglaophenia cf. plumosa	Hydroid	Native
Aglaophenia delicatula	Hydroid	Native
Aglaophenia parvula	Hydroid	Native
Aglaophenia plumosa	Hydroid	Native
Agnewia tritoniformis	Mollusca	Native
Akera soluta	Mollusca	Native
Alabes dorsalis	Chordata	Native
Aliaporcellana cf. pygmaea	Arthropoda	Native
Aliaporcellana suluensis	Arthropoda	Native

Alitta succinea	Annelida	Non-native
Allorchestes compressus	Arthropoda	Native
Alope orientalis	Arthropoda	Native
Alpheus australiensis	Arthropoda	Native
Alpheus cf. australiensis	Arthropoda	Native
Alpheus cf. eulimene	Arthropoda	Native
Alpheus cf. facetus	Arthropoda	Native
Alpheus cf. paracrinitus	Arthropoda	Native
Alpheus cf. parasocialis	Arthropoda	Native
Alpheus cf. spongiarum	Arthropoda	Native
Alpheus cf. villosus	Arthropoda	Native
Alpheus chiragricus	Arthropoda	Native
Alpheus cristatus	Arthropoda	Native
Alpheus facetus	Arthropoda	Native
Alpheus gracilis	Arthropoda	Native
Alpheus hippothoe	Arthropoda	Native
Alpheus novaezelandiae	Arthropoda	Native
Alpheus richardsoni	Arthropoda	Native
Alpheus socialis	Arthropoda	Native
Alpheus villosus	Arthropoda	Native
Amarinus laevis	Arthropoda	Native
Amaryllis macrophthalmus	Arthropoda	Native
Amastigia cf. texta	Bryozoa	Native
Amathia biseriata	Bryozoa	Native
Amathia brongniartii	Bryozoa	Native
Amathia cf. connexa	Bryozoa	Native
Amathia cf. distans	Bryozoa	Non-native
Amathia cf. semiconvoluta	Bryozoa	Native
Amathia connexa	Bryozoa	Native
Amathia distans	Bryozoa	Non-native
Amathia tortuosa	Bryozoa	Cryptogenic
Amathia vidovici	Bryozoa	Native
Amblychilepas oblonga	Mollusca	Native
Ammothea ovatoides	Arthropoda	Native
Ammothella stocki	Arthropoda	Native
Amphipholis squamata	Echinodermata	Native
Amphisbetia minima	Cnidaria	Native
Amphitrite pachyderma	Annelida	Native
Amphitritides ithya	Annelida	Native
Amphiura (Amphiura) constricta	Echinodermata	Native
Amphiura (Amphiura) poecila	Echinodermata	Native
Amphiura (Amphiura) tenuis	Echinodermata	Native
Amphiura (Amphiura) trisacantha	Echinodermata	Native
Amphiura (Ophiopeltis) parviscutata	Echinodermata	Native

Anachis atkinsoni	Mollusca	Native
Anachis troglodytes	Mollusca	Native
Anadara granosa	Mollusca	Native
Anapella amygdala	Mollusca	Native
Ancorina robusta	Porifera	Native
Ancorina suina	Porifera	Native
Anisodonta subalata	Mollusca	Native
Anodontia omissa	Mollusca	Native
Anomia trigonopsis	Mollusca	Native
Anoplodactylus digitatus	Arthropoda	Native
Anoplodactylus evansi	Arthropoda	Native
Anoplodactylus glandulifer	Arthropoda	Native
Anotrichium elongatum	Rhodophyta	Native
Anotrichium subtile	Rhodophyta	Native
Antedon incommoda	Echinodermata	Native
Antennella secundaria	Cnidaria	Non-native
Anthohebella parasitica	Cnidaria	Native
Anthothoe albocincta	Cnidaria	Native
Anthothoe cf. albocincta	Cnidaria	Native
Antithamnion pinnafolium	Rhodophyta	Native
Antithamnionella glandifera	Rhodophyta	Native
Antithamnionella ternifolia	Rhodophyta	Cryptogenic
Aora maculata	Arthropoda	Native
Aplidium cf. lenticulum	Chordata	Native
Aplysilla cf. rosea	Porifera	Non-native
Apocorophium acutum	Arthropoda	Non-native
Arachnopusia unicornis	Bryozoa	Non-native
Arca avellana	Mollusca	Native
Arca navicularis	Mollusca	Native
Armandia intermedia	Annelida	Native
Artacamella dibranchiata	Annelida	Native
Arthrocardia wardii	Rhodophyta	Native
Ascidia cf. latesiphonica	Chordata	Native
Ascidia cf. liberata	Chordata	Native
Ascidia cf. munda	Chordata	Native
Ascidia cf. sydneiensis	Chordata	Non-native
Ascidia cf. thompsoni	Chordata	Native
Ascidia challengeri	Chordata	Native
Ascidia decepta	Chordata	Native
Ascidia empheres	Chordata	Native
Ascidia latesiphonica	Chordata	Native
Ascidia munda	Chordata	Native
Ascidia sydneiensis	Chordata	Non-native
Ascidiella aspersa	Chordata	Non-native

Ascorhynchus tenuirostris	Arthropoda	Native
Asparagopsis taxiformis	Rhodophyta	Native
Asterias amurensis	Chordata	Non-native
Asterocarpa humilis	Chordata	Native
Astralium pileolum	Mollusca	Native
Astralium tentoriformis	Mollusca	Native
Astrangia woodsi	Cnidaria	Native
Athanas dimorphus	Arthropoda	Native
Athanas parvus	Arthropoda	Native
Atys cylindrica	Mollusca	Native
Audouinella caespitosum	Rhodophyta	Native
Augeneria verdis	Annelida	Native
Augenerilepidonotus dictyolepis	Annelida	Native
Austraeolis cacaotica	Mollusca	Native
Austrobalanus imperator	Arthropoda	Native
Austrodecus tubiferum	Arthropoda	Native
Austromegabalanus nigrescens	Arthropoda	Native
Austrophyllis alcicornis	Rhodophyta	Native
Balanus amphitrite	Arthropoda	Cryptogenic
Balanus cf. amphitrite	Arthropoda	Cryptogenic
Balanus cf. reticulatus	Arthropoda	Native
Balanus cf. variegatus	Arthropoda	Native
Balanus cf. vestitus	Arthropoda	Native
Balanus improvisus	Arthropoda	Non-native
Balanus reticulatus	Arthropoda	Non-native
Balanus trigonus	Arthropoda	Cryptogenic
Balanus variegatus	Arthropoda	Native
Barbatia bistrigata	Mollusca	Native
Barbatia cf. helblingi	Mollusca	Native
Barbatia cf. pistachia	Mollusca	Native
Barbatia foliata	Mollusca	Native
Barbatia helblingi	Mollusca	Native
Barbatia pistachia	Mollusca	Native
Barbatia riculata	Mollusca	Native
Barbatia wendti	Mollusca	Native
Beania magellanica	Bryozoa	Native
Beania mirabilis	Bryozoa	Native
Bedeva hanleyi	Mollusca	Native
Bedeva paivae	Mollusca	Native
Bembicium auratum	Mollusca	Native
Bembicium nanum	Mollusca	Native
Bhawania amboinensis	Annelida	Native
Bhawania cf. amboinensis	Annelida	Native
Bicellariella ciliata	Bryozoa	Native

Bicellariella gracilis	Bryozoa	Native
Bicrisia edwardsiana	Bryozoa	Native
Biffarius arenosus	Arthropoda	Native
Biflustra perfragilis	Bryozoa	Native
Bimeria australis	Cnidaria	Native
Bimeria currumbinensis	Cnidaria	Native
Bispira cf. porifera	Annelida	Native
Bittium granarium	Mollusca	Native
Boccardia cf. chilensis	Annelida	Non-native
Boccardia chilensis	Annelida	Cryptogenic
Boccardia proboscidea	Annelida	Non-native
Boccardiella cf. bihamata	Annelida	Native
Botrylloides leachi	Chordata	Non-native
Botrylloides magnicoecum	Chordata	Cryptogenic
Botrylloides perspicuus	Chordata	Native
Botryllus cf. tuberatus	Chordata	Native
Botryllus schlosseri	Chordata	Non-native
Botryllus tuberatus	Chordata	Native
Botryocladia obovata	Rhodophyta	Native
Botryocladia sonderi	Rhodophyta	Native
Bougainvillia cf. balei	Cnidaria	Native
Bougainvillia muscus	Cnidaria	Non-native
Bowerbankia gracilis	Bryozoa	Non-native
Bowerbankia imbricata	Bryozoa	Non-native
Brachidontes cf. rostratus	Mollusca	Native
Brachidontes erosa	Mollusca	Native
Brachidontes maritimus	Mollusca	Native
Brachidontes rostratus	Mollusca	Native
Branchiomma nigromaculata	Annelida	Native
Branchiosyllis australis	Annelida	Native
Branchiosyllis exilis	Annelida	Native
Bryopsis plumosa	Chlorophyta	Non-native
Bugula cf. avicularia	Bryozoa	Non-native
Bugula cf. flabellata	Bryozoa	Non-native
Bugula cf. robusta	Bryozoa	Native
Bugula cf. serrata	Bryozoa	Native
Bugula cf. stolonifera	Bryozoa	Non-native
Bugula dentata	Bryozoa	Native
Bugula flabellata	Bryozoa	Non-native
Bugula neritina	Bryozoa	Non-native
Bugula phillipinata	Bryozoa	Native
Bugula robusta	Bryozoa	Native
Bugula serrata	Bryozoa	Native
Bugula stolonifera	Bryozoa	Non-native

Bugula vectifera	Bryozoa	Native
Bulla punctulata	Mollusca	Native
Caberea boryi	Bryozoa	Native
Caberea dichotoma	Bryozoa	Native
Caberea dolabrata	Bryozoa	Native
Caberea helicina	Bryozoa	Native
Caberea lata	Bryozoa	Native
Caberea rostrata	Bryozoa	Native
Cabestana tabulata	Mollusca	Native
Callipallene emaciata micracantha	Arthropoda	Native
CallistoMollusca antiquus	Mollusca	Native
Callithamnion violaceum	Rhodophyta	Native
Callogobius mucosus	Chordata	Native
Callophyllis lambertii	Rhodophyta	Native
Callucina lacteola	Mollusca	Native
Calthalotia mundula	Mollusca	Native
Calyptotheca cf. wasinensis	Bryozoa	Native
Calyptotheca triangula	Bryozoa	Native
Canda cf arachnoides	Bryozoa	Native
Caprella acanthogaster	Arthropoda	Non-native
Caprella cf. danilevskii	Arthropoda	Non-native
Caprella cf. equilibra	Arthropoda	Non-native
Caprella equilibra	Arthropoda	Cryptogenic
Caprella penantis	Arthropoda	Cryptogenic
Caprella scaura	Arthropoda	Non-native
Cardita cf. crassicosta	Mollusca	Native
Cardita excavata	Mollusca	Native
Cardita muricata	Mollusca	Native
Cardita preissii	Mollusca	Native
Cardita variegata	Mollusca	Native
Carijoa cf. multiflora	Cnidaria	Native
Catenicella buskii	Bryozoa	Native
Catenicella cf. uberrima	Bryozoa	Native
Catenicella elegans	Bryozoa	Native
Caulerpa brownii	Chlorophyta	Native
Caulerpa cactoides	Chlorophyta	Native
Caulerpa cf. brachypus	Chlorophyta	Native
Caulerpa longifolia	Chlorophyta	Native
Caulerpa nummularia	Chlorophyta	Native
Caulerpa obscura	Chlorophyta	Native
Caulerpa peltata	Chlorophyta	Native
Caulerpa racemosa	Chlorophyta	Native
Caulerpa racemosa var. laetivirens	Chlorophyta	Native
Caulerpa racemosa var. turbinata	Chlorophyta	Native

