SPATIAL AND TEMPORAL GENETIC STRUCTURE OF THE NEW ZEALAND SCALLOP *Pecten novaezelandiae*: A MULTIDISCIPLINARY PERSPECTIVE

BY

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Abstract

Knowledge about the population genetic structure of species and the factors shaping such patterns is crucial for effective management and conservation. The complexity of New Zealand's marine environment presents a challenge for management and the classification of its marine biogeographic areas. As such, it is an interesting system to investigate marine connectivity dynamics and the evolutionary processes shaping the population structure of marine species. An accurate description of spatial and temporal patterns of dispersal and population structure requires the use of tools capable of incorporating the variability of the mechanisms involved. However, these techniques are yet to be broadly applied to New Zealand marine organisms.

This study used genetic markers to assess the genetic variation of the endemic New Zealand scallop, *Pecten novaezelandiae*, at different spatial and temporal scales. A multidisciplinary approach was used integrating genetic with environmental data (seascape genetics) and hydrodynamic modelling tools. *P. novaezelandiae* supports important commercial, recreational and customary fisheries but there is no previous information about its genetic structure. Therefore, twelve microsatellite markers were developed for this study (Chapter 2).

Samples (n=952) were collected from 15 locations to determine the genetic structure across the distribution range of *P. novaezelandiae*. The low genetic structure detected in this study is expected given the recent evolutionary history, the large reproductive potential and the pelagic larval duration of the species (approximately 3 weeks). A significant isolation by distance signal and a degree of differentiation from north to south was apparent, but this structure conflicted with some evidence of panmixia. A latitudinal genetic diversity gradient was observed that might reflect the colonisation and extinction events and insufficient time to reach migration-drift equilibrium during a recent range expansion (Chapter 3).

A seascape genetic approach was used to test for associations between patterns of genetic variation in *P. novaezelandiae* and environmental variables (three geospatial and six environmental variables). Although the geographic distance between populations was an important variable explaining the genetic variation among populations, it appears that levels of genetic differentiation are not a simple function of distance. Evidence suggests

that some environmental factors such as freshwater discharge and suspended particulate matter can be contributing to the patterns of genetic differentiation of *P. novaezelandiae* in New Zealand (Chapter 4).

Dispersal of *P. novaezelandiae* was investigated at a small spatial and temporal scale in the Coromandel fishery using genetic markers integrated with hydrodynamic modelling. For the spatial analysis, samples (n=402) were collected in 2012 from 5 locations and for the temporal analysis samples (n=383) were collected in 2012 and 2014 from 3 locations. Results showed small but significant spatial and temporal genetic differentiation, suggesting that the Coromandel fishery does not form a single panmictic unit with free gene flow and supporting a model of source-sink population dynamics (Chapter 5).

The importance of using multidisciplinary approaches at different spatial and temporal scales is widely recognized as a means to better understand the complex processes affecting marine connectivity. The outcomes of this study highlight the importance of incorporating these different approaches, provide vital information to assist in effective management and conservation of *P. novaezelandiae* and contribute to our understanding of evolutionary processes shaping population structure of marine species.

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“One planet, one experiment.”

E. O. Wilson

Table of contents

List of Figures

List of Tables

CHAPTER 1

Introduction

Marine connectivity and fisheries genetics

Most marine invertebrates have a planktonic larval stage of development (Strathmann *et al.* 2002). This period in the water column is typically the larval dispersal phase of the species and greatly determines population connectivity and patterns of population structure of species. Population connectivity can be defined as the exchange of individuals among geographically separated subpopulations (Cowen *et al.* 2007), with connectivity also being influenced by post-settlement mortality, growth, and fitness from settlement to successful reproduction (Pineda *et al.* 2007). Population connectivity is therefore an important process for population replenishment and the management of marine ecosystems. Understanding the patterns of genetic structure of marine species, and the processes driving such patterns, is essential not only for learning about the ecology and evolution of the species but also for implementing effective management strategies. To identify the most likely source populations, i.e. populations with larvae contributing to local recruitment, is particularly important in fisheries since it influences population growth in fished areas (Soria *et al.* 2012). Moreover, biologically distinctive populations play a key role in providing resilience and in assuring fisheries productivity (Aguirre & Marshall 2012). This is particularly important for organisms with large periodic population fluctuations and highly variable recruitment, such as most scallop species (Shumway & Parsons 2006).

Scallops support important fisheries around the world. More than 400 species are known to occur from the tropics to the poles and over 30 species are commercially important. King scallops (*Pecten* spp.) are the most commercially exploited species and are found mostly at high latitudes in both hemispheres, along the coasts of Europe, Africa, Asia, Australia, New Zealand and their neighbouring islands (Brand, 2006 in Shumway & Parsons, 2006). Because of the general interest in scallops associated with their high economic value, they have been subject of considerable research effort. Studies on population genetic structure have been conducted for *Aequipecten opercularis* (Arias *et al.* 2010), *Argopecten irradians irradians* (Bricelj & Krause 1992), *Chlamys farreri* (Zhan *et al.* 2009), *Chlamys opercularis* (Macleod *et al.* 1985), *Nodipecten subnodosus* (Petersen *et al.* 2010), *Patinopecten yessoensis* (Nagashima et al. 2005; Sato et al. 2005; Chen et al. 2009), *Pecten fumatus* (Woodburn 1990), *Pecten jacobaeus* (Rios *et al.* 2002), *Pecten maximus* (Wilding *et al.* 1997; Heipel *et al.* 1998; Rios *et al.* 2002) and *Placopecten magellanicus* (e.g. Kenchington et al. 2006). However, in New Zealand, the population genetic structure of the

endemic *Pecten novaezelandiae* Reeve, 1852 is currently unknown. As observed in other species, the New Zealand scallop has highly variable recruitment (Shumway & Parsons 2006) and the processes that result in large periodic population fluctuations are poorly understood; therefore fisheries managers are confronted with uncertainty during the decision-making process.

Typically, fisheries are divided into management units or stocks, which can be homogeneous groups regarding, for example, growth and mortality rates. There are several stock definitions (reviewed in Carvalho and Hauser 1994), but in general, a stock can be defined as a group of individuals sharing similar vital rates such as maturity, growth and mortality and with a closed life cycle in which recruits are originated by previous generations in the same group (Cadrin *et al.* 2005). In practice, the application of the stock definition is very complex. Populations are rarely differentiated by evident boundaries and in marine organisms this categorisation is even more complex when compared to terrestrial organisms. This is because marine organisms are commonly expected to show lower geographical differentiation. Such an assumption is the result of, for example, less physical barriers observed in an "open" ocean and the planktonic larval phases responsible for the dispersal of some marine species. Nevertheless, recent studies have highlighted the complexity of marine population dynamics and geographical differentiation across many species (e.g. Apte and Gardner 2002; Kenchington et al. 2006; Zhan et al. 2009).

An understanding of population genetic structure was incorporated in stock definition in the late twentieth-century. Larkin (1972) described a stock as "…a population of organisms which, sharing a common gene pool, is sufficiently discrete to warrant consideration as a self-perpetuating system which can be managed". In the past three decades a great variety of studies in the field of fisheries genetics have demonstrated that integrating genetic information with traditional methods of fishery stock assessment can extensively improve the quality of management recommendations (e.g. Sweijd et al. 2000; Ward 2000; Hauser & Carvalho 2008; Saillant et al. 2012). As a consequence, the importance of genetic diversity at the population level for assuring adaptive responses to natural modifications as well as environmental changes caused by man is now broadly recognized (Bonin *et al.* 2007; Aguirre & Marshall 2012; Allendorf *et al.* 2014).

Several different approaches have been used to identify stocks and investigate population structure and connectivity. Direct methods, such as tagging, have been

extremely useful for defining the movement of fish species (McFarlane *et al.* 1990). However, invertebrate species with a dispersal period as a pelagic larva are logistically very difficult to track due to the small sizes of larvae. The use of molecular markers can provide valuable information on the dispersal movement among populations or stocks, on the reproductive success of individuals and can also provide genetic information over previous generations (Selkoe & Toonen 2006). Consequently, they allow for the assessment of variability between stocks and a better understanding of the replenishment of fisheries (Carvalho & Hauser 1994).

Different genetic markers have been used for the assessment of population genetic structure and connectivity. For example, in the 1960s, protein allozymes were the first markers used to address genetic variation within individuals. However, as allozymes are proteins encoded by DNA and not all variation in DNA sequence results in different proteins, allozyme studies did not capture all the information contained in the DNA. It tended to underestimate levels of genetic variability and caused constraints on sample collection and storage (Carvalho 1998). With the technical advance of molecular biology, several types of molecular markers have become prevalent in ecological studies. Mitochondrial DNA (mtDNA) markers have been used extensively mainly because they are relatively easy to amplify without previous information on the DNA sequence, mutation rates are reasonably high, in most animals mtDNA is inherited maternally which makes individual lineages easy to track and because there are few copies of mtDNA (it is effectively a quarter of the size of diploid nuclear DNA) it is reasonably sensitive to demographic events. Nevertheless, the use of mtDNA has some limitations as it may not be representative of the whole population and the high probability of haplotype losses may underestimate the levels of genetic diversity (Park & Moran 1994). Another method that has been used since the 1990s is the PCR-based method named random amplified polymorphic DNA (RAPDs). Although RAPDs can be a relatively quick method, amplification of bands frequently varies and bands that are amplified from non-target DNA can be difficult to detect. Another method also used is the amplified fragment length polymorphism (AFLPs), which is more reliable than RAPDs but it is also more labour intensive. Finally, single nucleotide polymorphisms (SNPs) are becoming increasingly more popular for population genetic structure studies and although their development and use is relatively recent and expensive they hold great potential for a wide range of applications (Freeland 2005).

As a result of being easily influenced by migration, rapidly developed and because of their decreasing cost of development, microsatellites are currently the most popular and versatile DNA markers for ecological applications; their utility and limitations are well known (Freeland 2005; Selkoe & Toonen 2006). Microsatellites are short sequences of DNA consisting of tandem repeats of 2-10 bp. They are highly polymorphic (i.e., multiple alleles at each locus due to high rates of mutation), co-dominant (i.e., homozygous and heterozygous individuals can be identified, meaning that allele frequencies are easily calculated), usually species-specific, commonly considered as selectivity neutral and broadly distributed in the genome (Freeland 2005). Microsatellites are regarded as high resolution genetic markers and can reveal very high genetic diversity at fine geographical scales (e.g. Zhan et al. 2009). Microsatellites have high mutation rates compared to other types of sequences. Although these mutations can be highly variable, microsatellite estimated mutation rates, as for example $5.56x10^{-4}$ in the common carp (*Cyprinus carpio*) (Yue et al., 2007), are considerably higher than the estimated overall point mutation rate of nuclear DNA, which is approximately 10^{-9} to 10^{-10} (Li 1997). The high number of mutations in microsatellites is usually attributed to slipped-strand mis-pairing that occurs during DNA replication. This characteristic makes microsatellite data particularly appropriate for deducing comparatively recent population genetic events (Freeland et al., 2011). Microsatellite markers had been developed for many scallop species (e.g. Sato *et al.* 2005; Watts *et al.* 2005; Ma & Yu 2009; Arias *et al.* 2010; Charrier *et al.* 2012; Marín *et al.* 2012) and have shown high variability, suggesting that they are suitable for being used in the family Pectinidae.