Caulerpa sedoides f. geminata	Chlorophyta	Native
Caulerpa taxifolia	Chlorophyta	Native
Caulibugula dendrograpta	Bryozoa	Non-native
Caulibugula haddoni	Bryozoa	Native
Cellana conciliata	Mollusca	Native
Cellaria pilosa	Bryozoa	Native
Cellaria punctata	Bryozoa	Native
Cellaria tenuirostris	Bryozoa	Native
Celleporaria bispinata	Bryozoa	Native
Celleporaria cf. columnaris	Bryozoa	Native
Celleporaria cf. fusca	Bryozoa	Native
Celleporaria cf. mamillata	Bryozoa	Native
Celleporaria cf. nodulosa	Bryozoa	Native
Celleporaria cf. oculata	Bryozoa	Native
Celleporaria columnaris	Bryozoa	Native
Celleporaria foliata	Bryozoa	Native
Celleporaria fusca	Bryozoa	Native
Celleporaria nodulosa	Bryozoa	Native
Cenolia trichoptera	Echinodermata	Native
Centroceras clavulatum	Rhodophyta	Non-native
Ceramium cliftonianum	Rhodophyta	Native
Ceramium filiculum	Rhodophyta	Native
Ceramium flaccidum	Rhodophyta	Cryptogenic
Ceramium isogonum	Rhodophyta	Native
Ceramium macilentum	Rhodophyta	Native
Ceramium pusillum	Rhodophyta	Native
Ceramium sympodiale	Rhodophyta	Native
Ceramium tasmanicum	Rhodophyta	Native
Ceramium virgatum	Rhodophyta	Cryptogenic
Ceratonereis amphidonta	Annelida	Native
Ceratonereis cf. costae	Annelida	Native
Ceratonereis cf. mirabilis	Annelida	Native
Ceratonereis mirabilis	Annelida	Native
Ceratonereis perkinsi	Annelida	Native
Cerceis tridentata	Arthropoda	Native
Chaetozone setosa	Annelida	Native
Chama asperella	Mollusca	Native
Chama cf. fibula	Mollusca	Native
Chama cf. ruderalis	Mollusca	Native
Chama fibula	Mollusca	Non-native
Chama lazarus	Mollusca	Native
Chama limbula	Mollusca	Native
Chama pacifica	Mollusca	Native
Chama ruderalis	Mollusca	Native

Chamaesipho tasmanica	Arthropoda	Native
Champia parvula	Rhodophyta	Cryptogenic
Champia viridis	Rhodophyta	Native
Chaperiopsis cervicornis	Bryozoa	Native
Charybdis cf. anisodon	Arthropoda	Native
Charybdis cf. hellerii	Arthropoda	Native
Charybdis hellerii	Arthropoda	Non-native
Chelonaplysilla cf. violacea	Porifera	Native
Chelonaplysilla violacea	Porifera	Native
Chlamys aktinos	Mollusca	Native
Chlorodiella laevissima	Arthropoda	Native
Chlorotocella gibber	Arthropoda	Native
Chondria fusifolia	Rhodophyta	Native
Chondria simpliciuscula	Rhodophyta	Native
Chondria succulenta	Rhodophyta	Native
Chordaria cladosiphon	Ochrophyta	Native
Chorizocarpa cf. michaelseni	Chordata	Native
Chorizocarpa cf. sydneyensis	Chordata	Native
Chorizocarpa sydneyensis	Chordata	Native
Chromodoris cf. epicuria	Mollusca	Native
Chthamalus antennatus	Arthropodas	Native
Chthamalus malayensis	Arthropodas	Native
Cilicaea crassicaudata	Arthropoda	Native
Cilicaea latreillei	Arthropoda	Native
Ciona intestinalis	Chordata	Non-native
Cirolana erodiae	Arthropoda	Native
Cirolana harfordi	Ispods	Non-native
Cirriformia cf. capensis	Annelida	Native
Cirriformia cf. filigera	Annelida	Native
Cirriformia filigera	Annelida	Native
Cirriformia tentaculata	Annelida	Native
Cladophora albida	Chlorophyta	Native
Cladophora feredayi	Chlorophyta	Native
Cladophora lehmanniana	Chlorophyta	Non-native
Cladophora subsimplex	Chlorophyta	Native
Clanculus undatus	Mollusca	Native
Clarkcoma canaliculata	Echinodermata	Native
Clathrina adusta	Porifera	Native
Clava cf. simplex	Cnidaria	Native
Cleidothaerus cf. plicifera	Mollusca	Native
Cleotrivia globosa	Mollusca	Native
Clytia cf. gracilis	Cnidaria	Native
Clytia cf. hemisphaerica	Cnidaria	Non-native
Clytia cf. paulensis	Cnidaria	Non-native

Clytia gravieri	Cnidaria	Native
Clytia hemisphaerica	Cnidaria	Cryptogenic
Clytia johnstoni	Cnidaria	Native
Clytia paulensis	Cnidaria	Cryptogenic
Cnemidocarpa areolata	Chordata	Native
Cnemidocarpa cf. barbata	Chordata	Native
Cnemidocarpa completa	Chordata	Native
Cnemidocarpa fissa	Chordata	Native
Cnemidocarpa floccosa	Chordata	Native
Cnemidocarpa lobata	Chordata	Native
Cnemidocarpa radicosa	Chordata	Native
Cnemidocarpa stolonifera	Chordata	Native
Codium fragile ssp tomentosoides	Chlorophyta	Non-native
Coeloclonium cf. umbellulum	Rhodophyta	Native
Coeloclonium umbellulum	Rhodophyta	Native
Colpomenia sinuosa	Ochrophyta	Cryptogenic
Conopeum cf. seurati	Bryozoa	Native
Conopeum reticulum	Bryozoa	Non-native
Corallina officinalis	Rhodophyta	Cryptogenic
Coralliophila mira	Mollusca	Native
Cordylophora caspia	Cnidaria	Non-native
Corella eumyota	Chordata	Native
Corydendrium parasiticum	Cnidaria	Native
Coscinasterias muricata	Chordata	Native
Cosmetalepas concatenatus	Mollusca	Native
Craspedoplax variabilis	Mollusca	Native
Crassimarginatella cf. papulifera	Bryozoa	Native
Crassimarginatella papulifera	Bryozoa	Native
Crassostrea gigas	Mollusca	Non-native
Cricophorus nutrix	Cnidaria	Native
Crisia acropora	Bryozoa	Native
Crisia cf. acropora	Bryozoa	Native
Crisia margaritacea	Bryozoa	Native
Cronia avellana	Mollusca	Native
Crucigera cf. inconstans	Annelida	Native
Crucigera inconstans	Annelida	Native
Cryptodromia cf. tumida	Arthropoda	Native
Cryptoplax striata	Mollusca	Native
Cryptosula pallasiana	Bryozoa	Non-native
Culicia australiensis	Cnidaria	Native
Culicia cf. tenella	Cnidaria	Native
Culicia tenella	Cnidaria	Cryptogenic
Cutleria multifida	Ochrophyta	Non-native
Cyamiomactra cf. problematica	Mollusca	Native

Cyclicopora longipora	Bryozoa	Native
Cymatium exaratum	Mollusca	Native
Cymatium labiosum	Mollusca	Native
Cypraea helvola	Mollusca	Native
Cypraea subviridis	Mollusca	Native
Cystiscus angasi	Mollusca	Native
Dasya capillaris	Rhodophyta	Native
Dasya cf. caraibica	Rhodophyta	Native
Dasya crescens	Rhodophyta	Native
Dasya extensa	Rhodophyta	Native
Dasya hookeri	Rhodophyta	Native
Dasya iyengarii	Rhodophyta	Native
Dasya villosa	Rhodophyta	Native
Demonax leucaspis	Annelida	Native
Dendostrea cf. folium	Mollusca	Native
Dendostrea cf. sandvichensis	Mollusca	Native
Dendostrea folium	Mollusca	Native
Dendostrea sandvichensis	Mollusca	Native
Dendrilla cactos	Porifera	Native
Dendrilla cf. rosea	Porifera	Native
Densipora corrugata	Bryozoa	Native
Dictyopteris muelleri	Ochrophyta	Native
Dictyopteris nigricans	Ochrophyta	Native
Dictyopteris plagiogramma	Ochrophyta	Native
Dictyota bartayresiana	Ochrophyta	Native
Dictyota cervicornis	Ochrophyta	Native
Dictyota dichotoma	Ochrophyta	Cryptogenic
Dictyota divaricata	Ochrophyta	Native
Dictyota furcellata	Ochrophyta	Native
Dilophus marginatus	Ochrophyta	Native
Dimorphostylis colefaxi	Arthropoda	Native
Diodora cf. jukesii	Mollusca	Native
Diodora cf. lincolnensis	Mollusca	Native
Diodora jukesii	Mollusca	Native
Diopatra dentata	Annelida	Native
Diphasia digitalis	Cnidaria	Native
Diphasia subcarinata	Cnidaria	Native
Diplosoma ferrugem	Chordata	Native
Diplosoma listerianum	Chordata	Non-native
Diplosoma velatum	Chordata	Native
Dipolydora flava	Annelida	Cryptogenic
Dipolydora giardi	Annelida	Cryptogenic
Dipolydora socialis	Annelida	Non-native
Distaplia cf. australensis	Chordata	Native

Distaplia stylifera	Chordata	Native
Distaplia violetta	Chordata	Native
Distaplia viridis	Chordata	Native
Dofleinia armata	Cnidaria	Native
Doriopsilla peculiaris	Mollusca	Native
Doris cameroni	Mollusca	Native
Dorvillea australiensis	Annelida	Native
Dulichiella australis	Arthropoda	Native
Dumea latipes	Arthropoda	Native
Durvillaea potatorum	Ochrophyta	Native
Dynamena crisoides	Cnidaria	Native
Dynamena mertoni	Cnidaria	Native
Echinothamnion hookeri	Rhodophyta	Native
Ecklonia radiata	Ochrophyta	Native
Ecteinascidia cf. diaphanis	Chordata	Native
Ecteinascidia rubricollis	Chordata	Native
Ectocarpus siliculosus	Ochrophyta	Non-native
Ehlersia ferrugina	Annelida	Native
Elasmopus rapax	Arthropoda	Non-native
Electra tenella	Bryozoa	Cryptogenic
Electroma georgiana	Mollusca	Native
Electroma physoides	Mollusca	Native
Elminius covertus s	Arthropodas	Native
Elminius modestus s	Arthropodas	Native
Elysia ornata	Mollusca	Native
Elzerina blainvillii	Bryozoa	Native
Emarginula devota	Mollusca	Native
Emarginula patula	Mollusca	Native
Endeis straughani	Arthropoda	Native
Engina armillata	Mollusca	Native
Ensiculus cultellus	Mollusca	Native
Enteromorpha intestinalis	Chlorophyta	Cryptogenic
Epitonium cf. perplexum	Mollusca	Native
Epopella simplex s	Arthropodas	Native
Ericthonius pugnax	Arthropoda	Native
Euchelus cf. ampullus	Mollusca	Native
Euchone limnicola	Annelida	Non-native
Euclavella claviformis	Chordata	Native
Eucoelium mariae	Chordata	Native
Eudendrium aylingae	Cnidaria	Native
Eudendrium capillare	Cnidaria	Native
Eudendrium cf. capillare	Cnidaria	Native
Eudendrium cf. generale	Cnidaria	Native
Eudendrium cf. kirkpatricki	Cnidaria	Native

Eudendrium glomeratum	Cnidaria	Native
Eudendrium pennycuikae	Cnidaria	Native
Eudistoma laysani	Chordata	Native
Eumarcia fumigata	Mollusca	Native
Eumida cf. sanguinea	Annelida	Native
Eumida fuscolutata	Annelida	Native
Eumida sanguinea	Annelida	Native
Eunice afra punctuata	Annelida	Native
Eunice antennata	Annelida	Native
Eunice australis	Annelida	Native
Eunice bassensis	Annelida	Native
Eunice cf. afra punctuata	Annelida	Native
Eunice cf. australis	Annelida	Native
Eunice cf. bowerbanki	Annelida	Native
Eunice cf. complanata	Annelida	Native
Eunice cf. hirschi	Annelida	Native
Eunice cf. ornata	Annelida	Native
Eunice cf. plicata	Annelida	Native
Eunice complanata	Annelida	Native
Eunice hirschi	Annelida	Native
Eunice laticeps	Annelida	Native
Eunice siciliensis	Annelida	Native
Eunice torresiensis	Annelida	Native
Eunice tubifex	Annelida	Native
Eunice vittata	Annelida	Native
Eupolymnia koorangia	Annelida	Native
Euptilota articulata	Rhodophyta	Native
Euraphia withersi	Arthropoda	Native
Euthelepus cf. marchinbar	Annelida	Native
Fenestrulina mutabilis	Bryozoa	Native
Ficopomatus enigmaticus	Annelida	Non-native
Filellum serratum	Cnidaria	Cryptogenic
Fragum retusum	Mollusca	Native
Fultodromia cf. nodipes	Arthropoda	Native
Fulvia tenuicostata	Mollusca	Native
Galathea australiensis	Arthropoda	Native
Galeolaria caespitosa	Annelida	Native
Gastrochaena cuneiformis	Mollusca	Native
Gelidium pusillum	Rhodophyta	Non-native
Gnathia biorbis	Arthropoda	Native
Gonothyraea loveni	Cnidaria	Non-native
Gracilaria arcuata	Rhodophyta	Native
Gracilaria cf. secundata	Rhodophyta	Native
Grahamina gymnota	Chordata	Non-native

Granata imbricata	Mollusca	Native
Grateloupia filicina luxurians	Rhodophyta	Native
Gregarinidra serrata	Bryozoa	Native
Griffithsia monilis	Rhodophyta	Native
Griffithsia subcylindrica	Rhodophyta	Native
Griffithsia teges	Rhodophyta	Native
Gymnangium gracilicaule	Cnidaria	Native
Gymnangium hians	Cnidaria	Native
Gymnangium longirostre	Cnidaria	Native
Halecium cf. lighti	Cnidaria	Native
Halecium cf. tenellum	Cnidaria	Native
Halecium cf. undulatum	Cnidaria	Native
Halecium delicatulum	Cnidaria	Cryptogenic
Halecium fragile	Cnidaria	Native
Halecium sessile	Cnidaria	Native
Halicarcinus innominatus	Arthropoda	Non-native
Halicarcinus ovatus	Arthropoda	Native
Halicarcinus rostratus	Arthropoda	Native
Halimeda cuneata N_Chlorophyta	Chlorophyta	Native
Haliotis cf. conicopora	Mollusca	Native
Haliplanella lineata	Cnidaria	Non-native
Halocynthia dumosa	Chordata	Native
Halopteris buskii	Cnidaria	Native
Halopteris campanula	Cnidaria	Native
Halopteris novaezelandiae	Ochrophyta	Native
Halopteris plagiocampa	Cnidaria	Native
Halopteris ramulosa	Ochrophyta	Native
Hapalochlaena maculosa	Mollusca	Native
Haraldiophyllum sinuosum	Rhodophyta	Native
Harmothoe cf. praeclara	Annelida	Native
Harmothoe cf. waahli	Annelida	Native
Harmothoe charlottae	Annelida	Native
Harmothoe dictyophora	Annelida	Native
Harmothoe phillipensis	Annelida	Native
Harmothoe praeclara	Annelida	Native
Harmothoe waahli	Annelida	Native
Hartmeyeria formosa	Chordata	Native
Hebella costata	Cnidaria	Native
Hebellopsis scandens	Cnidaria	Native
Heliocidaris erythrogramma	Echinodermata	Native
Helograpsus haswellianus	Arthropoda	Native
Hemiaegina minuta	Arthropoda	Native
Hemitoma subemarginata	Mollusca	Native
Herdmania momus	Chordata	Non-native

Hermaea evelinemarcusae	Mollusca	Native
Herpetopoma aspersa	Mollusca	Native
Herpetopoma atrata	Mollusca	Native
Herpetopoma rubra	Mollusca	Native
Herposiphonia rostrata	Rhodophyta	Native
Heteroclinus perspicillatus	Chordata	Native
Heteropanope cf. changensis	Arthropoda	Native
Heteropanope cf. longipedes	Arthropoda	Native
Heterozostera tasmanica	Tracheophyta	Native
Hexaminius popeiana	Arthropoda	Native
Hiatella arctica	Mollusca	Non-native
Hiatella australis	Mollusca	Native
Hincksia granulosa	Ochrophyta	Non-native
Hincksia sandriana	Ochrophyta	Non-native
Hincksia sordida	Ochrophyta	Native
Hincksinoflustra denticulata	Bryozoa	Native
Hippolyte caradina	Arthropoda	Native
Hippopetraliella magna	Bryozoa	Native
Hippothoa distans	Bryozoa	Non-native
Holothuria cf. fuscocinerea	Echinodermata	Native
Huenia bifurcata	Arthropoda	Native
Hyastenus auctus	Arthropoda	Native
Hyastenus cf. convexus	Arthropoda	Native
Hyastenus convexus	Arthropoda	Native
Hyastenus elatus	Arthropoda	Native
Hyastenus sebae	Arthropoda	Native
Hyatella intestinalis	Porifera	Native
Hyboscolex dicranochaetus	Annelida	Native
Hydrococcus brazieri	Mollusca	Native
Hydroides cf. brachyacanthus	Annelida	Native
Hydroides cf. ezoensis	Annelida	Non-native
Hydroides diramphus	Annelida	Non-native
Hydroides elegans	Annelida	Cryptogenic
Hydroides ezoensis	Annelida	Non-native
Hydroides lunulifera	Annelida	Native
Hydroides minax	Annelida	Native
Hydroides recta	Annelida	Native
Hydroides tambalagamensis	Annelida	Native
Hydroides trivesiculosus	Annelida	Native
Hydroides tuberculatus	Annelida	Native
Hydroides uncinata	Annelida	Native
Hymenena curdieana	Rhodophyta	Native
Hyotissa cf. hyotis	Mollusca	Native
Hyotissa hyotis	Mollusca	Native

Hypnea cervicornis	Rhodophyta	Native
Hypnea cf. spinella	Rhodophyta	Native
Hypnea charoides	Rhodophyta	Native
Hypnea musciformis	Rhodophyta	Non-native
Hypnea ramentacea	Rhodophyta	Native
Hypnea valentiae	Rhodophyta	Native
Hypselodoris obscura	Mollusca	Native
Iais californica	Arthropoda	Native
Ibla cumingi	Arthropoda	Native
Ibla quadrivalvis	Arthropoda	Native
Idanthyrsus armatus	Annelida	Native
Idanthyrsus australiensis	Annelida	Native
Idiellana pristis	Cnidaria	Native
Inermonephtys cf. palpata	Annelida	Native
Iphione muricata	Annelida	Native
Irus carditoides	Mollusca	Native
Irus crebrelamellatus	Mollusca	Native
Irus crenatus	Mollusca	Native
Irus cumingii	Mollusca	Native
Irus griseus	Mollusca	Native
Irus irus	Mollusca	Native
Isanemonia australis	Cnidaria	Native
IschnoMollusca cf. arbutus	Mollusca	Native
IschnoMollusca virgatus	Mollusca	Native
Isognomon albisoror	Mollusca	Native
Isognomon cf. ephippium	Mollusca	Native
Isognomon cf. isognomon	Mollusca	Native
Isognomon cf. nucleus	Mollusca	Native
Isognomon cf. perna	Mollusca	Native
Isognomon ephippium	Mollusca	Native
Isognomon isognomon	Mollusca	Native
Isognomon nucleus	Mollusca	Native
Isognomon perna	Mollusca	Native
Isolda pulchella	Annelida	Native
Istiblennius meleagris	Chordata	Native
Jania adhaerens	Rhodophyta	Native
Jania verrucosa	Rhodophyta	Native
Jasmineira elegans	Annelida	Native
Jassa marmorata	Arthropoda	Non-native
Jassa slatteryi	Arthropoda	Cryptogenic
Jellyella tuberculata	Bryozoa	Cryptogenic
Jujubinus lepidus	Mollusca	Native
Kellia adamsi	Mollusca	Native
Kellia cf. adamsi	Mollusca	Native

Kellia cf. yorkensis	Mollusca	Native
Kellia physema	Mollusca	Native
Kellia rotunda	Mollusca	Native
Kellia tumida	Mollusca	Native
Lafoeina amirantensis	Cnidaria	Native
Langerhansia cervantensis	Annelida	Native
Lanice bidewa	Annelida	Native
Lanice cf. bidewa	Annelida	Native
Lanicides attenuata	Annelida	Native
Lanicides cf. fascia	Annelida	Native
Lanicola lobata	Annelida	Native
Lasaea australis	Mollusca	Native
Laurencia arbuscula	Rhodophyta	Native
Laurencia filiformis	Rhodophyta	Native
Laurencia majuscula	Rhodophyta	Native
Lauridromia dehaani	Arthropoda	Native
Leitoscoloplos bifurcatus	Annelida	Native
Lenormandia marginata	Rhodophyta	Native
Leonnates cf. decipens	Annelida	Native
Leonnates cf. stephensoni	Annelida	Native
Leonnates decipens	Annelida	Native
Leonnates jousseaumei	Annelida	Native
Lepidonotus carinulatus	Annelida	Native
Lepidonotus cf. carinulatus	Annelida	Native
Lepidonotus cf. glaucus	Annelida	Native
Lepidonotus glaucus	Annelida	Native
Lepidonotus purpureus	Annelida	Native
Lepidonotus yorkianus	Annelida	Native
Leptochelia cf. dubia	Arthropoda	Native
Leptochelia dubia	Arthropoda	Cryptogenic
Leptograpsus variegatus	Arthropoda	Native
Leptomithrax gaimardii	Arthropoda	Native
Leptomithrax sternocostulatus	Arthropoda	Native
LeptoMollusca badius	Mollusca	Native
LeptoMollusca liratus	Mollusca	Native
LeptoMollusca mathewsianus	Mollusca	Native
Leptosynapta dolabrifera	Echinodermata	Native
Leucothoe commensalis	Arthropoda	Native
Leucothoe goowera	Arthropoda	Native
Ligia australiensis	Arthropoda	Native
Limaria cf. fragilis	Mollusca	Native
Limaria fragilis	Mollusca	Native
Limaria orientalis	Mollusca	Non-native
Limnoria quadripunctata	Arthropoda	Non-native

Lissoclinum cf. roseum	Chordata	Native
Lissodendoryx cf. isodictyalis	Porifera	Native
Lissoporcellana cf. spinuligera	Arthropoda	Native
Lithophaga malaccana	Mollusca	Native
Lithophaga teres	Mollusca	Native
Litocheira bispinosa	Arthropoda	Native
Litozamia peterdi	Mollusca	Native
Littoraria articulata	Mollusca	Native
Littorina acutispira	Mollusca	Native
Lobopelma microscala	Annelida	Native
Lobophora variegata	Ochrophyta	Native
Lobospira bicuspidata	Ochrophyta	Native
Loimia cf. ingens	Annelida	Native
Loimia ingens	Annelida	Native
Lomentaria monochlamydea	Rhodophyta	Native
Lomis hirta	Arthropoda	Native
Longicarpus modestus	Annelida	Native
Lopha cristagalli	Mollusca	Native
Lophurella periclados	Rhodophyta	Native
Lovenella chiquitita	Cnidaria	Native
Lumbrineris cf. coccinea	Annelida	Native
Lumbrineris cf. latreilli	Annelida	Native
Lumbrineris cf. tetraura	Annelida	Native
Lumbrineris coccinea	Annelida	Native
Lumbrineris inflata	Annelida	Native
Lumbrineris latreilli	Annelida	Native
Lumbrineris setosa	Annelida	Native
Lysidice cf. natalensis	Annelida	Native
Lysidice collaris	Annelida	Cryptogenic
Lysidice ninetta	Annelida	Native
Lysilla cf. laciniata	Annelida	Native
Lysilla jennacubinae	Annelida	Native
Lysilla laciniata	Annelida	Native
Macrobrachium intermedium	Arthropoda	Native
Macrocystis angustifolia	Ochrophyta	Native
Macromedaeus cf. distinguendus	Arthropoda	Native
Macrophiothrix cf. variabilis	Echinodermata	Native
Macrorhynchia cf. philippina	Cnidaria	Native
Macrorhynchia philippina	Cnidaria	Native
Macrorhynchia phoenicia	Cnidaria	Native
Macrothamnion cf. secundum	Rhodophyta	Native
Macrothamnion pellucidum	Rhodophyta	Native
Malleus decurtatus	Mollusca	Native
Malleus meridianus	Mollusca	Native