Population genetics is a powerful tool to address marine connectivity and population dynamics. Although random genetic drift, gene flow, mutation and selection are the main forces shaping the patterns of genetic structure, stochastic processes add an inevitable uncertainty in the recruitment of organisms (Siegel *et al.* 2008). Indirect techniques such as the use of molecular markers have been widely used to understand dispersal patterns and marine connectivity (Hellberg *et al.* 2002). However, the integrated use of molecular markers with other methods is recognized as a better approach to help clarify the complex dynamics of marine populations (Cowen & Sponaugle 2009). Multidisciplinary approaches combining genetic and ecological information are particularly valuable when genetic differentiation is low, which is the case for many marine species (Selkoe *et al.* 2008).

Environmental factors affecting genetic variation

Population genetic structure of organisms can be strongly influenced by biological factors such as the pelagic larval duration of the species and also by current and historical environmental features. For example, it is commonly recognized that connectivity among marine populations is strongly influenced by coastal currents (Ross *et al.* 2009; White *et al.* 2010). Understanding the effects that environmental variation has on population genetic structure is a central topic for management and conservation. Consequently, approaches that integrate biological characteristics, spatial structure and oceanographic features are valuable tools for understanding connectivity among populations (Selkoe *et al.* 2010).

Landscape genetics is a discipline that analyses the influence of landscape characteristics on genetic structure of populations (Manel *et al.* 2003). In the aquatic environment it is often named seascape genetics and aims to understand the factors (e.g. ocean currents) that shape gene flow dynamics; however, compared to landscape genetics, studies applying this concept in the marine environment are still scarce (but see Galindo *et al.* 2006; White *et al.* 2010; Schunter *et al.* 2011; Wei *et al.* 2013b; Constable 2014; Hannan 2014) and in only one recent study with the rock scallop *Spondylus calcifer* (Soria *et al.* 2012).

Seascape genetics is an increasingly powerful tool to identify marine environmental features that can be correlated with the genetic structure of species (Liggins *et al.* 2013). The influence of environmental variables on population subdivision can be measured using two different approaches: (1) comparing simulations of physical oceanographic models, e.g. based on ocean currents and larval characteristics, with genetic data represent a powerful tool for predicting larvae dispersal (e.g. Galindo et al. 2006, Galindo et al. 2010); and (2) assessing the influence of environmental factors such as sea surface temperature and tidal current on geographic genetic variation, i.e. testing the hypothesis that environmental features can explain the genetic structure of populations (González-Wangüemert et al. 2010; Wei et al. 2013b).

When inferring gene flow, it is also essential to consider different spatial scales. Important factors affecting dispersal might not be obvious in a large spatial scale study, since seascape effects on migration and genetic drift might be difficult to distinguish from microevolutionary forces such as mutations. On the other hand, studies considering only a

fine spatial scale can be affected by noise in the genetic data associated with population subunits that persist across generations (intrademic structure). Therefore, the choice of sampling scale introduces different features that may affect interpretations of patterns of gene flow (Conover *et al.* 2006; Anderson *et al.* 2010).

Temporal variation in genetic structure can also be the result of environmental factors and it is very well documented in many marine invertebrates (e.g. Kovach *et al.* 2010; Perrier *et al.* 2013; Owen & Rawson 2013; Kesäniemi *et al.* 2014; Pusack *et al.* 2014). Environmental conditions may lead to 'sweepstake recruitment', where random events determine which adults are successful each spawning season (Hedgecock 1994). Variation in oceanic currents can also affect the movement of larvae and consequently the patterns of genetic structure of species (Sotka *et al.* 2004; Selkoe & Toonen 2006). These complex recruitment dynamics, which are characteristic of many marine invertebrate species, have very important consequences for fisheries management. However this represents a challenge for assessing the size of the fishable component of stocks, which is dependent on the successful recruitment of individuals. Therefore, population genetic studies at different spatial and temporal scales can potentially provide a clearer interpretation of the factors influencing population dynamics.

Finally, historical environmental processes such as glacial periods and changes in sea level can also affect the distribution of species and consequently lead to the observed population genetic structure (Gaggiotti *et al.* 2009). For example, in New Zealand several species have shown a genetic break at around 41-42° S, just south of the Cook Strait (Gardner *et al.* 2010) and studies suggest that this genetic split is the result of historic land subdivision combined with the complex hydrography of the Cook Strait region (Apte & Gardner 2002; Goldstien *et al.* 2006). Therefore, historical barriers can restrict connectivity between populations even if currently connected by strong oceanic currents, such as observed for a reef system in Indonesia where the patterns of genetic structure reflect the separation of ocean basins during the Pleistocene low-sea-levels (Barber *et al.* 2000).

The New Zealand marine environment

New Zealand is an archipelago of more than 700 islands with a complex oceanography. Extending from the subtropical Kermadec Islands at 29ºS to the subantarctic

Campbell Islands at 52°S, it is located in the subtropical convergence, the division between subtropical water in the north and subantarctic water in the south (Wallis & Trewick 2009). The complexity of the region, for example due to several small currents and eddies, variable wind, waves and tides as well as coastal currents shaped by interactions with ocean floor topography, makes it difficult to predict the influence of the marine environment on marine populations structure (Ross *et al.* 2009). On the other hand, it is an ideal system to investigate the influence of these current systems and environmental variability on patterns of genetic structure and connectivity in coastal marine species.

Identifying spatial and temporal genetic boundaries across species in the New Zealand marine environment can bring insights about the processes that shape patterns of genetic structure and marine connectivity at the ecosystem level, which is required for management efforts. Fifty-eight studies concerning the genetic structure of 42 coastal marine taxa were conducted during the past 32 years in New Zealand (Gardner *et al.* 2010). Twenty (33%) of these studies reported north-south divergence, 16 (28%) reported no genetic structure among populations, 12 (21%) reported divergence within and/or among populations, 9 (16%) reported isolation by distance and one (2%) reported east-west divergence. Studies that described north-south differentiation frequently reported the location of the genetic break at around 41-42° S, just south of the Cook Strait (Gardner *et al.* 2010).

Gardner *et al.* (2010) drew attention to gaps in knowledge concerning coastal population structure particularly in estuarine and soft substrate habitats. To fully understand the patterns of regional connectivity in New Zealand and characterize the geographic units of genetic diversity for conservation, these gaps in knowledge must be addressed. Furthermore, knowledge of population connectivity among these fragile habitats is essential because they hold assemblages of commercially important species and are subjected to intense human activity, such as dredging and port activities (Cole *et al.* 2000).

Study species

The New Zealand scallop, *Pecten novaezelandiae*, is a large bivalve with a flat upper left valve and a convex lower right valve. Growth to 100 mm shell length takes between 1.5 and 3.5 years although growth rates are spatially and temporally variable. Morrison (1999)

observed that the maximum average size and average growth rates diminish with increasing depth and the maximum reported age in unexploited populations is 7 years.

The New Zealand scallop is an exceptionally fecund hermaphroditic species. Size at full maturity is reported at 65 mm shell height in the Hauraki Gulf and the smallest mature individuals reported are 55 mm shell height (Williams & Babcock 2005). However, studies suggest that scallops might reach maturity at different sizes in different locations (Williams & Babcock 2005). This species generally breeds in early summer even though partial spawning may occur from August to February (Williams & Parkinson 2010) and individual populations are usually synchronous, i.e. individuals spawn at the same time (Shumway & Parsons 2006). Factors such as latitude, depth and temperature may influence the spawning dynamics of *P. novaezelandiae*. For example, it has been demonstrated for other scallop species, such as *Argopecten irradians* and *Pecten maximus*, that higher latitude populations spawn earlier in the season and over longer periods of time (reviewed in Shumway & Parsons 2006). Tunbridge (1968) showed that *Pecten novaezelandiae* spawned first in the deeper beds (28-40 m) among seven sites ranging from 6-40 m depth. Finally, evidence suggests that elevated food (chlorophyll *a*) levels and temperature can also influence spawning dynamics in *Argopecten purpuratus*, populations of which exhibited intense spawning during an El Niño period (Shumway & Parsons 2006).

The endemic New Zealand scallop is an epibenthic organism found in diverse types of soft substrate from low tide to 90 m deep and patchily distributed throughout coastal waters (Bull 1976; Williams & Parkinson 2010). Similarly to other scallops, *P. novaezelandiae* is able to move quickly by clapping its valves, thereby propelling the animal forward. However, most species become rapidly exhausted after moving short distances (Morrison 1999) which possibly means that they are potentially unable to achieve movement on the large scale of large beds and therefore the main dispersal period occurs through the larval stage. The duration of scallop larvae stages generally ranges from 6 - 70 days (Shumway & Parsons 2006) and has been shown to vary within species depending on temperature (Beaumont & Barnes 1992). The estimated pelagic larval duration of *P. novaezelandiae* is three to four weeks (Bull 1976; Jong 2013), which is within the range described for other species such as 25 days for *Pecten maximus* (Pennec *et al.* 2003; Figure 1.1).

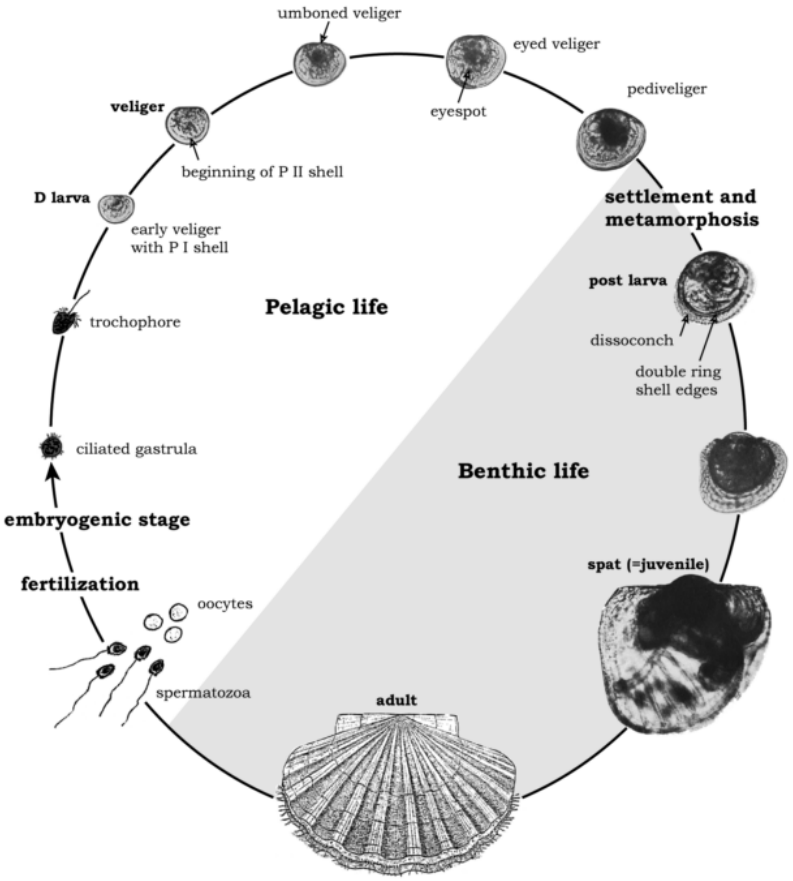

Figure 1.1 Diagrammatic representation of the life cycle *of Pecten maximus* (Pennec *et al.* 2003)

The New Zealand scallop is a highly valued species, supporting important commercial, recreational and customary fisheries. However, its exploitation faces several problems mainly because its recruitment is highly variable and the processes that result in large periodic population fluctuations are poorly understood (Ministry of Primary Industries 2013a). Spat variability can also be the result of human-induced processes such as fishing-related changes to habitat that affect juvenile scallop survival and an increase in sedimentation input, which can affect adults and consequently reduce the likelihood of future larval settlement (Talman *et al.* 2004; Szostek *et al.* 2013). In New Zealand, evidence of declining stocks is found: (1) in the Coromandel fishery, which has been declining in terms of recruited biomass since 2005-06 (Williams & Parkinson 2010); (2) in Golden Bay, which was effectively closed to commercial fishing in 2011 and in 2012 two scallop stocks or sub-stocks were considered to be overfished; and (3) in Tasman Bay,

which has undergone a voluntary closure to commercial fishing since 2006 due to fishery collapse (Ministry of Primary Industries, 2012).