Maoricolpus roseus	Mollusca	Non-native
Margaretta barbata	Bryozoa	Native
Marphysa sanguinea species complex	Annelida	Native
Megabalanus occator	Arthropoda	Non-native
Megabalanus rosa	Arthropoda	Non-native
Megabalanus tintinnabulum	Arthropoda	Non-native
Melita matilda	Arthropoda	Native
Membranipora membranacea	Bryozoa	Cryptogenic
Menaethius monoceros	Arthropoda	Native
Menipea roborata	Bryozoa	Native
Metagoniolithon radiatum	Rhodophyta	Native
Metaprotella cf. haswelliana	Arthropoda	Native
Metavermilia acanthophora	Annelida	Native
Metavermilia cf. acanthophora	Annelida	Native
Microcosmus australis	Chordata	Native
Microcosmus cf. australis	Chordata	Native
Microcosmus cf. squamiger	Chordata	Native
Microcosmus cf. stoloniferus	Chordata	Native
Microcosmus exasperatus	Chordata	Native
Microcosmus helleri	Chordata	Native
Microcosmus pupa	Chordata	Native
Microcosmus squamiger	Chordata	Native
Microcosmus stoloniferus	Chordata	Native
Microporella lunifera	Bryozoa	Native
Mimachlamys asperrima	Mollusca	Native
Mimachlamys australis	Mollusca	Native
Mimachlamys famigerator	Mollusca	Native
Minuspio cirrifera	Annelida	Native
Mitrella cf. eximia	Mollusca	Native
Mitrella cf. lincolnensis	Mollusca	Native
Mitrella lincolnensis	Mollusca	Native
Mitrella semiconvexa	Mollusca	Native
Mitrella tayloriana	Mollusca	Native
Mitrella venulata	Mollusca	Native
Modiolus albicostatus	Mollusca	Native
Modiolus areolatus	Mollusca	Native
Modiolus auriculatus	Mollusca	Native
Modiolus cf. albicostatus	Mollusca	Native
Modiolus cf. areolatus	Mollusca	Native
Modiolus victoriae	Mollusca	Native
Molgula ficus	Chordata	Native
Monia zelandica	Mollusca	Native
Monocorophium acherusicum	Arthropoda	Non-native
Monocorophium insidiosum	Arthropoda	Non-native

Monomyces radiatus	Cnidaria	Native
Monophorus angasi	Mollusca	Native
Monostaechas quadridens	Cnidaria	Native
Monotheca cf. obliqua	Cnidaria	Native
Monotheca compressa	Cnidaria	Native
Monotheca flexuosa	Cnidaria	Native
Monotheca pulchella	Cnidaria	Native
Montfortula rugosa	Mollusca	Native
Mopsella klunzingeri	Cnidaria	Native
Mopsella zimmeri	Cnidaria	Native
Mucropetraliella cf. vultur	Bryozoa	Native
Mucropetraliella ellerii	Bryozoa	Native
Mucropetraliella nodulosa	Bryozoa	Native
Mucropetraliella vultur	Bryozoa	Native
Musculista senhousia	Mollusca	Non-native
Musculus cf. imus	Mollusca	Native
Musculus cf. miranda	Mollusca	Native
Musculus cf. nanus	Mollusca	Native
Musculus chinensis	Mollusca	Native
Musculus cumingianus	Mollusca	Native
Musculus impactus	Mollusca	Native
Musculus nanus	Mollusca	Native
Myriogramme gunniana	Rhodophyta	Native
Myriogramme pulchella	Rhodophyta	Native
Mytilus edulis	Mollusca	Cryptogenic
Mytilus edulis planulatus	Mollusca	Native
Mytilus galloprovincialis	Mollusca	Non-native
Mytilus planulatus	Mollusca	Native
Myxicola infundibulum	Annelida	Non-native
Naineris australis	Annelida	Native
Naineris cf. australis	Annelida	Native
Nannastacus inflatus	Arthropoda	Native
Nassarius burchardi	Mollusca	Native
Nassarius nigellus	Mollusca	Native
Nassarius pauperatus	Mollusca	Native
Nassarius pyrrhus	Mollusca	Native
Naxia tumida	Arthropoda	Native
Neanthes cf. flindersi	Annelida	Native
Neanthes cf. kerguelensis	Annelida	Native
Neanthes cricognatha	Annelida	Native
Neanthes kerguelensis	Annelida	Native
Neanthes uniseriata	Annelida	Native
Neanthes vaalii	Annelida	Native
Nectocarcinus integrifrons	Arthropoda	Native

Nectocarcinus tuberculosus	Arthropoda	Native
Nellia oculata	Bryozoa	Native
Nellia tenella	Bryozoa	Native
Nematonereis unicornis	Annelida	Native
Nematonereis unicornis species complex	Annelida	Native
Neoleprea booligal	Annelida	Native
Neorhynchoplax cf. minima	Arthropoda	Native
Neorhynchoplax octagonalis	Arthropoda	Native
Neovermilia cf. globula	Annelida	Native
Neovermilia globula	Annelida	Native
Nephtys australiensis	Annelida	Native
Nephtys longipes	Annelida	Native
Nereis bifida	Annelida	Native
Nereis cf. denhamensis	Annelida	Native
Nereis cockburnensis	Annelida	Native
Nereis denhamensis	Annelida	Native
Nicolea amnis	Annelida	Native
Nicolea cf. amnis	Annelida	Native
Nizymenia australis	Rhodophyta	Native
Nodilittorina praetermissa	Mollusca	Native
Nolella alta	Bryozoa	Native
Notoacmea flammea	Mollusca	Native
Notoacmea petterdi	Mollusca	Native
Notomastus estuarius	Annelida	Native
Notomastus latericeus	Annelida	Native
Notomithrax cf. ursus	Arthropoda	Native
Notomithrax minor	Arthropoda	Native
Notomithrax ursus	Arthropoda	Native
Notophyllum splendens	Annelida	Native
Notoplax addenda	Mollusca	Native
Notopontonia cf. platycheles	Arthropoda	Native
Nymphon molleri	Arthropoda	Native
Obelia angulosa	Cnidaria	Native
Obelia bicuspidata	Cnidaria	Native
Obelia bispinosa	Cnidaria	Native
Obelia cf. dichotoma	Cnidaria	Native
Obelia cf. geniculata	Cnidaria	Native
Obelia cf. longissima	Cnidaria	Native
Obelia dichotoma	Cnidaria	Non-native
Obelia longissima	Cnidaria	Cryptogenic
Odontosyllis australiensis	Annelida	Native
Odostomia occultidens	Mollusca	Native
Oenone fulgida	Annelida	Non-native
Onchidella cf. patelloides	Mollusca	Native

Onchidella patelloides	Mollusca	Native
Opercularella humilis	Cnidaria	Native
Opheliidae Travisia	Annelida	Native
Ophiacantha heterotyla	Echinodermata	Native
Ophiacantha pica	Echinodermata	Native
Ophiactis cf. resiliens	Echinodermata	Native
Ophiactis cf. savignyi	Echinodermata	Native
Ophiactis macrolepidota	Echinodermata	Native
Ophiactis resiliens	Echinodermata	Native
Ophiactis savignyi	Echinodermata	Native
Ophiocentrus pilosa	Echinodermata	Native
Ophiocentrus verticillata	Echinodermata	Native
Ophiodissa carchesium	Cnidaria	Native
Ophiomyxa australis	Echinodermata	Native
Ophiothrix caespitosa	Echinodermata	Native
Ophiothrix martensi	Echinodermata	Native
Ophiothrix spongicola	Echinodermata	Native
Ophiothrix vicina	Echinodermata	Native
Orthopyxis caliculata	Cnidaria	Native
Orthopyxis integra	Cnidaria	Native
Orthopyxis mollis	Cnidaria	Native
Ostrea angasi	Mollusca	Native
Oulactis muscosa	Cnidaria	Non-native
Oxynoe viridis	Mollusca	Native
Pachycheles sculptus	Arthropoda	Native
Padina elegans	Ochrophyta	Native
Padina sanctae-crucis	Ochrophyta	Native
Pagurus cf. hirtimanus	Arthropoda	Native
Palaemon cf. serenus	Arthropoda	Native
Palaemon serenus	Arthropoda	Native
Palaemonella cf. rotumana	Arthropoda	Native
Palaemonella rotumana	Arthropoda	Native
Paleanotus chrysolepis	Annelida	Native
Palola cf. siciliensis	Annelida	Native
Palola siciliensis	Annelida	Native
Paphies striata	Mollusca	Native
Parablennius tasmanianus	Chordata	Native
Paracalix ambiplica	Cnidaria	Native
Paracerceis sculpta	Arthropoda	Non-native
Paracilicaea gigas	Arthropoda	Native
Paracilicaea septemdentata	Arthropoda	Native
Paradella dianae	Arthropoda	Non-native
Paradella octaphymata	Arthropoda	Native
Paradexamine churinga	Arthropoda	Native

Paradexamine moorhousei	Arthropoda	Native
Paragrapsus gaimardii	Arthropoda	Native
Paragrapsus quadridentatus	Arthropoda	Native
Parahyotissa imbricata	Mollusca	Native
Parahyotissa numisma	Mollusca	Native
Paralepidonotus ampulliferus	Annelida	Native
Paraleucothoe novaehollandiae	Arthropoda	Native
Paranchialina angusta	Arthropoda	Native
Parascyphus simplex	Cnidaria	Native
Parasmittina cf. cheilodon	Bryozoa	Native
Parasmittina cf. delicatula	Bryozoa	Native
Paratanais ignotus	Arthropoda	Native
Parawaldeckia dilkera	Arthropoda	Native
Parawaldeckia yamba	Arthropoda	Native
Paridotea ungulata	Arthropoda	Native
Parthenope cf. longispinus	Arthropoda	Native
Patelloida insignis	Mollusca	Native
Patelloida mufria	Mollusca	Native
Patiriella brevispina	Chordata	Native
Patiriella regularis	Chordata	Non-native
Pecten fumatus	Mollusca	Native
Pennaria disticha	Cnidaria	Non-native
Pennaria wilsoni	Cnidaria	Native
Periclimenes andamanensis	Arthropoda	Native
Periclimenes cf. andamanensis	Arthropoda	Native
Periclimenes cf. elegans	Arthropoda	Native
Periclimenes grandis	Arthropoda	Native
Periclimenes obscurus	Arthropoda	Native
Perinereis amblyodonta	Annelida	Native
Perinereis nigropunctata	Annelida	Native
Perinereis variodentata	Annelida	Native
Perithallia caudata	Ochrophyta	Native
Petrolisthes elongatus	Arthropoda	Non-native
Petrolisthes militaris	Arthropoda	Native
Peyssonnelia capensis	Rhodophyta	Native
Peyssonnelia cf. capensis	Rhodophyta	Native
Phallusia arabica	Chordata	Native
Phallusia barbarica	Chordata	Native
Phallusia julinea	Chordata	Native
Phallusia obesa	Chordata	Native
Phascolosoma annulatum	Sipuncula	Native
Phascolosoma stephensoni	Sipuncula	Native
Phasianella variegata	Mollusca	Native
Phasianotrochus irisodontes	Mollusca	Native

Pherusa cf. parmata	Annelida	Native
Pherusa parmata	Annelida	Native
Phialella quadrata	Cnidaria	Non-native
Philippia lutea	Mollusca	Native
Phlyctenanthus australis	Cnidaria	Native
Phycodrys australasica	Rhodophyta	Native
Phyllamphicteis cf. foliata	Annelida	Native
Phyllodoce novaehollandiae	Annelida	Native
Pileolaria cf. roseopigmentata	Annelida	Native
Pilodius miersi	Arthropoda	Native
Pilumnopeus cf. serratifrons	Arthropoda	Native
Pilumnopeus serratifrons	Arthropoda	Non-native
Pilumnus acer	Arthropoda	Native
Pilumnus cf. australis	Arthropoda	Native
Pilumnus cf. longicornis	Arthropoda	Native
Pilumnus cf. minutus	Arthropoda	Non-native
Pilumnus cf. rufopunctatus	Arthropoda	Native
Pilumnus cf. tomentosus	Arthropoda	Native
Pilumnus etheridgei	Arthropoda	Native
Pilumnus fissifrons	Arthropoda	Native
Pilumnus longicornis	Arthropoda	Native
Pilumnus minutus	Arthropoda	Non-native
Pilumnus monilifer	Arthropoda	Native
Pilumnus semilanatus	Arthropoda	Native
Pilumnus terraereginae	Arthropoda	Native
Pilumnus tomentosus	Arthropoda	Native
Pinctada albina	Mollusca	Native
Pinctada cf. sugillata	Mollusca	Native
Pinctada maculata	Mollusca	Native
Pinctada margaritifera	Mollusca	Native
Pinctada sugillata	Mollusca	Native
Pinna bicolor	Mollusca	Native
Pinnotheres hickmani	Arthropoda	Native
Pisidia dispar	Arthropoda	Native
Pisidia gordoni	Arthropoda	Native
Pista australis	Annelida	Native
Pista cf. brevibranchia	Annelida	Native
Pista trunca	Annelida	Native
Pista typha	Annelida	Native
Pistorius bidens	Arthropoda	Native
Plagusia chabrus	Arthropoda	Non-native
Plagusia glabra	Arthropoda	Native
Planopilumnus penicillatus	Arthropoda	Native
Planostrea pestigris	Mollusca	Native