Currently, the New Zealand scallop is managed under the Quota Management System (QMS). The New Zealand Ministry of Primary Industries (MPI) works closely with stakeholders to establish a sustainable and cautious Total Allowable Commercial Catch (TACC) for each quota management area (QMA; Figure 1.2). Thus, an annual pre-season research survey is carried out to estimate abundance and determine sustainable yields and to determine the quantity that the commercial fishery can catch of each stock or QMA in that year. Additionally, there is also a size limit, measured in terms of shell length, which varies accordingly to each QMA (Williams & Parkinson 2010). However, there is little information on the stock structure and population dynamics of this species and this substantial uncertainty may lead to inappropriate estimates of TACC.

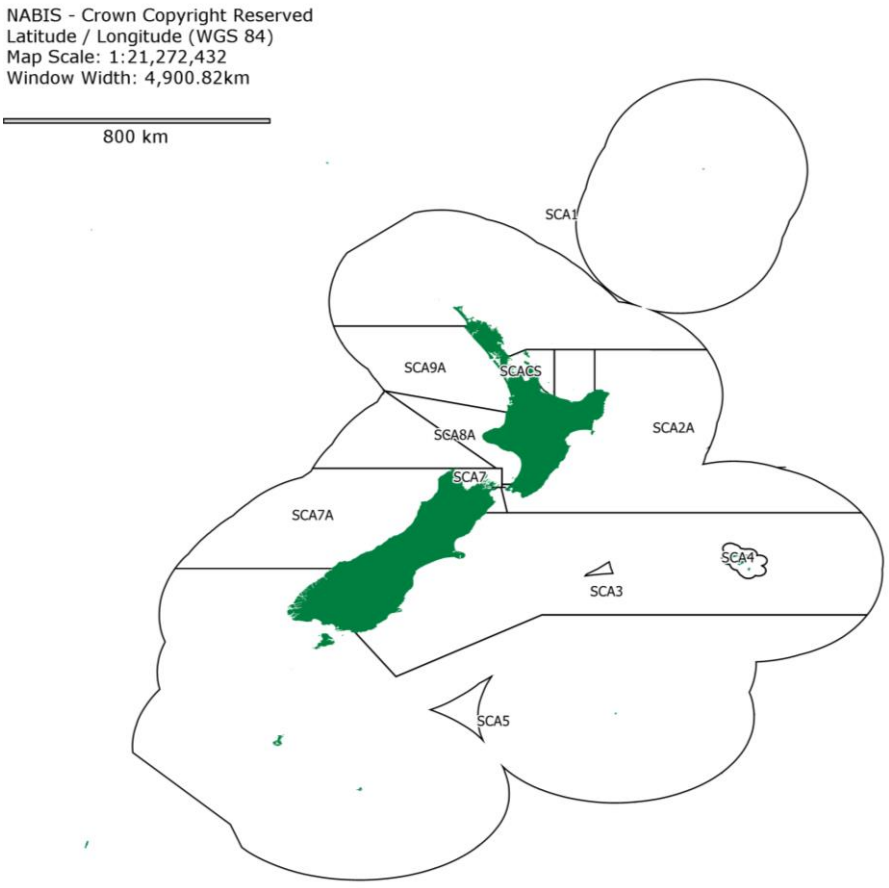

Figure 1.2 Map of the location of quota management areas (QMAs) used for management of the commercial and recreational fishery of *Pecten novaezelandiae* (sourced from www.nabis.govt.nz)

Aims and thesis structure

The overall aim of this PhD thesis was to investigate the patterns of connectivity and genetic structure of the endemic scallop *Pecten novaezelandiae*. This study brings together information for management of the New Zealand scallop and also knowledge about population dynamics of scallops in general, an important step to fully understand the processes that regulate scallops biomass fluctuations and to achieve sustainable fisheries management. It also provides information about the patterns of gene flow and the processes shaping those patterns in the New Zealand marine environment. Specific objectives and hypotheses tested included:

1) To develop and characterize a set of microsatellite markers for *P. novaezelandiae*;
2) To characterize the genetic variability of populations of *P. novaezelandiae* encompassing the species' range; evaluate the genetic differentiation and understand factors shaping the patterns found; test the null hypothesis of panmixia; and compare the observed patterns with other species, based on hypotheses of evolutionary age;
3) To identify environmental variables likely to explain the observed patterns of genetic structure across the species' range; test the null hypothesis that environmental variables are not correlated with genetic variation;
4) To estimate spatial and temporal genetic variation of *P. novaezelandiae* at a small scale (within the limits of the Coromandel fishery) using microsatellites and a hydrodynamic model; test the null hypothesis of panmixia and temporal stability; and study the possibility of a model of source-sink population dynamics.

This work is part of the project "Multi-species coastal marine connectivity" (ZBD2009_10) funded by the Ministry of Primary Industries (MPI), formerly Ministry of Fisheries. Sampling comprised small and large scale dredging and diving carried out from February 2012 until August 2014.

Each data chapter of this thesis (i.e. except Chapters 1 and 6) represents a different unit with specific objectives and individual sections of Introduction, Methods, Results and Discussion. The purpose of Chapter 1 (present chapter) is to give a general introduction to the research topics and an overview on the approaches used. Chapter 2 describes the

microsatellites markers developed for *P. novaezelandiae* from 454 sequence data and corresponds to a manuscript published in *Conservation Genetics Resources* "Silva CNS, Gardner JPA (2014). Development and characterisation of 12 microsatellite markers for the New Zealand endemic scallop *Pecten novaezelandiae*. 6(2), 327-328". In Chapter 3 the genetic structure of *P. novaezelandiae* is described, the null hypothesis of panmixia (i.e., no genetic structure) is tested and the factors that shape the patterns observed are characterized. In Chapter 4 a seascape genetics approach is used to identify associations between the genetic structure of the New Zealand scallop across its distribution range and nine environmental variables. Chapter 5 describes a spatial and temporal analysis of dispersal of *P. novaezelandiae* in the Coromandel fishery region, using microsatellites integrated with hydrodynamic modelling to test the null hypothesis of panmixia. Finally, Chapter 6 summarizes the key findings, indicates future directions and provides recommendation about the sustainable management of the New Zealand scallop.

CHAPTER 2

Development of microsatellite DNA markers for the New Zealand scallop *Pecten novaezelandiae*

Manuscript published in *Conservation Genetics Resources*:

Silva CNS, Gardner JPA (2014). Development and characterisation of 12 microsatellite markers for the New Zealand endemic scallop *Pecten novaezelandiae*. Conservation Genetics Resources 6(2), 327-328.

Introduction

The New Zealand scallop (*Pecten novaezelandiae* Reeve, 1853), (Bivalvia: Pectinidae) is distributed throughout coastal and semi-estuarine waters in the North, South, Stewart and Chatham Islands. It is a highly valued species supporting important fisheries although stocks have been declining and there is still substantial uncertainty about stock status (Williams & Parkinson 2010). Despite its ecological and economic importance, there is still a lack of genomic resources for the New Zealand scallop and no studies of population connectivity have been conducted to date.

Marine species commonly have vast population sizes and widespread dispersal capabilities and the expectations are populations exhibiting high levels of genetic diversity. Therefore, studies of population connectivity and stock structure require sensitive tools to detect low levels of differentiation such as the use of microsatellite markers (Avise 2004). Microsatellites are currently the most popular and versatile DNA markers for ecological applications. With the advances in next generation sequencing (NGS) technologies, the development of microsatellite markers has become cheaper, easier and much faster compared to traditional methods (Abdelkrim *et al.* 2009). A commonly used NGS technology uses the GS-FLX Titanium platform (Roche 454 Life Science, USA) and is generally named as 454 sequencing.

The analysis of PCR products by laser detection requires one of the primers to be fluorescently labelled and these dyes are very expensive. To overcome this issue, Schuelke (2000) developed the M13 protocol which enables a single set of fluorescently labelled markers to be used in conjunction with a range of PCR primers and it can also be multiplexed (PCR-amplified as a multiplex of loci) or pooled together after single PCRs (pool-plexed).

In this study, microsatellite markers were developed *de novo* for the New Zealand scallop *Pecten novaezelandiae* using NGS (454 sequencing). These markers were developed with the intention of investigating genetic diversity and population structure connectivity among populations.

Materials and methods

High quality genomic DNA was extracted from the adductor muscle of one individual of *Pecten novaezelandiae* collected from Wellington Harbour using a Phenol-Chloroform-Isoamyl method. In order to precipitate the polysaccharides present in the mucus, a volume of 100 µL of saturated KCl solution (40 g/100 ml) was added to the digested DNA. Samples were sent to the High-Throughput DNA Sequencing Unit at University of Otago (Dunedin, New Zealand) for microsatellite-enriched library preparation and 454 sequencing on a Roche GS-FLX instrument. The software iQDD V1.3 (Meglécz *et al.* 2010) was used to search for Short Tandem Repeats (STRs) and design possible primers for PCR amplification, setting 90 bp as minimum PCR product size and 100 bp as minimum sequence length. The minimum repeat length for di-, tri-, tetra- and pentanucleotide motifs was set to 8, 6, 4 and 4, respectively. The best primer pair for each repeat sequence was selected and a total of 49 primers were retained for PCR amplification.

A M13 (5'-TGT AAA ACG ACG GCC AGT) tail was added to the 5' end of each forward primer for detection purposes following Schuelke (2000). Four primers each labelled with a fluorescent dye with the same M13 primer sequence were ordered. The fluorochrome labels 6-FAM, NED, PET and VIC were used: 5'-FAM- ACG ACG TTG TAA AAC GAC-3', 5'-NED- ACG ACG TTG TAA AAC GAC-3', 5'-PET- ACG ACG TTG TAA AAC GAC-3', 5'-VIC- ACG ACG TTG TAA AAC GAC-3'. PCR amplification conditions were: 94°C (5 min), 30 cycles at 94°C (30 s) / 56°C (45 s) / 72°C (45 s), followed by 8 cycles 94°C (30 s) / 53°C (45 s) / 72°C (45 s), and a final extension at 72°C for 10 min (Schuelke 2000). Each reaction (15 µL) contained 70 ng of DNA template, 0.5 units/µL Taq DNA polymerase, 67 mM Tris-Hcl pH 8.8, 16 mM $(NH_4)SO_4$, 2 mM $MgCl_2$, 0.2 mM dNTPs, 0.075 µM of Forward primer, 0.3 µM of Reverse and M13 primers and ddH_2O to volume.