Platynereis antipoda	Annelida	Native
Platynereis polyscalma	Annelida	Native
Platysiphonia delicata	Rhodophyta	Non-native
Platythalia quercifolia	Ochrophyta	Native
Plaxiphora albida	Mollusca	Native
Plaxiphora matthewsi	Mollusca	Native
Plesiocolochirus ignava	Echinodermata	Native
Pleurobranchaea maculata	Mollusca	Native
Plocamium angustum	Rhodophyta	Native
Plumularia branchiata	Cnidaria	Native
Plumularia caliculata	Cnidaria	Native
Plumularia cf. setacea	Cnidaria	Non-native
Plumularia setacea	Cnidaria	Non-native
Plumularia setaceoides	Cnidaria	Native
Podarke angustifrons	Annelida	Native
Podarkeopsis galangaui	Annelida	Native
Polyandrocarpa australiensis	Chordata	Native
Polyandrocarpa sagamiensis	Chordata	Non-native
Polycarpa aurita	Chordata	Native
Polycarpa biforis	Chordata	Native
Polycarpa cf. obscura	Chordata	Native
Polycarpa cf. olitoria	Chordata	Native
Polycarpa cf. pedunculata	Chordata	Native
Polycarpa contecta	Chordata	Native
Polycarpa nigricans	Chordata	Native
Polycarpa obscura	Chordata	Native
Polycarpa olitoria	Chordata	Native
Polycarpa papillata	Chordata	Native
Polycarpa pedunculata	Chordata	Native
Polycarpa pigmentata	Chordata	Native
Polycarpa stirpes	Chordata	Native
Polycarpa viridis	Chordata	Native
Polycirrus boholensis	Annelida	Native
Polydora cornuta	Annelida	Non-native
Polydora hoplura	Annelida	Cryptogenic
Polydora protuberata	Annelida	Native
Polyonyx cf. obesulus	Arthropoda	Native
Polyonyx obesulus	Arthropoda	Native
Polyophthalmus cf. pictus	Annelida	Native
Polyophthalmus pictus	Annelida	Native
Polysiphonia blandii	Rhodophyta	Non-native
Polysiphonia brodiei	Rhodophyta	Non-native
Polysiphonia cf. infestans	Rhodophyta	Native
Polysiphonia cf. subtilissima	Rhodophyta	Native

Polysiphonia crassiuscula	Rhodophyta	Native
Polysiphonia decipiens	Rhodophyta	Native
Polysiphonia ferulacea	Rhodophyta	Native
Polysiphonia infestans	Rhodophyta	Cryptogenic
Polysiphonia scopulorum	Rhodophyta	Native
Polysiphonia senticulosa	Rhodophyta	Non-native
Polysiphonia subtilissima	Rhodophyta	Non-native
Polysyncraton cf. millepore	Chordata	Native
Polysyncraton rugosum	Chordata	Native
Pomatoceros taeniata	Annelida	Native
Pomatoleios kraussii	Annelida	Native
Pomatostegus stellatus	Annelida	Native
Poricellaria ratoniensis	Bryozoa	Native
Porina tubulifera	Bryozoa	Native
Portunus pelagicus	Arthropoda	Native
Potamilla cf. laciniosa	Annelida	Native
Potamilla laciniosa	Annelida	Native
Potamilla neglecta	Annelida	Native
Pretostrea rosacea	Mollusca	Native
Priolepis nuchifasciata	Chordata	Native
Prionospio multipinnulata	Annelida	Native
Proceraea filiformis	Annelida	Native
Proterato lachryma	Mollusca	Native
Protocirrineris chrysoderma	Annelida	Native
Protula cf. palliata	Annelida	Native
Pseudoamphicteis papillosa	Annelida	Native
Pseudobranchiomma cf. orientalis	Annelida	Native
Pseudobranchiomma orientalis	Annelida	Native
Pseudocerceis furculata	Arthropoda	Native
Pseudocerceis trilobata	Arthropoda	Native
Pseudoceros reticularis	Platyhelminthes	Native
Pseudonereis anomala	Annelida	Native
Pseudopolydora cf. kempi	Annelida	Native
Pseudopolydora kempi	Annelida	Cryptogenic
Pseudopotamilla cf. laciniosa	Annelida	Native
Pseudopotamilla laciniosa	Annelida	Native
Pseudopotamilla reniformis	Annelida	Native
Pseudoproclea australis	Annelida	Native
Pteria cf. coturnix	Mollusca	Native
Pterocirrus cf. magalhaensis	Annelida	Native
Pterocladia rectangularis	Rhodophyta	Native
Pterosiphonia pennata	Rhodophyta	Native
Pustulostrea cf. tuberculata	Mollusca	Native
Pustulostrea tuberculata	Mollusca	Native

Pyrene bidentata	Mollusca	Native
Pyrene scripta	Mollusca	Native
Pyrene testudinaria	Mollusca	Native
Pyura australis	Chordata	Native
Pyura cf. robusta	Chordata	Native
Pyura cf. stolonifera	Chordata	Native
Pyura confragosa	Chordata	Native
Pyura elongata	Chordata	Native
Pyura fissa	Chordata	Native
Pyura gibbosa draschii	Chordata	Native
Pyura gibbosa	Chordata	Native
Pyura irregularis	Chordata	Native
Pyura molguloides	Chordata	Native
Pyura robusta	Chordata	Native
Pyura sacciformis	Chordata	Native
Pyura stolonifera	Chordata	Native
Pyura tasmanensis	Chordata	Native
Redigobius macrostoma	Chordata	Native
Reteporella fissa	Bryozoa	Native
Reteporella subimmersa "Fossil"	Bryozoa	Native
Rhabdozoum wilsoni	Bryozoa	Native
Rhinothelepus lobatus	Annelida	Native
Rhodoglossum gigartinoides	Rhodophyta	Native
Rhodosoma turcicum	Chordata	Native
Rhodymenia cf. sonderi	Rhodophyta	Native
Rhodymenia leptophylla	Rhodophyta	Native
Rhodymenia sonderi	Rhodophyta	Native
Rhynchozoon cf. splendens	Bryozoa	Native
Ruditapes largillierti	Mollusca	Non-native
Sabella cf. spallanzanii	Annelida	Native
Sabella spallanzanii	Annelida	Non-native
Sabellate australiensis	Annelida	Native
Sabellate cf. indica	Annelida	Native
Sabellate cf. spectabilis	Annelida	Native
Sabellate indica	Annelida	Native
Saccostrea cucullata	Mollusca	Native
Saccostrea echinata	Mollusca	Native
Saccostrea glomerata	Mollusca	Native
Salmacina australis	Annelida	Native
Salmacis belli	Echinodermata	Native
Salmacis cf. belli	Echinodermata	Native
Sarsia cf. eximia	Cnidaria	Native
Sarsia cf. radiata	Cnidaria	Native
Sarsia eximia	Cnidaria	Cryptogenic

Sarsia radiata	Cnidaria	Native
Sassia subdistorta	Mollusca	Native
Savignyella lafontii	Bryozoa	Cryptogenic
Scaeochlamys livida	Mollusca	Native
Schistomeringos loveni	Annelida	Native
Schizophrys aspera	Arthropoda	Native
Schizoporella errata	Bryozoa	Non-native
Schizoporella unicornis	Bryozoa	Non-native
Schottera nicaeensis	Rhodophyta	Non-native
Scoloplos cf. novaehollandiae	Annelida	Native
Scoloplos cylindrifer	Annelida	Native
Scoloplos normalis	Annelida	Native
Scoloplos simplex	Annelida	Native
Scruparia ambigua	Bryozoa	Non-native
Scrupocellaria cf. diadema	Bryozoa	Native
Scrupocellaria cf. maderensis	Bryozoa	Native
Scrupocellaria cf. spatulata	Bryozoa	Native
Scrupocellaria ornithorhynchus	Bryozoa	Native
Scyllarides haanii	Arthropoda	Native
Septifer bilocularis	Mollusca	Native
Septifer cf. bilocularis	Mollusca	Native
Serpula cf. jukesii	Annelida	Native
Serpula cf. rubens	Annelida	Native
Serpula cf. vittata	Annelida	Native
Serpula cf. watsoni	Annelida	Native
Serpula jukesii	Annelida	Native
Serpula rubens	Annelida	Native
Sertularella cf. robusta	Cnidaria	Native
Sertularella diaphana	Cnidaria	Native
Sertularella robusta	Cnidaria	Native
Sertularella simplex	Cnidaria	Native
Sertularella tricuspidata	Cnidaria	Native
Sertularia cf. longa	Cnidaria	Native
Sertularia ligulata	Cnidaria	Native
Sertularia orthogonalis	Cnidaria	Cryptogenic
Sertularia stechowi	Cnidaria	Native
Sertularia tenuis	Cnidaria	Native
Sidneioides cf. tamaramae	Chordata	Native
Sinum cf. zonale	Mollusca	Native
Siphonaria diemenensis	Mollusca	Native
Siphonaria funiculata	Mollusca	Native
Siphonaria zelandica	Mollusca	Native
Smittoidea maunganuiensis	Bryozoa	Native
Sphacelaria cf. cirrosa	Ochrophyta	Native

Sphaeroma quoyanum	Arthropoda	Native
Sphaeroma sculpta	Arthropoda	Native
Sphaeroma walkeri	Arthropoda	Non-native
Spirobranchus cf. polytrema	Annelida	Native
Spirobranchus cf. tetraceros	Annelida	Native
Spirobranchus coronatus	Annelida	Native
Spirobranchus tetraceros	Annelida	Native
Spondylus nicobaricus	Mollusca	Native
Spondylus violascens	Mollusca	Native
Sporochnus comosus	Ochrophyta	Native
Spyridia dasyoides	Rhodophyta	Native
Spyridia filamentosa	Rhodophyta	Native
Stavelia cf. subdistorta	Mollusca	Native
Stavelia subdistorta	Mollusca	Native
Stelletta cf. clavosa	Porifera	Native
Stenothoe cf. marina	Arthropoda	Native
Stenothoe miersi	Arthropoda	Native
Stenothoe valida	Arthropoda	Cryptogenic
Stephanollona orbicularis	Bryozoa	Native
Stereotheca elongata	Cnidaria	Native
Sthenelais pettiboneae	Annelida	Native
Stichopus mollis	Echinodermata	Native
Stictosiphonia intricata	Rhodophyta	Native
Stimdromia lateralis	Arthropoda	Native
Stolonica australis	Chordata	Native
Stomatella impertusa	Mollusca	Native
Streblosoma acymatum	Annelida	Native
Streblosoma cf. atos	Annelida	Native
Streblosoma cf. latitudinum	Annelida	Native
Streblosoma latitudinum	Annelida	Native
Striatobalanus amaryllis	Arthropoda	Native
Striatobalanus cf. amaryllis	Arthropoda	Native
Striostrea cf. mytiloides	Mollusca	Native
Striostrea mytiloides	Mollusca	Native
Strombiformis topaziaca	Mollusca	Native
Styela canopus	Chordata	Non-native
Styela clava	Chordata	Non-native
Styela plicata	Chordata	Non-native
Stylactis betkensis	Cnidaria	Native
Stylomma palmatum	Annelida	Native
Stylopallene cheilorhynchus	Arthropoda	Native
Subadyte pellucida	Annelida	Native
Suberites cupuloides	Porifera	Native
Sycozoa brevicauda	Chordata	Native