After locus validation, 12 loci were selected and successfully combined in four multiplex groups (Table 2.1) using the software Multiplex Manager 1.0 (Holleley & Geerts 2009). Conditions of the PCR amplification were as follows: 94ºC (5 min), then 36 cycles at 94ºC (30 s) / 60ºC (45 s) / 74ºC (60 s) and a final extension at 74ºC (10 min). Each reaction (15 µL) contained 70 ng of DNA template, 0.5 units/µL Taq DNA polymerase, 67 mM Tris-HCl pH 8.8, 16 mM $(NH_4)SO_4$, 2 mM $MgCl_2$, 0.2 mM dNTPs, 0.3 µM of Forward and Reverse primers and ddH_2O to volume. A total of 32 STRs (65%) were

successfully amplified. PCR products were sent for genotyping on an ABI3730 Genetic Analyzer (Macrogen Inc., Korea) and fragment sizes were scored manually. To improve cost-effectiveness, the PCR products were mixed together in two groups and analyzed simultaneously (PCR pool-plexing). The markers were tested for polymorphism in 122 randomly selected individuals collected from Little Barrier Island (-36° 13' 51.0", +175° 4' 17.40") and Wellington Harbour (-41° 18' 05.0", +174° 48' 35.0") and basic statistics were calculated for each locus. Microchecker (Van Oosterhout *et al.* 2004) was used to check for null alleles, stuttering and large allele dropout. Tests of linkage disequilibrium, departure from Hardy-Weinberg equilibrium (HWE), estimates of diversity and the expected and observed heterozygosities (H_e and H_o) were performed in GENEPOP (Rousset 2008).

Results

The runs yielded a total of 315,404 DNA sequences (Figure 2.1) and iQDD identified 448 perfect microsatellite motif sequences with primers. The best primer pairs were selected and a total of 49 primers were tested for PCR amplification. Loci were discarded if they failed to amplify, showed high levels of allelic drop out, were confounded by artefacts or were monomorphic. Of these, 12 loci gave consistent results and were retained. All loci were polymorphic and the number of alleles ranged from 6 to 37 (Table 2.1). No evidence of stuttering or large allele dropout was detected and no significant linkage disequilibrium was detected between locus pairs (GENEPOP v.4.2 using the Markov chain method and Fisher´s exact test). The observed (H_o) and expected (H_e) heterozygosities ranged from 0.209 to 0.926 and from 0.318 to 0.961, respectively. Three loci (*Pnova*_01, *Pnova*_24 and *Pnova*_27) showed significant deviation from HWE and evidence of null alleles.

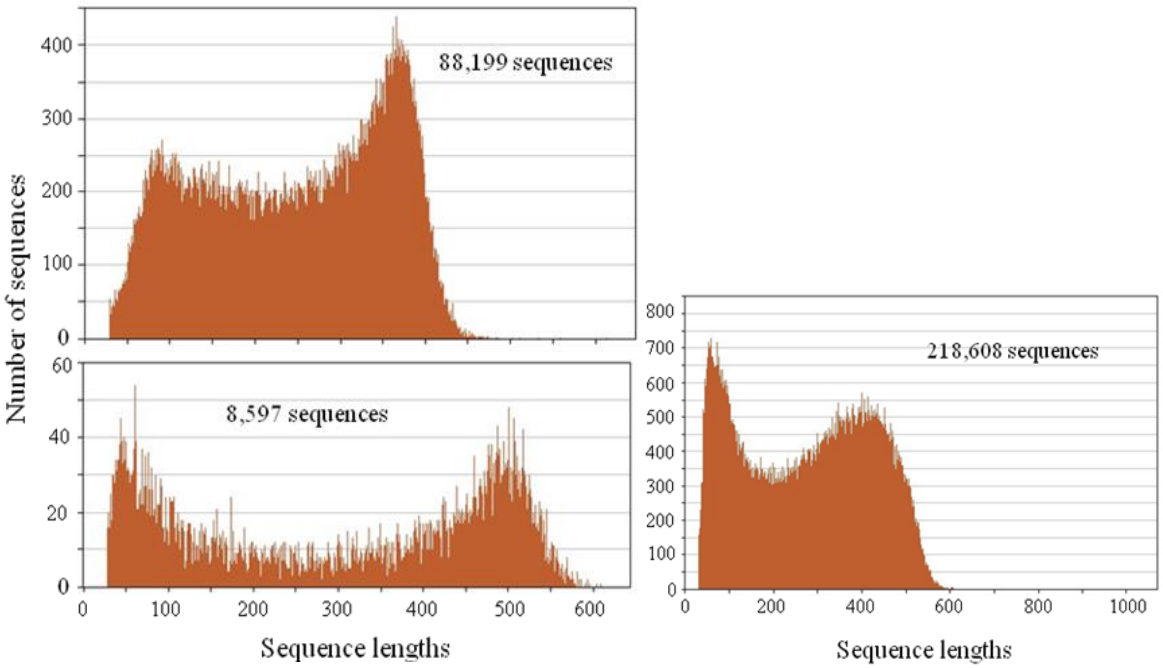

Figure 2.1 Length frequency of the 88199, 8597 and 218608 reads, respectively, obtained with a 1/8th run on a 454 GS FLX instrument for *Pecten novaezelandiae*.

Discussion

The method used in this study allows a relatively rapid and affordable development of microsatellite markers. The next generation sequencing yields a vast amount of data (over 100,000 sequences produced by the 454 method) and the software iQDD V1.3 (Meglécz *et al.* 2010) scans potential primers, therefore prioritizing a potential number of primers before the laboratory testing phase. In addition, using the M13(-21) primer genotyping protocol (Schuelke 2000) and PCR pool-plexing can save thousands of dollars offering a better alternative for small research budgets.

Microsatellite development can be challenging particularly for highly fecund marine bivalves with high mutation rates. Previous studies have reported null alleles (i.e. alleles that fail to amplify by the polymerase chain reaction) in bivalves (Hedgecock *et al.* 2004; Marín *et al.* 2012) causing the underestimation of heterozygotes and consequently deviations from Hardy-Weinberg equilibrium (HWE) expectations. For that reason the

markers *Pnova*_01, *Pnova*_24 and *Pnova*_27 should be used with caution having in mind the scale to which they might influence results.

The scallop *Pecten novaezelandiae* has been widely studied in New Zealand as an important and valued fishery resource (e.g. Williams and Babcock 2004; Williams and Babcock 2005). A few phylogenetic studies have been done to date to elucidate the evolutionary relationships and taxonomy of the family Pectinidae (Saavedra & Peña 2006; Puslednik & Serb 2008; Salvi *et al.* 2010). However, there was no previous information on the genetic structure of *P. novaezelandiae*. These newly developed microsatellite markers are particularly suitable for assessing current levels of genetic variability within and between populations of *P. novaezelandiae* as well as identifying the degree of differentiation between stocks and therefore are of great utility as a tool for informing conservation management.

Table 2.1 Polymorphic microsatellite markers for *P. novaezelandiae* with locus characteristics, number of alleles (N_a), observed heterozygosity (H_o), expected heterozygosity (H_e), probability of being out of Hardy-Weinberg Equilibrium (HWE).

Multiplex group	Locus	Accession no.	Repeat	Forward primer sequence (5´-3´)	Allele size range (bp)	N_a	H_o	H_e	HWE p-value
1 (Pool 1)	*Pnova*_09	KF732829	$(AGTT)_5$	GGCGTCCACTGACAGATAAG	112-144	7	0.351	0.349	0.870
	*Pnova*_24	KF732831	$(AGAC)_5$	CACTGACGAAACGTTGGTGT	116-140	7	0.307	0.395	0.003
2 (Pool 1)	*Pnova*_02	KF732826	$(TA)_{11}$	CAGTAGCTCCTGCCCCATTA	163-185	11	0.661	0.695	0.792
	*Pnova*_10	KF732830	$(TA)_{11}$	GGAAGGAAGCACAGCAGGTA	258-278	7	0.274	0.318	0.236
	*Pnova*_27	KF732832	$(TATC)_{33}$	CAGATACGTCAGAGTGCTGATTC	191-343	37	0.877	0.961	0.007
3 (Pool 1)	*Pnova*_01	KF732825	$(TA)_8$	GTAGCACACGCAAATGCCTA	207-229	6	0.209	0.377	0.000
	*Pnova*_04	KF732827	$(TTGT)_7$	AATGCAGGAAGGTTTTGGTTT	276-300	7	0.681	0.627	0.312
	*Pnova*_28	KF732833	$(CAA)_{19}$	AAGGCATATAACTCAGCTGGAA	254-377	34	0.926	0.959	0.138
4 (Pool 2)	*Pnova*_05	KF732828	$(ACAG)_7$	AGCGACATACAATGGGGAAG	131-163	9	0.764	0.749	0.679
	*Pnova*_31	KF732834	$(TA)_{11}$	TGCGCTACAGTGTCGTTCTT	108-122	8	0.681	0.617	0.034
	*Pnova*_32	KF732835	$(AT)_{11}$	GTGTCGTCTACAGCCGGAAT	175-185	6	0.458	0.496	0.626
	*Pnova*_33	KF732836	$(AATAT)_{10}$	CTCCAGGAGTAGAGCCGATG	164-214	10	0.691	0.789	0.380

CHAPTER 3

Genetic structure of *Pecten novaezelandiae* throughout its distribution range

Introduction

Many marine species have low levels of population genetic differentiation as a result of large population sizes, high fecundity and a pelagic larval stage (Cowen & Sponaugle 2009). Pelagic larvae provide species with a high dispersal capability and larval transport is expected to play an important role in determining population structure (Hedgecock 1986). The maximum dispersal ability can be related to the pelagic larval duration and the distance able to be travelled during that time (Bohonak 1999). There are now many examples of species showing extensive gene flow and panmixia (Apte & Gardner 2001; Neethling *et al.* 2008; Reisser *et al.* 2014), but it has become clear that even marine invertebrates with a long pelagic larval duration can exhibit significant genetic differentiation (Thomas & Bell 2013). The trade-off between potential and realised gene flow has only recently begun to be appreciated (Shanks 2009; Dawson *et al.* 2014; Reisser *et al.* 2014).

There are many factors that influence the population genetic structure of species, particularly life history strategy and ocean currents (Shanks 2009), which highlights the importance of considering each species independently. Usually, the observed population genetic structure of a species is shaped by historical factors, such as past glaciations or changes in sea level, which leave a present genetic signature (Hewitt 1996), and contemporary factors such as current barriers to gene flow. Therefore, the degree of genetic variation between populations is the result of the interaction between gene flow, genetic drift, mutation, natural selection and historical processes (Gaggiotti *et al.* 2009).

For widely distributed species, populations at the edges of their distributions are expected to have lower abundance as they become more spatially isolated from the geographical centre of their distribution (Vucetich & Waite 2003). This is commonly referred to as the ‘abundant centre’ model, which has been frequently discussed within the context of the ecology and evolution of species’ ranges (Sagarin & Gaines 2002). A resulting debate has ensued in evolutionary biology as to the degree to which the ‘abundant centre’ distribution model is expressed in the amount of genetic diversity among populations in the geographic range of the species. While some studies show a decline in genetic diversity and increased differentiation towards the species range limits (reviewed in Eckert et al. 2008), the mechanisms that create these patterns are not clear. Therefore, studies that can encompass the entire distribution range of a species can provide valuable

information about the relative roles of historical and contemporary factors in shaping genetic variability and patterns of genetic structure (Hasselman *et al.* 2013).

New Zealand has a wide diversity of habitats and high levels of endemism. Its marine environment ranges from 34° to 47° latitude south, with subtropical to sub-polar characteristics and a very complex oceanography (see Gordon *et al.* 2010). In New Zealand most studies on the population genetic structure of marine organisms are of rocky reef species; studies of species living on sandy and soft bottom habitats are scarce (see Gardner *et al.* 2010). The endemic New Zealand scallop *Pecten novaezelandiae* supports a number of important fisheries but there is no previous information regarding its genetic structure. On the one hand, the species has traits commonly associated with high potential for dispersal, as a broadcast spawner with high fecundity (Williams & Babcock 2004; Shumway & Parsons 2006). In contrast, these scallops have characteristics that might be expected to lead to population differentiation since they are relatively long-lived (>7 years), adults are sedentary and patchily distributed (Morrison 1999), and they have an estimated pelagic larval duration of approximately two to three weeks (Williams & Babcock 2004; Shumway & Parsons 2006). As a comparison, the New Zealand bivalve *Paphies subtriangulata*, which has a similar pelagic larval duration, showed evidence of strong differentiation between the Chatham Islands and the mainland populations (Hannan 2014), while *Perna canaliculus* with a longer pelagic larval duration (three to five weeks), shows north-south differentiation in New Zealand, with a genetic break at about 42° S latitude (Apte & Gardner 2002).

A variety of patterns of population genetic structure have been observed in New Zealand. Gardner *et al.* (2010) categorised these patterns as: (1) no structure; (2) isolation by distance; (3) divergence within and among populations; (4) east-west divergence; and (5) north-south divergence. Most of the studies (33%) reported a north-south split around the southern region of the Cook Strait, at about 42° S. For some species, such as *Perna canaliculus* and *Patiriella regularis*, the reported divergence time between North and South Island populations dates to approximately 1.3 Ma ago (Apte & Gardner 2002; Ayers & Waters 2005), which corresponds to a period of hydrographic change across the Cook Strait region (Lewis *et al.* 1994). In contrast, the contemporary North and South Island lineages of each of the three endemic intertidal limpets *Cellana ornata*, *Cellana radians* and *Cellana flava* diverged approximately 200 000 to 300 000 years ago (Goldstien *et al.* 2006).

While both historical and current factors are expected to shape existing patterns of genetic differentiation, examining their relative importance can be challenging. The recent evolutionary history of *Pecten novaezelandiae* might be indicative of a potentially weak genetic differentiation across its distributional range. Fossil records in New Zealand document the origin of the genus *Pecten* as a result of succession of populations during the Pleistocene, approximately 1 Ma ago (Beu 2010). Therefore, the recent evolutionary history of the New Zealand scallop allows for testing of the effects of more recent evolutionary processes in shaping species population genetic structure. In addition, evaluating latitudinal changes in genetic diversity of *Pecten novaezelandiae* can provide more information on its colonization history and on recent factors affecting gene flow. Finally, as microsatellite markers are highly variable, they are especially useful for the interpretation of recent demographic events. In this study, the null hypothesis of panmixia of *P. novaezelandiae* was tested using 12 microsatellites (Silva & Gardner 2014) and a range of statistical analyses.

Materials and methods

Sample collections

In total, 952 individuals of *Pecten novaezelandiae* were sampled throughout its distribution range between 2012 and 2014. Sampling was dependent on the hotspots of distribution of the species. Samples were collected from 15 populations (Figure 3.1) using dredging from depths between 15 – 50 m and SCUBA diving from depths between 7 – 15 m. The number of individuals per site varied between 10 and 99 (Table 3.1). After collection, scallops were measured (length of the top shell), size structure was analysed using the software R 3.1.0 (R Core Team 2014) and samples of the adductor muscle were preserved in 80% ethanol and frozen (-20^{o}C) for later processing.

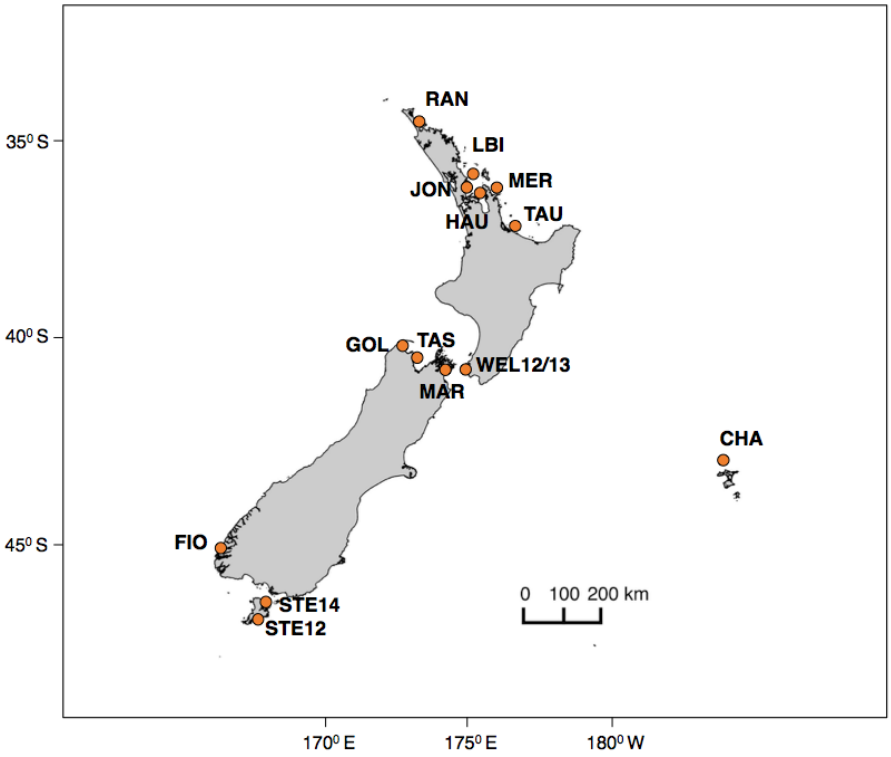

Figure 3.1 Map of sampling sites of *Pecten novaezelandiae* collected from New Zealand. Abbreviations as per Table 3.1

Table 3.1 *Pecten novaezelandiae* collecting site descriptions, sample sizes (N), mean depth (m), dates and geospatial coordinates

Code	Site Description	N	Depth (m)	Date collected	Latitude	Longitude
RAN	Rangaunu Bay	98	42	3/11/2012	-34° 49' 2.8"	+173° 18' 6.45"
LBI	Little Barrier Is	95	15	1/05/2012	-36° 13' 51.0"	+175° 4' 17.40"
JON	Jones Bay	40	10	15/11/2012	-36° 22' 53.6"	+174° 48' 59.48"
HAU	Hauraki Gulf	99	43	28/11/2012	-36° 34' 9.60"	+175° 14' 6.57"
MER	Mercury Is	69	15	1/05/2012	-36° 41' 3.60"	+175° 43' 33.60"
TAU	Tauranga	99	22	3/05/2012	-37° 40' 14.4"	+176° 24' 10.80"
WEL12	Wellington Harbour	67	10	3/02/2012	-41° 18' 05.0"	+174° 48' 35.0"
WEL13	Wellington Harbour	48	10	31/05/2013	-41° 18' 05.0"	+174° 48' 35.0"
MAR	Marlborough Sounds	50	15	11/12/2012	-41° 11' 54.8"	+174° 07' 09.2"
TAS	Tasman Bay	48	22	13/05/2014	-41° 04' 27.0"	+173° 05' 48.0"
GOL	Golden Bay	48	20	14/05/2014	-40° 36' 27.6"	+172° 46' 40.8"
FIO	Fiordland	35	9	1/10/2012	-45° 35' 7.51"	+166° 44' 4.34"
STE12	Stewart Is, Port Pegasus	10	10	11/05/2012	-47° 10' 6.53"	+167° 42' 0.97"
STE14	Stewart Is, Paterson Inlet	48	7	4/04/2014	-46° 55' 58.0"	+168° 04' 15.0"
CHA	Chatham Is	98	50	11/03/2013	-43° 42' 32.40"	-176° 23' 38.40"
Total		952				

Laboratory protocols

Total DNA was extracted from the adductor muscle using Geneaid Genomic DNA Mini Kits (Tissue) following the manufacturer´s instructions. DNA concentrations and the A260/A280 ratios were quantified using a NanoDrop™ ND-1000 (Thermo Scientific). Specimens were genotyped at 12 polymorphic microsatellite loci: *Pnova_01*, *Pnova_02*, *Pnova_04*, *Pnova_05*, *Pnova_09*, *Pnova_10*, *Pnova_24*, *Pnova_27*, *Pnova_28*, *Pnova_31*, *Pnova_32*, *Pnova_33* (Silva & Gardner 2014). Microsatellite loci were PCR-amplified in reactions (15 µL) containing 70 ng of DNA template, 0.5 units/µL *Taq* DNA polymerase, 67 mM Tris–HCl pH 8.8, 16 mM $(NH_4)SO_4$, 2 mM $MgCl_2$,0.2 mM dNTPs, 0.3 µM of Forward and Reverse primers and ddH_2O to volume. Based on the combinations recommended by the Multiplex Manager 1.0 program (Holleley & Geerts 2009), primer pairs were PCR multiplexed using the conditions described in Chapter 2, Supplementary Table 1. Primers were fluorescently labelled (FAM, NED, PET and VIC) and groups 1, 2 and 3 were pool-plexed. PCR products were visualized with an automated sequencer (ABI PRISM 3730 DNA Sequencer, Applied Biosystems) with the GeneScan-500 (LIZ) internal size standard. The software GeneMarker V2.2.0 (SoftGenetics) was used to analyse electropherograms for allele scoring and the alleles were binned with manual checking using the AutoBin program (Guichoux *et al.* 2011).

Analysis of genetic diversity

Genotyping artefacts were assessed using the software Micro-Checker v.2.2.0.3 (Van Oosterhout *et al.* 2004). Analysis of departure from Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium (LD) were performed using the software GenePop on the web using the Markov chain method and Fisher´s exact test (Rousset 2008). False discovery rate (FDR) control (Verhoeven *et al.* 2005) was applied to p-values in all statistical analyses that included multiple comparisons.

To determine whether sufficient sample size was achieved to accurately represent allelic variation, allele discovery curves were computed for the twelve loci using the package "PopGenKit" (Rioux Paquette 2011) in R 3.1.0 (R Core Team 2014). Data were combined from all populations for this analysis.