Sycozoa cerebriformis	Chordata	Native
Syllidia armata	Annelida	Native
Syllis australiensis	Annelida	Native
Syllis gracilis australiensis	Annelida	Native
Syllis gracilis	Annelida	Non-native
Symplectoscyphus indivisus	Cnidaria	Native
Synalpheus cf. bituberculatus	Arthropoda	Native
Synalpheus cf. neptunus	Arthropoda	Native
Synalpheus cf. streptodactylus	Arthropoda	Native
Synalpheus cf. tumidomanus	Arthropoda	Native
Synalpheus hastilicrassus	Arthropoda	Native
Synalpheus neomeris	Arthropoda	Native
Synalpheus neptunus	Arthropoda	Native
Synalpheus streptodactylus	Arthropoda	Native
Synalpheus tumidomanus	Arthropoda	Native
Synnotum aegyptiacum	Bryozoa	Native
Synnotum cf. aegyptiacum	Bryozoa	Native
Synnotum cf. pembaense	Bryozoa	Native
SypharoMollusca pellisserpentis	Mollusca	Native
Tanais cf. dulongi	Arthropoda	Native
Tellina albinella	Mollusca	Native
Tellina botanica	Mollusca	Native
Tellina cf. tenuilamellata	Mollusca	Native
Tellina parvitas	Mollusca	Native
Temnopleurus michaelseni	Echinodermata	Native
Terebella cf. ehrenbergi	Annelida	Native
Terebella tantabiddycreekensis	Annelida	Native
Tesseropora cf. wireni	Arthropoda	Non-native
Tesseropora rosea	Arthropoda	Native
Tethya communis	Porifera	Native
Tetraclita coerulescens	Arthropoda	Native
Tetraclita squamosa	Arthropoda	Native
Tetraclitella purpurascens	Arthropoda	Native
Thais echinata	Mollusca	Native
Thais orbita	Mollusca	Native
Thalamita cf. spinimana	Arthropoda	Native
Thalamita danae	Arthropoda	Native
Thalamoporella gothica	Bryozoa	Non-native
Thamnoclonium dichotomum	Rhodophyta	Native
Thelepus alatus	Annelida	Native
Thelepus australiensis	Annelida	Native
Thelepus cf. alatus	Annelida	Native
Thelepus cf. boja	Annelida	Native
Thelepus cf. extensus	Annelida	Native

Thelepus extensus	Annelida	Native
Thelepus robustus	Annelida	Native
Themiste cf. fusca	Sipuncula	Native
Theora cf. lubrica I_Mollusca	Mollusca	Non-native
Theora lubrica I_Mollusca	Mollusca	Non-native
Thor amboinensis	Arthropoda	Native
Thor paschalis	Arthropoda	Native
Thormora argus	Annelida	Native
Thormora jukesii	Annelida	Native
Thusaenys irami	Arthropoda	Native
Timoclea cardioides	Mollusca	Native
Tosia australis	Chordata	Native
Trachinops caudimaculatus	Chordata	Native
Tricellaria aculeata	Bryozoa	Native
Tricellaria cf. inopinata	Bryozoa	Non-native
Tricellaria inopinata	Bryozoa	Cryptogenic
Tricellaria occidentalis	Bryozoa	Non-native
Tricellaria porteri	Bryozoa	Cryptogenic
Trichomusculus barbatus	Mollusca	Native
Trichomusculus cf. barbatus	Mollusca	Native
Trichomya hirsutus	Mollusca	Native
Tricolia tomlini	Mollusca	Native
Tridentiger trigonocephalus	Chordata	Non-native
Trinorfolkia clarkei N_bony Chordata	Chordata	Native
Triphyllozoon cf. moniliferum	Bryozoa	Native
Triphyllozoon moniliferum	Bryozoa	Native
Triphyllozoon munitum	Bryozoa	Native
Trypanosyllis gigantea	Annelida	Native
Trypanosyllis taeniformis	Annelida	Native
Trypostega venusta	Bryozoa	Native
Tubastrea coccinea	Stony Cnidaria	Native
Tubastrea diaphana	Stony Cnidaria	Native
Tubastrea micranthus	Stony Cnidaria	Native
Tubularia cf. crocea	Cnidaria	Non-native
Tubularia crocea	Cnidaria	Non-native
Tubulipora cf. maragitacea "Fossil"	Bryozoa	Native
Tugali cicatricosa	Mollusca	Native
Tugali parmophoidea	Mollusca	Native
Turritopsis cf. nutricula	Cnidaria	Native
Turritopsis nutricula	Cnidaria	Non-native
Typosyllis armillaris	Annelida	Native
Typosyllis cervantensis	Annelida	Native
Typosyllis cf. armillaris	Annelida	Native
Typosyllis cf. cervantensis	Annelida	Native

Typosyllis cf. crassicirrata	Annelida	Native
Typosyllis cf. gerhardi	Annelida	Native
Typosyllis hyalina	Annelida	Native
Typosyllis lutea	Annelida	Native
Typosyllis pseudopapillata	Annelida	Native
Typosyllis raygeorgei	Annelida	Native
Ulva australis	Chlorophyta	Native
Ulva lactuca	Chlorophyta	Cryptogenic
Ulva laetevirens	Chlorophyta	Native
Ulva rigida	Chlorophyta	Cryptogenic
Ulva stenophylla	Chlorophyta	Non-native
Undaria pinnatifida	Ochrophyta	Non-native
Uniophora dyscrita	Chordata	Native
Uniophora granifera	Chordata	Native
Venerupis anomala	Mollusca	Native
Venerupis cf. anomala	Mollusca	Native
Venerupis galactites	Mollusca	Native
Venerupis iridescens	Mollusca	Native
Vermiliopsis cf. infundibilum	Annelida	Native
Vulsella spongiarum	Mollusca	Native
Vulsella vulsella	Mollusca	Native
Wallucina assimilis	Mollusca	Native
Watersipora arcuata	Bryozoa	Non-native
Watersipora subtorquata	Bryozoa	Non-native
Xenostrobus cf. inconstans	Mollusca	Native
Xenostrobus cf. pulex	Mollusca	Native
Xenostrobus inconstans	Mollusca	Native
Xenostrobus pulex	Mollusca	Native
Xenostrobus securis	Mollusca	Native
Yoldia lata	Mollusca	Native
Zonaria crenata	Ochrophyta	Native
Zonaria turneriana	Ochrophyta	Native
Zoobotryon verticillatum	Bryozoa	Non-native
Zuzara venosa	Arthropoda	Native
Zygometra cf. microdiscus	Echinodermata	Native

Table A3. Species identified in the 15 port surveys around New Zealand and species status – native, non-native and cryptogenic species.

Species	Phyla	Species status
Acanthochitona violacea	Mollusca	Native
Acanthochitona zelandica	Mollusca	Native
Acanthoclinus fuscus	Chordata	Native
Acanthoclinus littoreus	Chordata	Native
Achelia assimilis	Arthropoda	Native
Acontiostoma tuberculata	Arthropoda	Native
Acraspedanthus elongatus	Echinodermata	Native
Acrocirrus trisectus	Annelida	Native
Acrosorium decumbens	Rhodophyta	Native
Adamsiella chauvinii	Rhodophyta	Native
Adocia cf.parietalioides	Porifera	Native
Adocia cf.venustina	Porifera	Native
Aetea australis	Bryozoa	Cryptogenic
Aetea truncata	Bryozoa	Native
Aiptasiomorpha minima	Echinodermata	Native
Alloiodoris lanuginata	Mollusca	Native
Allostichaster insignis	Chordata	Native
Allostichaster polyplax	Chordata	Native
Alpheus novaezealandiae	Arthropoda	Native
Alpheus socialis	Arthropoda	Native
Amaryllis macrophthalma	Arthropoda	Native
Amphilochus filidactylus	Arthropoda	Native
Amphipholis squamata	Echinodermata	Native
Amphisbetia bispinosa	Hydroid	Native
Amphisbetia fasciculata	Hydroid	Native
Amphisbetia minima	Hydroid	Native
Anguinella palmata	Bryozoa	Non-native
Anisoiphimedia haurakiensis	Arthropoda	Native
Anotrichium crinitum	Rhodophyta	Native
Antithamnion applicitum	Rhodophyta	Native
Antithamnion pectinatum	Rhodophyta	Native
Antithamnionella adnata	Rhodophyta	Native
Aora maculata	Arthropoda	Native
Aora typica	Arthropoda	Native
Aplidium adamsi	Chordata	Native
Aplidium benhami	Chordata	Native
Aplidium knoxi	Chordata	Native
Aplidium phortax	Chordata	Cryptogenic
Apocorophium acutum	Arthropoda	Non-native
Apoglossum montagneanum	Rhodophyta	Native

Apoglossum oppositifolium	Rhodophyta	Native
Archidoris nanula	Mollusca	Native
Archidoris wellingtonensis	Mollusca	Native
Armandia maculata	Annelida	Native
Ascidiella aspersa	Chordata	Non-native
Asteracmea suteri	Mollusca	Native
Asterocarpa cerea	Chordata	Cryptogenic
Asterocarpa coerulea	Chordata	Native
Aulacomya atra maoriana	Mollusca	Native
Austrolittorina antipodum	Mollusca	Native
Austrominius modestus	Arthropoda	Native
Balanus trigonus	Arthropoda	Cryptogenic
Beania discodermiae	Bryozoa	Native
Beania magellanica	Bryozoa	Native
Beania plurispinosa	Bryozoa	Native
Betaeopsis aequimanus	Arthropoda	Native
Bicellariella ciliata	Bryozoa	Native
Biemna rhabderemioides	Porifera	Native
Bitectipora mucronifera	Bryozoa	Native
Bitectipora rostrata	Bryozoa	Native
Boccardia acus	Annelida	Native
Boccardia chilensis	Annelida	Native
Boccardia knoxi	Annelida	Native
Boccardia lamellata	Annelida	Native
Boccardia otakouica	Annelida	Native
Boccardia syrtis	Annelida	Native
Borniola reniformis	Mollusca	Native
Bostrychia harveyi	Rhodophyta	Native
Bostrychia moritziana	Rhodophyta	Native
Bostrychia tenuissima	Rhodophyta	Native
Botrylliodes leachii	Chordata	Cryptogenic
Botryllus stewartensis	Chordata	Native
Bougainvillia muscus	Hydroid	Cryptogenic
Branchiomma curta	Annelida	Native
Brongniartella australis	Rhodophyta	Native
Bryopsis vestita	Chlorophyta	Native
Buccinulum linea	Mollusca	Native
Buccinulum vittatum	Mollusca	Native
Bugula dentata	Bryozoa	Native
Bugula flabellata	Bryozoa	Non-native
Bugula neritina	Bryozoa	Non-native
Bugula stolonifera	Bryozoa	Non-native
Caberea rostrata	Bryozoa	Native
Caberea zelandica	Bryozoa	Native

Cabestana spengleri	Mollusca	Native
Cadlina willani	Mollusca	Native
Calliostoma tigris	Mollusca	Native
Callipallene novaezealandiae	Arthropoda	Native
Callophyllis calliblepharoides	Rhodophyta	Native
Callophyllis variegata	Rhodophyta	Native
Callyspongia cf. bathami	Porifera	Native
Callyspongia cf.irregularis	Porifera	Native
Callyspongia diffusa	Porifera	Cryptogenic
Callyspongia ramosa	Porifera	Cryptogenic
Callyspongia stellata	Porifera	Native
Caloglossa leprieurii	Rhodophyta	Native
Cancer amphioetus	Arthropoda	Non-native
Cancer gibbosulus	Arthropoda	Non-native
Cancer novaezelandiae	Arthropoda	Native
Caprella equilibra	Arthropoda	Native
Caprella mutica	Arthropoda	Non-native
Caprellina longicollis	Arthropoda	Native
Capreolia implexa	Rhodophyta	Native
Carazziella quadricirrata	Annelida	Native
Carpophyllum flexuosum	Ochrophyta	Native
Caulerpa brownii	Chlorophyta	Native
Cellana ornata	Mollusca	Native
Cellaria tenuirostris	Bryozoa	Native
Celleporaria nodulosa	Bryozoa	Non-native
Celleporella delta	Bryozoa	Native
Celleporella tongima	Bryozoa	Native
Celleporina proximalis	Bryozoa	Native
Ceradocopsis carnleyi	Arthropoda	Native
Ceramium aff. Apiculatum	Rhodophyta	Native
Ceramium apiculatum	Rhodophyta	Native
Ceramium flaccidum	Rhodophyta	Native
Ceramium rubrum	Rhodophyta	Native
Ceramium vestitum	Rhodophyta	Native
Chaemosipho columna	Arthropoda	Native
Chaperia granulosa	Bryozoa	Native
Chaperiopsis cervicornis	Bryozoa	Native
Chelonaplysilla cf.violacea	Porifera	Cryptogenic
Chiastosella watersi	Bryozoa	Native
Chondracanthus chapmanii	Rhodophyta	Native
Chondropsis topsentii	Porifera	Non-native
Chromodoris aureomarginata	Mollusca	Native
Cilicaea canaliculata	Arthropoda	Native
Ciona intestinalis	Chordata	Non-native

Cirolana kokoru	Arthropoda	Native
Cirolana quechso	Arthropoda	Native
Cladophora feredayi	Chlorophyta	Native
Cladophoropsis herpestica	Chlorophyta	Native
Cladostephus spongiosus	Ochrophyta	Native
Clathria (Isociella) cf. incrustans	Porifera	Native
Clathria (Microciona) dendyi	Porifera	Native
Clathria (Microciona)coccinea	Porifera	Native
Clathria cf.lissosclera	Porifera	Native
Clathria cf.terraenovae	Porifera	Native
Clavisyllis alternata	Annelida	Native
Cleantis tubicola	Arthropoda	Native
Cliona celata	Porifera	Non-native
Clytia elongata	Hydroid	Native
Clytia hemisphaerica	Hydroid	Cryptogenic
Cnemidocarpa bicornuta	Chordata	Native
Cnemidocarpa nisiotus	Chordata	Native
Cnemidocarpa otagoensis	Chordata	Native
Cnemidocarpa regalis	Chordata	Native
Colomastix magnirama	Arthropoda	Native
Colomastix subcastellata	Arthropoda	Native
Cominella glandiformis	Mollusca	Native
Cominella quoyana	Mollusca	Native
Conopeum seurati	Bryozoa	Non-native
Cookia sulcata	Mollusca	Native
Coralline (Melobesia)	Rhodophyta	Cryptogenic
Corella eumyota	Chordata	Cryptogenic
Corynactis australis	Echinodermata	Cryptogenic
Coscinasterias muricata	Chordata	Native
Crassicorophium bonnellii	Arthropoda	Non-native
Crassimarginatella fossa	Bryozoa	Native
Crassostrea gigas	Mollusca	Non-native
Crella (Pytheas) incrustans	Porifera	Cryptogenic
Crella (Pytheas)affinis	Porifera	Native
Crepidacantha crinispina	Bryozoa	Native
Crisia tenuis	Bryozoa	Native
Cryptogenicconchus porosus	Mollusca	Native
Cryptogenicsula pallasiana	Bryozoa	Non-native
Cutleria multifida	Ochrophyta	Non-native
Cyclicopora longipora	Bryozoa	Non-native
Dasya collabens	Rhodophyta	Native
Dasya subtilis	Rhodophyta	Native
Delesserian epiphytes	Rhodophyta	Native
Dellichthys morelandi	Chordata	Native

Demonax aberrans	Annelida	Native
Dendrodoris citrina	Mollusca	Native
Desmacella ambigua	Porifera	Native
Desmarestia ligulata	Ochrophyta	Native
Diadumene neozelandica	Echinodermata	Native
Dicithais orbita	Mollusca	Native
Dictyociona cf.atoxa C2_Porifera	Porifera	Cryptogenic
Dictyodendrilla dendyi	Porifera	Native
Dictyota dichotoma	Ochrophyta	Native
Didemnum incanum	Chordata	Cryptogenic
Didemnum vexillum	Chordata	Cryptogenic
Diplosoma listerianum	Chordata	Cryptogenic
Dipolydora armata	Annelida	Non-native
Dipolydora flava	Annelida	Non-native
Dodecaceria berkeleyi	Annelida	Native
Dorvillea australiensis	Annelida	Native
Dromia wilsoni	Arthropoda	Cryptogenic
Ecklonia radiata	Ochrophyta	Native
Electra tenella	Bryozoa	Non-native
Endarachne binghamiae	Ochrophyta	Native
Epopella plicata	Arthropoda	Native
Ericthonius pugnax	Arthropoda	Non-native
Erythroglossum undulatissimum	Rhodophyta	Native
Escharoides angela	Bryozoa	Native
Escharoides excavata	Bryozoa	Native
Eudendrium capillare	Hydroid	Non-native
Eudendrium generale	Hydroid	Non-native
Eulalia bilineata	Annelida	Cryptogenic
Eulalia capensis	Annelida	Native
Eulalia microphylla	Annelida	Native
Eunice australis	Annelida	Native
Euplacella communis	Porifera	Cryptogenic
Euryspongia cf. arenaria	Porifera	Native
Eurystomella foraminigera	Bryozoa	Native
Eusiroides monoculoides	Arthropoda	Native
Ficopomatus enigmaticus	Annelida	Non-native
Filellum serpens	Hydroid	Non-native
Filograna implexa	Annelida	Native
Flabelligera affinis	Annelida	Native
Forsterygion lapillum	Chordata	Native
Galeolaria hystrix	Annelida	Native
Galeopsis porcellanicus	Bryozoa	Native
Gammaropsis chiltoni	Arthropoda	Native
Gammaropsis dentifera	Arthropoda	Native

Gammaropsis haswelli	Arthropoda	Native
Gammaropsis longimana	Arthropoda	Native
Gammaropsis typica	Arthropoda	Native
Gigartina atropurpurea	Rhodophyta	Native
Gloiocladia saccata	Rhodophyta	Native
Glossophora kunthii	Ochrophyta	Native
Glycera benhami	Annelida	Native
Gondogeneia danai	Arthropoda	Native
Gracilaria truncata	Rhodophyta	Native
Grahamina capito	Chordata	Native
Grahamina gymnota	Chordata	Native
Grantessa intusarticulata	Porifera	Non-native
Griffithsia antarctica	Rhodophyta	Native
Griffithsia crassiuscula	Rhodophyta	Non-native
Griffithsia teges	Rhodophyta	Cryptogenic
Halecium corrrugatissimum	Hydroid	Native
Halecium sessile	Hydroid	Cryptogenic
Halicarcinus cookii	Arthropoda	Native
Halicarcinus innominatus	Arthropoda	Native
Halicarcinus tongi	Arthropoda	Native
Halicarcinus varius	Arthropoda	Native
Halicarcinus whitei	Arthropoda	Native
Halichondria panicea	Porifera	Cryptogenic
Haliclona cf.isodictyale	Porifera	Native
Haliclona cf.punctata	Porifera	Native
Haliclona cf.tenacior	Porifera	Native
Haliclona glabra	Porifera	Native
Haliclona heterofibrosa	Porifera	Cryptogenic
Haliclona maxima	Porifera	Native
Haliclona stelliderma	Porifera	Native
Halimena aoteoroa	Arthropoda	Native
Haliplanella lineata	Echinodermata	Non-native
Halisarca dujardini	Porifera	Non-native
Haplocheira barbimana	Arthropoda	Native
Haplosyllis spongicola	Annelida	Native
Harmothoe macrolepidota	Annelida	Native
Hebellopsis scandens	Hydroid	Native
Helice crassa	Arthropoda	Native
Heterosiphonia concinna	Rhodophyta	Native
Heterosiphonia squarrosa	Rhodophyta	Native
Hiatella arctica	Mollusca	Native
Hincksia mitchelliae	Ochrophyta	Native
Hippolyte bifidirostris	Arthropoda	Native
Hippolyte multicolorata	Arthropoda	Native

Homaxinella erecta	Porifera	Native
Hyale rubra	Arthropoda	Native
Hyboscolex longiseta	Annelida	Native
Hydroides elegans	Annelida	Non-native
Hydroides ezoensis	Annelida	Non-native
Hymenena curdieana	Rhodophyta	Cryptogenic
Hymenena variolosa	Rhodophyta	Native
Hymeniacidon perleve	Porifera	Cryptogenic
Hymenosoma depressum	Arthropoda	Native
Hypsistozoa fasmeriana	Chordata	Native
Iophon proximum	Porifera	Cryptogenic
Ircinia akaroa	Porifera	Native
Irus reflexus	Mollusca	Native
Ischyrocerus longimanus	Arthropoda	Native
Ischyromene cordiforaminalis	Arthropoda	Native
Jassa marmorata	Arthropoda	Non-native
Jassa slatteryi	Arthropoda	Non-native
Jassa staudei	Arthropoda	Non-native
Jasus edwardsi	Arthropoda	Native
Joeropsis neozelandica	Arthropoda	Cryptogenic
Kellia cycladiformis	Mollusca	Native
Lafoeina amirantensis	Hydroid	Non-native
Lamellaria cerebroides	Mollusca	Native
Lamellaria ophione	Mollusca	Native
Lasaea hinemoa	Mollusca	Native
Lepidastheniella comma	Annelida	Native
Lepidonotus banksi	Annelida	Native
Lepidonotus fiordlandica	Annelida	Native
Lepidonotus jacksoni	Annelida	Native
Lepidonotus polychromus	Annelida	Native
Leptograpsus variegatus	Arthropoda	Native
Leptomya retiaria	Mollusca	Native
Leuconopsis obsoleta	Mollusca	Native
Leucosolenia cf. discoveryi	Porifera	Non-native
Leucothoe trailli	Arthropoda	Native
Liljeborgia akaroica	Arthropoda	Native
Liljeborgia barhami	Arthropoda	Native
Liljeborgia hansoni	Arthropoda	Native
Limaria orientalis	Mollusca	Non-native
Lissoclinum notti	Chordata	Native
Lissodendoryx isodictyalis	Porifera	Cryptogenic
Lomentaria umbellata	Rhodophyta	Native
Lophopagurus (L.)thompsoni	Arthropoda	Native
Lophopagurus (Lophopagurus)pumilus	Arthropoda	Native

Lophothamnion hirtum	Rhodophyta	Native
Lumbricalus aotearoae	Annelida	Native
Lumbrineris sphaerocephala	Annelida	Native
Lysidice ninetta	Annelida	Native
Macroclymenella stewartensis	Annelida	Native
Mallacoota subcarinata	Arthropoda	Native
Maoricrypta costata	Mollusca	Native
Marphysa capensis	Annelida	Native
Marphysa unibranchiata	Annelida	Native
Megabalanus tintinnabulum linzei	Arthropoda	Native
Megalomma kaikourense	Annelida	Native
Megalomma suspiciens	Annelida	Native
Melita festiva	Arthropoda	Native
Melita inaequistylis	Arthropoda	Native
Meridiastra mortenseni	Chordata	Native
Mesanthura affinis	Arthropoda	Native
Micrelenchus tenebrosus	Mollusca	Native
Microcladia novae-zelandiae	Rhodophyta	Native
Microcosmus australis	Chordata	Native
Microcosmus hirsutus	Chordata	Native
Microcosmus squamiger	Chordata	Cryptogenic
Microporella agonistes	Bryozoa	Native
Microporella speculum	Bryozoa	Native
Microzonia velutina	Ochrophyta	Native
Modiolarca impacta	Mollusca	Native
Modiolus areolatus	Mollusca	Native
Molgula amokurae	Chordata	Native
Molgula mortenseni	Chordata	Native
Monocorophium acherusicum	Arthropoda	Non-native
Monocorophium sextonae	Arthropoda	Non-native
Monocorophium sp. aff. M. insidiosum	Arthropoda	Cryptogenic
Monotheca flexuosa	Hydroid	Native
Musculista senhousia	Mollusca	Non-native
Mycale (Carmia) hentscheli	Porifera	Native
Mycale (Carmia) tasmani	Porifera	Native
Myriogramme denticulata	Rhodophyta	Native
Myrionema strangulans	Ochrophyta	Native
Mytilus galloprovincialis	Mollusca	Cryptogenic
Natatolana rossi	Arthropoda	Native
Nauticaris marionis	Arthropoda	Native
Neanthes cricognatha	Annelida	Native
Neanthes kerguelensis	Annelida	Native
Neastacilla aff. Tuberculata	Arthropoda	Native
Neohymenicus pubescens	Arthropoda	Native

Neoleprea papilla	Annelida	Native
Neosabellaria kaiparaensis	Annelida	Native
Neovermilia sphaeropomatus	Annelida	Native
Nereiphylla castanea	Annelida	Native
Nereis falcaria	Annelida	Native
Nicolea armilla	Annelida	Native
Nicolea maxima	Annelida	Native
Notoacmea helmsi	Mollusca	Native
Notoacmea parviconoidea	Mollusca	Native
Notobalanus vestitus	Arthropoda	Native
Notomegabalanus decorus	Arthropoda	Native
Notomithrax minor	Arthropoda	Native
Notomithrax peronii	Arthropoda	Native
Notomithrax ursus	Arthropoda	Native
Obelia bidentata	Hydroid	Cryptogenic
Obelia dichotoma	Hydroid	Cryptogenic
Obelia geniculata	Hydroid	Native
Obelia longissima	Hydroid	Non-native
Onchidella nigricans	Mollusca	Native
Onithochiton neglectus	Mollusca	Native
Opercularella humilis	Hydroid	Native
Ophiactis resiliens	Echinodermata	Native
Ophiocentrus novaezealandiae	Echinodermata	Native
Ophiodromus angustifrons	Annelida	Native
Ophionereis fasciata	Echinodermata	Native
Ophlitospongia reticulata	Porifera	Native
Orchomene aahu	Arthropoda	Native
Orchomene sp. Aff. O. aahu	Arthropoda	Cryptogenic
Ostrea aupouria	Mollusca	Native
Ostrea chilensis	Mollusca	Native
Paguristes setosus	Arthropoda	Native
Pagurus novizealandiae	Arthropoda	Native
Pagurus traversi	Arthropoda	Native
Palaemon affinis	Arthropoda	Native
Pallenopsis obliqua	Arthropoda	Native
Paradexamine pacifica	Arthropoda	Native
Paraidanthyrsus quadricornis	Annelida	Native
Paranthura cf. flagellata	Arthropoda	Native
Parascyphus simplex	Hydroid	Native
Parawaldeckia angusta	Arthropoda	Native
Parawaldeckia sp. aff. Angusta	Arthropoda	Cryptogenic
Parawaldeckia sp. aff. P. karaka	Arthropoda	Cryptogenic
Parawaldeckia sp. aff. P. stephenseni	Arthropoda	Cryptogenic
Parawaldeckia stephenseni	Arthropoda	Native