An outlier analysis was performed using the software Lositan (Antao *et al.* 2008), which identifies any outlier loci that have excessively high or low F_{ST} values compared to neutral expectations, considering the relationship between F_{ST} and H_E (expected heterozygosity) in an island model. Fifty thousand simulations were run with a confidence interval (CI) of 0.95 under the infinite alleles model (IAM) for a sample size of 50. The average neutral F_{ST} was used and the "force mean F_{ST}" option was selected to increase the reliability of mean F_{ST}.

The software HP-Rare (Kalinowski 2005) was used to quantify genetic diversity as allelic richness (A_R) and private allelic richness (PA_R) with a rarefaction sample size of 24 individuals and a minimum sample size of 16 genes due to missing data. GenAlEx 6.5 (Peakall & Smouse 2012) was used to quantify the number of private alleles per site (Pa), observed (H_O) and expected (H_E) heterozygosity, and the fixation index (F_{IS}).

Population structure

Genetic differentiation among populations was assessed using different approaches. Pairwise F_{ST} values were calculated using the software GenePop on the web (Rousset 2008). This F_{ST} value, formally known as theta (θ), was adapted by Weir & Cockerham (1984) for using with multiallelic loci, it is unbiased to different sample sizes and uses an ANOVA approach to standardize variation within and among populations. An Exact G-test (Goudet *et al.* 1996) was also calculated in GenePop (Markov-chain parameters: 10,000 dememorization steps, 1,000 batches and 10,000 iterations per batch) for each population pair using the G log likelihood ratio. All p-values were corrected using the False Discovery Rate (FDR) (Verhoeven *et al.* 2005) and comparisons were considered significant at $p < 0.05$.

Pairwise R_{ST} values were calculated using the software Arlequin 3.5.1.3 (Excoffier & Lischer 2010) with 10,000 permutations for significance. R_{ST} is an F_{ST} analogue (Slatkin 1995) that considers a stepwise mutation model in microsatellite loci, meaning that each mutation changes an allele´s length by only one repeat unit. All p-values were adjusted for multiple comparisons using FDR (Verhoeven *et al.* 2005).

Modified pairwise statistics (F'_{ST}) were calculated using the software GenoDive 2.0b25 (Meirmans & Van Tienderen 2004). The F'_{ST} index is based on the AMOVA (analysis of

molecular variance) framework (Excoffier et al., 1992). It is a standardised measure based on a maximum possible value given the observed amount of within-population diversity and therefore has no p-value associated with it.

Pairwise Jost's D values (Jost 2008) were calculated using the software GenoDive 2.0b25 (Meirmans & Van Tienderen 2004). Jost (2008) proposed the D_{ST} metric, which takes total variation and differentiation into account and has no p-value associated with it.

Powsim 4.1 (Ryman & Palm 2006) was used to assess the statistical power and estimate the probability of detecting differentiation at F_{ST} values of 0.001, 0.0025, 0.005 and 0.01. Using 20 replications, the $\chi^2$and Fisher´s exact tests were used for a set of simulations with different combinations of N_{ef} (effective population size) and t (generations of drift).

A principal components analysis (PCoA) was performed in GenAlEx 6.5 (Peakall & Smouse 2006) to examine the variation among populations using co-dominant genetic distance. GenAlEx 6.5 (Peakall & Smouse 2012) was also used to conduct the Analysis of Molecular Variation (AMOVA) using 999 permutations. The sampling sites were grouped according to the PCoA and the F_{ST} values. The 15 populations were grouped into 4 regions (North: RAN, LBI, JON, HAU, MER, TAU; Central: WEL12, WEL13, MAR, TAS, GOL; South: FIO, STE12, STE14; and Chatham Islands: CHA). An AMOVA was also conducted in GenAlEx 6.5 for the populations WEL12 and WEL13 to test if the temporal sampling differences (2012 versus 2013) explained any of the variation in the Wellington Harbour dataset. The following analyses were conducted using WEL as one single population because temporal differences did not explain any of the variation in the datasets of WEL12 and WEL13 (see Results section).

The neighbor joining (NJ) method (Saitou & Nei 1987) was used to generate a population tree using the software PopTreeW (Takezaki *et al.* 2014) based on F_{ST} values with 1000 bootstrap replicates.

The software package AWclust (Gao & Starmer 2008) was used to evaluate population genetic structure among populations. AWclust is a nonparametric analysis and therefore does not assume HWE or linkage disequilibrium. This analysis was specifically designed for SNPs, so each microsatellite allele at each locus was coded as zero, one (heterozygous) or two (homozygous), following the approach of Gruber *et al.* (2013) and Wei *et al.* (2013a). The gap statistic was calculated for values of K ranging from 1 to 14 using 100

null simulations. As a comparison, Bayesian cluster analysis was performed in Structure 2.3.4 (Pritchard *et al.* 2000) using 100,000 interactions, a burn-in length of 10,000, 'admixture' model, 'correlated allele frequencies' and sampling regions were used as 'prior' for k=1 through k=14. LOCPRIOR models were used because they are best suited for cases of low genetic structure (Pritchard *et al.* 2000). Results were evaluated using the software Structure Harvester (Earl & VonHoldt 2012) and the appropriate number of clusters was determined by plotting the log probability (L(K)) and ΔK across multiple runs according to Evanno *et al.* (2005). A Spearman correlation test was done using the r software (R Core Team 2014) to test the correlation between the proportions of clusters with latitude. A spatial Bayesian analysis was also conducted in Geneland (Guillot *et al.* 2012) in order to incorporate information on the spatial distribution of samples and to relate observed patterns to geography. The model was implemented in a Markov Chain Monte Carlo scheme, using 100,000 interactions, and the correlated frequency model was used, which allows the detection of structure in the presence of low genetic differentiation.

Mantel tests were calculated in GenAlEx (Peakall & Smouse 2012) using both F_{ST} and R_{ST} and the shortest coastal distances as measured on Google Earth. Isolation by distance was first tested using all the 14 mainland populations (CHA was excluded), then excluding STE12 (due to low sample size) and then only the north and central group were used (edge populations STE12, STE14 and FIO were excluded).

To test whether genetic variation within populations is related to geographical gradients, a linear regression analysis was carried out in the software R 3.1.0 (R Core Team 2014). Latitude was plotted as a function of allelic richness (A_R) and private allelic richness (PA_R).

Estimates of migration

Assignment tests were used to identify first-generation migrants as well as the proportion of individuals recruiting to a location. Assignment tests are known to be more effective when genetic structure is high, therefore populations were grouped based on the four regions identified by the significance of previous analyses. The Bayesian program Geneclass 2 (Piry *et al.* 2004) was used with the Markov chain Monte Carlo (MCMC) resembling the algorithm of Paetkau et al. (2004). The likelihood ratio 'L_home/L_max' was used with a 0.01 rejection level and a simulated population size of 10,000 individuals per site. This approach pulls an individual's genotype from the location in which it was

sampled over the highest likelihood observed for this genotype in any location (Paetkau *et al.* 2004). The individuals were assigned to the region with the highest probability.

Results

All scallops sampled were >55 mm in shell length and classified as mature (Williams & Babcock 2005). The average size of all individuals was 99.68 ± 11.55 mm (Figure 3.2) and at this length they are likely to have recruited between 1.5 and 3.5 years prior to collection (2009–2011).

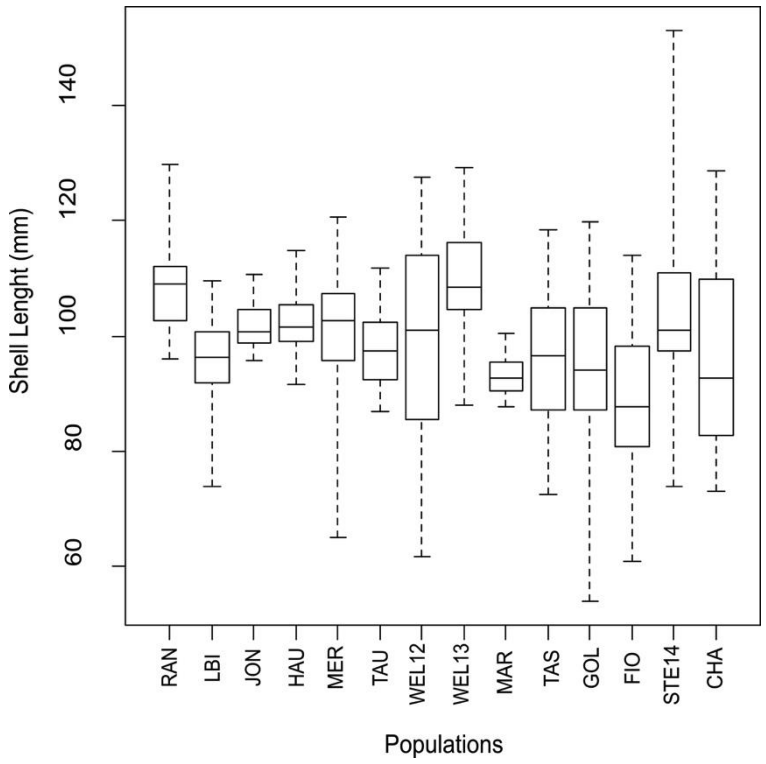

Figure 3.2 Size structure of *Pecten novaezelandiae* from 14 study sites in New Zealand (shells from samples collected in STE12 were not available). Dashed lines represent the maximum and minimum size at each site, while the bars represent the 25th and 75th quartile of size ranges, with the median indicated within each bar.

Genetic diversity

In total, 952 individuals were genotyped for variation at 12 microsatellite loci. *Pnova_24* and *Pnova_31* had the most missing data at 21.3% and 19.1%, respectively. The other 10 loci had an average of 2.7% of missing data.

Micro-Checker identified putative null alleles at *Pnova_02*, *Pnova_05*, *Pnova_10*, *Pnova_24*, *Pnova_27* and *Pnova_33* due to homozygote excess at each locus. However, no pattern or trend of null allele frequency as a function of either population or locus was identified. No long allele dropout was detected. After FDR correction for multiple tests, *Pnova_24* and *Pnova_33* were identified as being significantly out of HWE at more than half of the populations. No evidence of significant linkage disequilibrium was detected between locus pairs. Most of the allele discovery curves reached a plateau, with the exception of *Pnova_01*. The loci *Pnova_27* and *Pnova_28* were found to be the most polymorphic (Supplementary Figure 1).

Pnova_27 and *Pnova_28* were identified as candidates for balancing selection under the stepwise mutation model and *Pnova_27, Pnova_28* and *Pnova_33* under the infinite alleles model. However, this is possibly an artefact due to the very low values of F_{ST}. *Pnova_01, Pnova_02, Pnova_04, Pnova_05, Pnova_09, Pnova_10* and *Pnova_32* were identified as neutral markers under the infinite allele and stepwise mutation models. *Pnova_24* and *Pnova_31* were identified as F_{ST} outliers and candidates for positive selection under the infinite allele and stepwise mutation models. *Pnova_24* and *Pnova_31* were therefore excluded from the following analyses due to a combination of factors (i.e. missing data and F_{ST} outliers).