Parawaldeckia vesca	Arthropoda	Native
Parorchestia tenuis	Arthropoda	Native
Patelloida corticata	Mollusca	Native
Patiriella mortenseni	Chordata	Native
Patiriella oliveri	Chordata	Cryptogenic
Patiriella regularis	Chordata	Native
Pectinaria australis	Annelida	Native
Peltopes peninsulae	Arthropoda	Native
Pennaria disticha	Hydroid	Non-native
Pentagonaster pulchellus	Chordata	Native
Periclimenes yaldwyni	Arthropoda	Native
Perinereis amblyodonta	Annelida	Native
Perinereis camiguinoides	Annelida	Native
Perinereis pseudocamiguina	Annelida	Native
Perinereis vallata	Annelida	Native
Perna canaliculus	Mollusca	Native
Petrocheles spinosus	Arthropoda	Native
Petrolisthes elongatus	Arthropoda	Native
Petrolisthes novaezelandiae	Arthropoda	Native
Pherusa parmata	Annelida	Native
Phialella quadrata	Hydroid	Cryptogenic
Phorbas cf.anchorata	Porifera	Native
Phorbas fulva	Porifera	Native
Phycodrys quercifolia	Rhodophyta	Native
Pilumnopeus serratifrons	Arthropoda	Cryptogenic
Pilumnus lumpinus	Arthropoda	Native
Pilumnus novaezealandiae	Arthropoda	Native
Pinnotheres atrinocola	Arthropoda	Native
Pinnotheres novaezelandiae	Arthropoda	Native
Pista pegma	Annelida	Native
Plagusia chabrus	Arthropoda	Cryptogenic
Plakina monolopha	Porifera	Cryptogenic
Plakina trilopha	Porifera	Cryptogenic
Plaxiphora caelata	Mollusca	Native
Plaxiphora obtecta	Mollusca	Native
Pleurobranchaea maculata	Mollusca	Native
Plocamia novizelanicum	Porifera	Native
Plocamium angustum	Rhodophyta	Native
Plocamium cartilagineum	Rhodophyta	Native
Plocamium cirrhosum	Rhodophyta	Native
Plocamium leptophyllum	Rhodophyta	Native
Plocamium microcladioides	Rhodophyta	Native
Plumularia brachiata	Hydroid	Native
Plumularia setacea	Hydroid	Cryptogenic

Plumularia setaceoides	Hydroid	Native
Plumularia spirocladia	Hydroid	Native
Podocerus cristatus	Arthropoda	Native
Podocerus karu	Arthropoda	Native
Podocerus manawatu	Arthropoda	Native
Podocerus wanganui	Arthropoda	Native
Pododesmus zelandicus	Mollusca	Native
Polycarpa pegasus	Chordata	Native
Polycera hedgpathi	Mollusca	Cryptogenic
Polycheria obtusa	Arthropoda	Native
Polycheria sp. aff. P. obtusa	Arthropoda	Cryptogenic
Polyclinum sluteri	Chordata	Native
Polydora hoplura	Annelida	Non-native
Polysiphonia abscissoides	Rhodophyta	Native
Polysiphonia brodiaei	Rhodophyta	Non-native
Polysiphonia sertularioides	Rhodophyta	Non-native
Polysiphonia subtilissima	Rhodophyta	Non-native
Polyzoa reticulata	Chordata	Native
Pontophilus australis	Arthropoda	Native
Pratulum pulchellum	Mollusca	Native
Proscoloplos bondi	Annelida	Native
Protocirrineris nuchalis	Annelida	Native
Psammoclema cf. crassum	Porifera	Non-native
Pseudaxinella australis	Porifera	Native
Pseudophycis breviuscula	Chordata	Native
Pseudopista rostrata	Annelida	Native
Pseudopolydora paucibranchiata	Annelida	Non-native
Pseudopotamilla alba	Annelida	Native
Pseudopotamilla laciniosa	Annelida	Native
Pseudosphaeroma campbellense	Arthropoda	Native
Pseudosuberites sulcatus	Porifera	Cryptogenic
Pterocirrus brevicornis	Annelida	Native
Pterothamnion simile	Rhodophyta	Native
Pyromaia tuberculata	Arthropoda	Non-native
Pyura cancellata	Chordata	Native
Pyura carnea	Chordata	Native
Pyura lutea	Chordata	Native
Pyura pachydermatina	Chordata	Native
Pyura picta	Chordata	Native
Pyura pulla	Chordata	Native
Pyura rugata	Chordata	Native
Pyura spinosissima	Chordata	Native
Pyura subuculata	Chordata	Native
Pyura suteri	Chordata	Native

Pyura trita	Chordata	Native
Ranella australasia	Mollusca	Native
Rhizoclonium implexum	Chlorophyta	Native
Rhodophyllis centrocarpa	Rhodophyta	Native
Rhodophyllis lacerata	Rhodophyta	Cryptogenic
Rhodymenia aff.dichotoma	Rhodophyta	Cryptogenic
Rhodymenia foliifera	Rhodophyta	Native
Rhodymenia leptophylla	Rhodophyta	Native
Rhodymenia linearis	Rhodophyta	Native
Rhodymenia obtusa	Rhodophyta	Native
Rhynchozoon larreyi	Bryozoa	Cryptogenic
Rhyssoplax aerea	Mollusca	Native
Risellopsis varia	Mollusca	Native
Romanchella perrieri	Annelida	Native
Ruditapes largillierti	Mollusca	Native
Rynkatorpa uncinata	Echinodermata	Native
Sabellidae Indet	Annelida	Cryptogenic
Salacia bicalycula	Hydroid	Native
Sarcothalia livida	Rhodophyta	Native
Sargassum scabridum	Ochrophyta	Native
Sargassum sinclairii	Ochrophyta	Native
Schistomeringos loveni	Annelida	Native
Schizoporella errata	Bryozoa	Non-native
Schizoseris dichotoma	Rhodophyta	Native
Schizoseris griffithsia	Rhodophyta	Native
Schizosmittina cinctipora	Bryozoa	Native
Schottea cf.taupoensis	Arthropoda	Native
Schottea sp.	Arthropoda	Native
Scoloplos cylindrifer	Annelida	Native
Scoloplos simplex	Annelida	Native
Scruparia ambigua	Bryozoa	Cryptogenic
Scrupocellaria ornithorhyncus	Bryozoa	Native
Scutus breviculus	Mollusca	Native
Scytosiphon lomentaria	Ochrophyta	Native
Seba typica	Arthropoda	Native
sedis Adenocystis utricularis	Ochrophyta	Native
Sertularella robusta	Hydroid	Native
Sertularia marginata	Hydroid	Non-native
Sigapatella novaezelandiae	Mollusca	Native
Sigapatella tenuis	Mollusca	Native
Siphonaria australis	Mollusca	Native
Smittina rosacea	Bryozoa	Native
Smittina torques	Bryozoa	Native
Smittoidea maunganuiensis	Bryozoa	Native

Spirobranchus cariniferus	Annelida	Native
Spirobranchus polytrema	Annelida	Non-native
Steginoporella magnifica	Bryozoa	Native
Stenothoe miersii	Arthropoda	Cryptogenic
Stenothoe moe	Arthropoda	Native
Stenothoe sp. aff. S. gallensis	Arthropoda	Non-native
Stenothoe valida	Arthropoda	Cryptogenic
Stereotheca elongata	Hydroid	Native
Stichopus mollis	Echinodermata	Native
Stictosiphonia hookeri	Rhodophyta	Native
Stictosiphonia vaga	Rhodophyta	Native
Stomacontion sp. aff. S. pungpunga	Arthropoda	Cryptogenic
Streblosoma toddae	Annelida	Native
Styela clava	Chordata	Non-native
Styela plicata	Chordata	Cryptogenic
Stylotella agminata	Porifera	Non-native
Suberites cf. affinis	Porifera	Native
Sycon cf. ornatum	Porifera	Native
Symplectoscyphus johnstoni	Hydroid	Native
Symplectoscyphus subarticulatus	Hydroid	Native
Synthecium campylocarpum	Hydroid	Non-native
Synthecium elegans	Hydroid	Native
Synthecium subventricosum	Hydroid	Non-native
Sypharochiton pelliserpentis	Mollusca	Native
Sypharochiton sinclairi	Mollusca	Native
Talochlamys zelandiae	Mollusca	Native
Tedania battershilli	Porifera	Native
Tedania diversiraphidiophora	Porifera	Native
Tedania spinostylota	Porifera	Native
Terebella plagiostoma	Annelida	Native
Terebellides narribri	Annelida	Native
Tethya burtoni	Porifera	Native
Thelepus extensus	Annelida	Native
Timarete anchylochaetus	Annelida	Native
Trematocarpus aciculare	Rhodophyta	Native
Tricellaria inopinata	Bryozoa	Non-native
Trichomusculus barbatus	Mollusca	Native
Trochus tiaratus	Mollusca	Native
Trochus viridus	Mollusca	Native
Trypanosyllis gigantea	Annelida	Native
Trypanosyllis zebra	Annelida	Native
Tubulipora cf.connata	Bryozoa	Native
Tugali suteri	Mollusca	Native
Turbo smaragdus	Mollusca	Native

Typosyllis prolifera	Annelida	Native
Ulva spathulata	Chlorophyta	Native
Undaria pinnatifida	Ochrophyta	Non-native
Valdemunitella valdemunitella	Bryozoa	Native
Ventojassa frequens	Arthropoda	Native
Vosmaeria torquata	Porifera	Native
Vosmaeropsis cf macera	Porifera	Non-native
Watersipora arcuata	Bryozoa	Non-native
Watersipora subtorquata	Bryozoa	Non-native
Wittrockiella salina	Chlorophyta	Native
Xanthidae sexlobata	Arthropoda	Cryptogenic
Xenostrobus pulex	Mollusca	Native
Xenostrobus securis	Mollusca	Native
Xymene huttoni	Mollusca	Native
Xymene plebeius	Mollusca	Native
Xymene traversi	Mollusca	Native
Zoobotryon verticillatum	Bryozoa	Non-native

Table A4. Pairwise PERMANOVA test for the community composition for the interaction factors; Habitat × Sample interval and Substratum × Sample interval. Significance marked in bold ($P < 0.05$).

	t	***P* (perm)**	**Avg. similarity**		
Habitat × Sample interval			**Reef**	**Marina**	**Reef × Marina**
Time 1	2.3252	**0.0001**	53.26	34.635	38.531
Time 2	2.5417	**0.0001**	53.506	28.553	34.692
Time 3	2.9758	**0.0001**	38.784	34.948	28.262
Time 4	2.7269	**0.0001**	46.081	39.424	36.314
Time 5	2.7292	**0.0001**	33.818	46.235	33.038
Time 6	2.8138	**0.0001**	39.637	31.627	27.887
Time 7	2.6967	**0.0001**	31.772	27.918	22.611
Time 8	1.9043	**0.0003**	28.754	31.092	26.693
Substratum × Sample interval			**Slate**	**PVC**	**PVC × Slate**
Time 1	0.918	0.5365	38.265	44.499	41.011
Time 2	1.7555	**0.0043**	35.717	41.666	36.952
Time 3	1.4254	**0.0299**	28.808	37.251	31.971
Time 4	2.1249	**0.0003**	34.432	47.581	38.002
Time 5	1.8585	**0.0013**	33.124	42.273	35.289
Time 6	1.5002	**0.0221**	32.321	32.372	31.063
Time 7	1.8748	**0.0003**	26.386	28.844	24.767
Time 8	1.9284	**0.0005**	27.166	32.606	26.729