Allelic richness ranged from 4.91 in FIO to 5.89 in RAN. Private allelic richness ranged from 0.08 in FIO to 0.26 in WEL13. In total there were 27 private alleles across all populations; RAN had the higher number (8). Overall, there were lower levels of observed heterozygosity H_O = 0.616, than expected heterozygosity H_E = 0.659. F_{IS} ranged from -0.090 at STE12 to 0.146 at HAU (Table 3.2).

Table 3.2 Descriptive measures of genetic variation in *P. novaezelandiae* for 10 loci. Allelic richness (A_R), private allelic richness (PA_R), number of private alleles per site (Pa), observed heterozygosity (H_O), expected heterozygosity (H_E) and fixation index (F_{IS})

Population	A_R	PA_R	Pa	H_O	H_E	F_{IS}
RAN	5.89	0.25	8	0.616	0.676	0.078
LBI	5.83	0.21	2	0.605	0.665	0.088
JON	5.76	0.17	1	0.596	0.668	0.115
HAU	5.85	0.19	2	0.564	0.671	0.146
MER	5.87	0.21	5	0.662	0.670	0.006
TAU	5.70	0.19	1	0.596	0.658	0.083
WEL12	5.73	0.16	1	0.639	0.648	-0.001
WEL13	5.75	0.26	1	0.608	0.651	0.058
MAR	5.69	0.16	0	0.609	0.661	0.095
TAS	5.45	0.12	1	0.575	0.642	0.088
GOL	5.66	0.11	0	0.583	0.641	0.062
FIO	4.91	0.08	0	0.593	0.635	0.059
STE12	5.28	0.09	0	0.695	0.650	-0.090
STE14	5.41	0.12	4	0.689	0.680	-0.013
CHA	5.50	0.12	1	0.611	0.663	0.074

Population structure

The pairwise F_{ST} analysis for all comparisons ranged from 0 to 0.027 (Table 3.3). Of the 105 comparisons between pairs of populations, 44 were significant after FDR corrections. FIO, STE14 and CHA had the highest values of F_{ST} and therefore the highest number of statistically significant pairwise comparison outcomes. There were 6 significant comparisons between populations in the northern and central groups (WEL12–MER, WEL13–TAU, MAR–MER, MAR–TAU, TAS–HAU, TAS–MER), however there were no significant comparisons between sample sites within groups (northern and central). In terms of the mean F_{ST} per population, HAU had the lowest value (0.0038) and FIO had the highest (0.0154; Table 3.3). Similar patterns were seen in values of R_{ST}, which ranged from 0 to 0.026. However, more (45) significant R_{ST} comparisons were observed, including one within the northern group (MER–LBI; Table 3.3). In total, 42% of the comparisons of F_{ST} values and 43% of R_{ST} values were significantly different.

The F'_{ST} values ranged from 0 to 0.082 (Table 3.4). The populations FIO, STE12, STE14 and CHA had the highest values of F'_{ST} when compared to other populations. A similar pattern was observed for values of D_{ST} that ranged from 0 to 0.060 and had the highest values for the populations FIO, STE12, STE14 and CHA (Table 3.4).

Power analysis indicated that pairwise F_{ST} values as low as 0.0025 had a probability of 100% of detecting a true F_{ST} value for both Fisher´s exact test and χ^2. This indicates that there is sufficient resolution to detect weak differentiation among populations using 10 microsatellite loci.

Table 3.3 Pairwise F_{ST} values for *Pecten novaezelandiae* using 10 loci are below the diagonal and R_{ST} values are above the diagonal. Significant values are in bold after FDR testing. Mean F_{ST} values for each population are in the bottom row.

Code	RAN	LBI	JON	HAU	MER	TAU	WEL 12	WEL 13	MAR	TAS	GOL	FIO	STE 12	STE14	CHA
RAN		-0.003	-0.004	-0.002	0.002	0.002	0.000	-0.002	-0.001	-0.001	0.000	**0.017**	0.005	**0.018**	**0.005**
LBI	0.000		-0.002	0.000	**0.004**	0.001	0.001	0.004	0.004	-0.002	0.000	**0.020**	0.012	**0.021**	**0.004**
JON	0.000	0.0010		0.001	-0.001	0.000	-0.003	-0.004	-0.002	-0.004	0.001	**0.017**	0.003	**0.019**	**0.006**
HAU	0.000	0.001	0.001		0.001	0.002	0.001	0.000	0.001	0.002	0.000	**0.015**	-0.001	**0.018**	**0.004**
MER	0.002	0.003	0.002	0.000		0.000	**0.008**	**0.006**	**0.008**	**0.007**	**0.008**	**0.016**	0.007	**0.026**	**0.010**
TAU	0.002	0.001	0.002	0.002	0.000		**0.005**	**0.007**	**0.009**	0.002	**0.004**	**0.018**	0.008	**0.023**	**0.008**
WEL12	0.002	0.001	0.002	0.002	**0.007**	0.006		0.001	0.003	0.002	-0.002	**0.011**	0.007	**0.016**	0.003
WEL13	0.001	0.004	0.000	0.001	0.006	**0.008**	0.000		0.003	0.002	0.002	**0.017**	-0.002	**0.015**	**0.007**
MAR	0.001	0.004	0.002	0.002	**0.008**	**0.009**	0.002	0.001		0.002	0.003	**0.011**	0.001	**0.016**	**0.006**
TAS	0.001	0.000	0.000	**0.003**	**0.006**	0.003	0.001	0.000	0.001		-0.002	**0.011**	0.003	**0.015**	**0.005**
GOL	0.003	0.000	0.005	0.001	0.007	0.006	0.000	0.002	0.003	0.000		**0.009**	0.011	**0.017**	**0.004**
FIO	**0.017**	**0.018**	**0.018**	**0.014**	**0.016**	**0.017**	**0.012**	**0.019**	**0.012**	**0.013**	**0.010**		0.016	**0.015**	**0.019**
STE12	0.005	0.011	0.004	0.000	0.009	0.008	0.011	0.003	0.004	**0.008**	0.015	**0.015**		-0.006	0.001
STE14	**0.020**	**0.022**	**0.023**	**0.021**	**0.027**	**0.024**	**0.018**	**0.017**	**0.019**	**0.018**	**0.022**	**0.016**	0.000		**0.017**
CHA	**0.005**	**0.005**	**0.007**	**0.005**	**0.011**	**0.008**	**0.005**	**0.009**	**0.008**	**0.008**	**0.008**	**0.018**	0.002	**0.018**	
Mean F_{ST}	0.0042	0.0051	0.0048	0.0038	0.0074	0.0069	0.0049	0.0051	0.0054	0.0044	0.0059	0.0154	0.0068	0.0189	0.0084

Table 3.4 F'_{ST} values for *Pecten novaezelandiae* using 10 loci below diagonal and D_{ST} values above diagonal.

Code	RAN	LBI	JON	HAU	MER	TAU	WEL 12	WEL 13	MAR	TAS	GOL	FIO	STE 12	STE14	CHA
RAN		-0.003	-0.002	-0.003	0.004	0.004	0.004	0.002	0.003	0.003	0.005	0.035	0.014	0.043	0.010
LBI	-0.008		0.003	0.002	0.007	0.002	0.003	0.009	0.009	-0.003	0.000	0.036	0.025	0.047	0.011
JON	-0.009	-0.002		0.003	0.004	0.005	0.003	0.000	0.004	0.001	0.01	0.036	0.009	0.048	0.014
HAU	-0.007	-0.001	-0.004		0.001	0.004	0.004	0.003	0.004	0.006	0.003	0.029	-0.002	0.045	0.011
MER	0.002	0.006	0.000	-0.002		0.001	0.015	0.012	0.018	0.012	0.014	0.032	0.020	0.060	0.022
TAU	0.003	0.000	0.001	0.003	-0.002		0.011	0.015	0.019	0.006	0.011	0.033	0.016	0.051	0.016
WEL12	0.001	0.000	-0.002	0.001	0.019	0.013		0.001	0.005	0.002	-0.003	0.023	0.023	0.036	0.010
WEL13	-0.003	0.008	-0.007	-0.001	0.014	0.018	-0.005		0.003	0.001	0.003	0.035	0.007	0.036	0.020
MAR	-0.002	0.008	-0.003	-0.001	0.021	0.022	0.000	-0.003		0.002	0.005	0.024	0.010	0.040	0.018
TAS	0.000	-0.009	-0.006	0.003	0.014	0.006	-0.002	-0.005	-0.005		-0.005	0.024	0.016	0.038	0.017
GOL	0.002	-0.005	0.005	-0.003	0.016	0.011	-0.011	-0.003	-0.002	-0.014		0.019	0.031	0.045	0.016
FIO	0.045	0.047	0.045	0.034	0.042	0.043	0.029	0.046	0.027	0.031	0.02		0.030	0.033	0.036
STE12	-0.003	0.014	-0.021	-0.032	0.012	0.002	0.015	-0.012	-0.015	0.002	0.014	0.023		-0.001	0.006
STE14	0.057	0.063	0.063	0.058	0.082	0.069	0.049	0.048	0.052	0.051	0.059	0.044	-0.014		0.038
CHA	0.012	0.014	0.017	0.014	0.030	0.021	0.012	0.026	0.023	0.023	0.020	0.050	-0.004	0.053	

Genetic structure was apparent from the principal components analysis (PCoA), which showed that Axis 1 explained 38% of the variation and Axis 2 explained 25.3% (Figure 3.3). The analysis grouped the populations sampled in the top of the North Island (RAN, LBI, JON, HAU, MER, TAU) in quadrant III and the populations sampled in central New Zealand (WEL12, WEL13, MAR, TAS, GOL) in quadrant II. Fiordland (FIO), Stewart (STE12, STE14) and Chatham Islands (CHA) were plotted separately from the remainder populations.

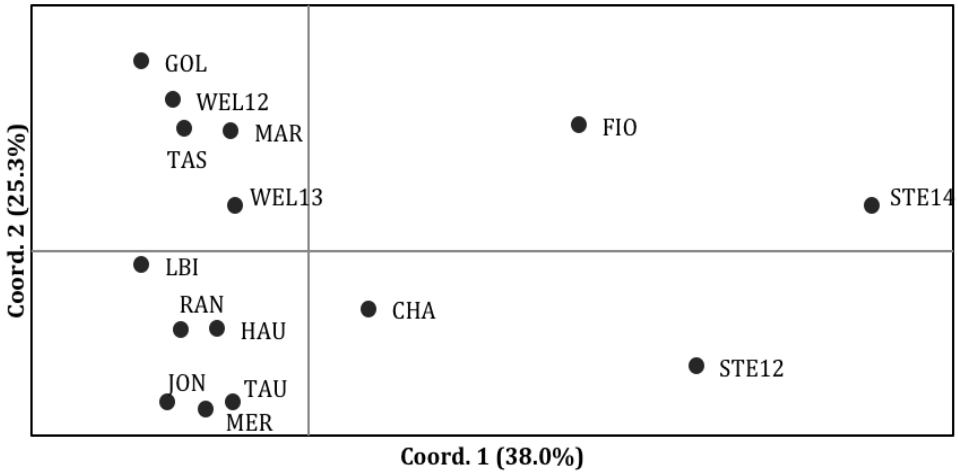

Figure 3.3 Principal components analysis (PCoA) for *Pecten novaezelandiae* using pairwise genetic distance based on 10 microsatellite loci.

AMOVA analysis for the four regions grouped in the PCoA analysis showed 86.2% of the variation was explained within populations, 12.8% explained among individuals, 0.3% explained among populations and 0.7% explained among regions: the model was significant at p=0.01 (Table 3.5). Temporal differences did not explain any of the variation in the datasets of WEL12 and WEL13 populations (AMOVA, p=0.05). Therefore the following analyses were conducted using WEL as one single population.

Table 3.5 Analysis of molecular variance (AMOVA) for 14 populations from 4 regions using 10 loci.

Source of variation	Degrees of Freedom	Sum of Squares	Estimated Variance	% Variation	Differentiation Indexes	Significance
Among Regions	3	44.999	0.024	0.7%	F_{RT} = 0.007	0.010
Among Populations	10	52.207	0.011	0.3%	F_{SR} = 0.003	0.010
Among Individuals	938	3589.77	0.437	12.8%	F_{ST} = 0.010	0.010
Within Populations	952	2811.00	2.953	86.2%	F_{IS} = 0.129	0.010
Total	1903	6497.97	3.425	100.0%	F_{IT} = 0.138	0.010

The NJ tree showed populations STE12 and STE14 grouped together with 70% support. The population FIO was grouped separately and CHA was grouped together with the north and central group but with low support (50% bootstrap). All the populations from the north and central groups (RAN, LBI, JON, HAU, MER, TAU, WEL, MAR, TAS, GOL) were grouped together with 30% support. The populations GOL and TAS were grouped together with 45% support and there was high support (70%) for the grouping of populations MER and TAU (Figure 3.4).

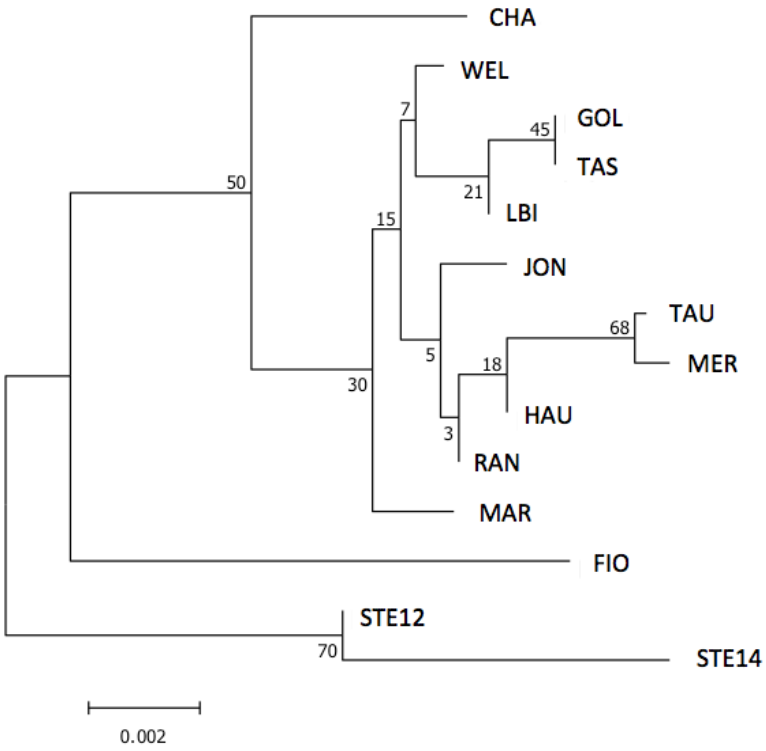

Figure 3.4 Neighbor joining population tree for *Pecten novaezelandiae* based on F_{ST} values using 14 populations.

The non-parametric (AWclust) analysis showed a large gap value at k=1 and an increase towards k=14 (Figure 3.5). For the Bayesian analysis (Structure) both the ΔK (Evanno *et al.* 2005) and the maximum log-likelihood of K methods showed the greatest value for 2 clusters (Table 3.6) and the bar plot showed a north-south cline of proportions of clusters (Figure 3.6). This cline was highly supported by a Spearman rank correlation test, which showed a significant decline in the proportion of Cluster 1 with increasing latitude (r=-0.890, p=0.000) and an increase of Cluster 2 with increasing latitude (r=0.890, p=0.000).

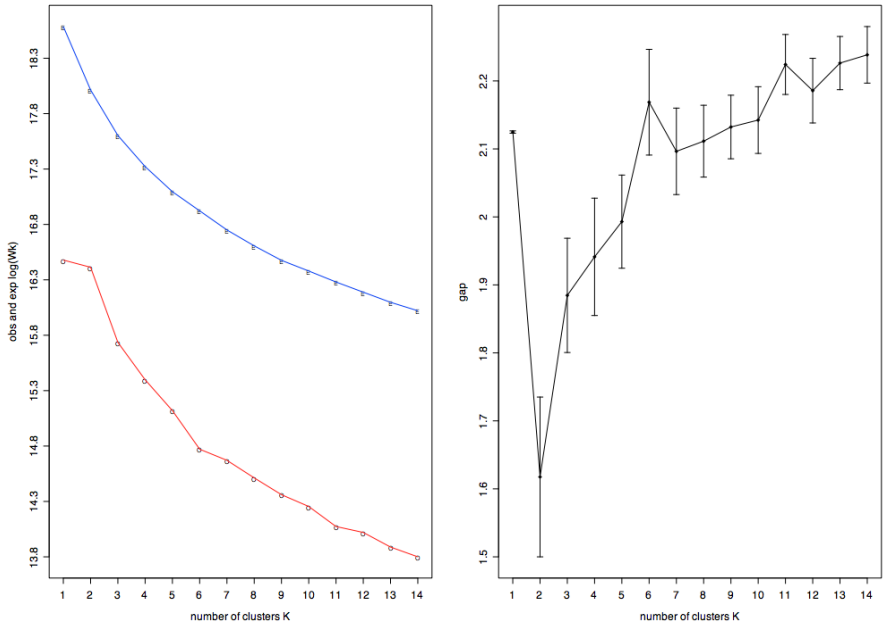

Figure 3.5 AWclust results for *Pecten novaezelandiae* using 10 loci: expected (E) and observed (O) log pooled with-in cluster sum of squares (Wk) (on the left) and gap statistic values between the observed and expected (on the right).

Table 3.6 Evanno table (Evanno *et al.* 2005) output for 14 populations from 4 regions of *Pecten novaezelandiae.*

K	Reps	Mean LnP(K)	Stdev LnP(K)	Ln'(K)	|Ln''(K)|	Delta K
1	5	-31200.08	0.4438	—	—	—
2	5	-31069.18	27.740	130.900	241.36	8.7006
3	5	-31179.64	171.174	-110.460	264.20	1.5435
4	5	-31554.30	195.677	-374.660	492.92	2.5190
5	5	-31436.04	169.526	118.260	637.22	3.7588
6	5	-31955.00	407.973	-518.960	199.40	0.4888
7	5	-32274.56	1093.434	-319.560	579.04	0.5296
8	5	-32015.08	590.824	259.480	422.80	0.7156
9	5	-32178.40	918.538	-163.320	393.60	0.4285
10	5	-31948.12	547.995	230.280	2425.10	4.4254
11	5	-34142.94	795.644	-2194.820	2853.92	3.5869
12	5	-33483.84	947.134	659.100	330.36	0.3488
13	5	-33155.10	552.145	328.740	934.76	1.6921
14	5	-33761.12	2471.232	-606.020	—	—

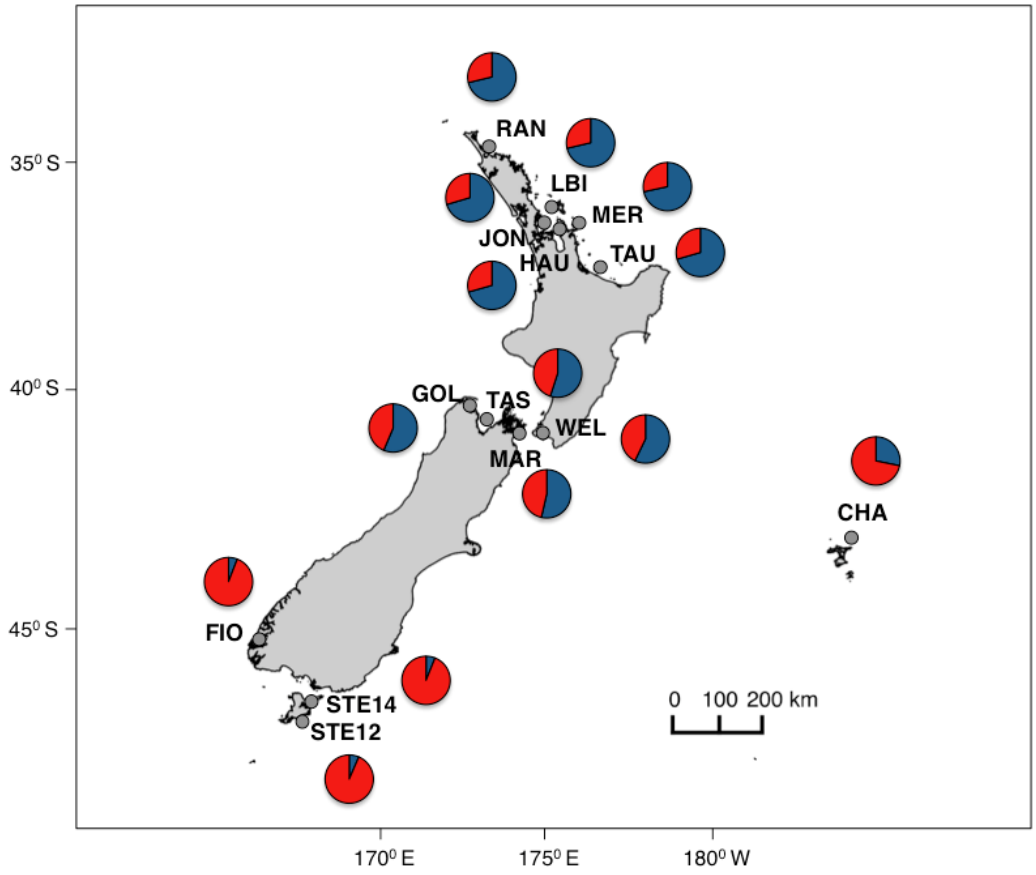

Figure 3.6 Bayesian cluster analysis (Structure) results for *Pecten novaezelandiae* using 10 loci (K=2). Samples were assigned to two colour coded-genetic clusters (blue and red).

Spatial Bayesian analysis showed that posterior distributions of K displayed a mode at K=5 (Figure 3.7a, b). The Geneland model identified 5 spatially coherent clusters with the following groups: north (Figure 3.8b), central (Figure 3.8c), Fiordland (Figure 3.8d), Stewart Island (Figure 3.8a) and Chatham Islands (Figure 3.8e). Each cluster had a probability of 0.65, 0.55, 0.45, 0.40 and 0.45 of belonging to the respective group (Figure 3.8). This structure was undetected under an uncorrelated frequencies model (results not shown), possibly due to the low levels of genetic differentiation observed between populations.

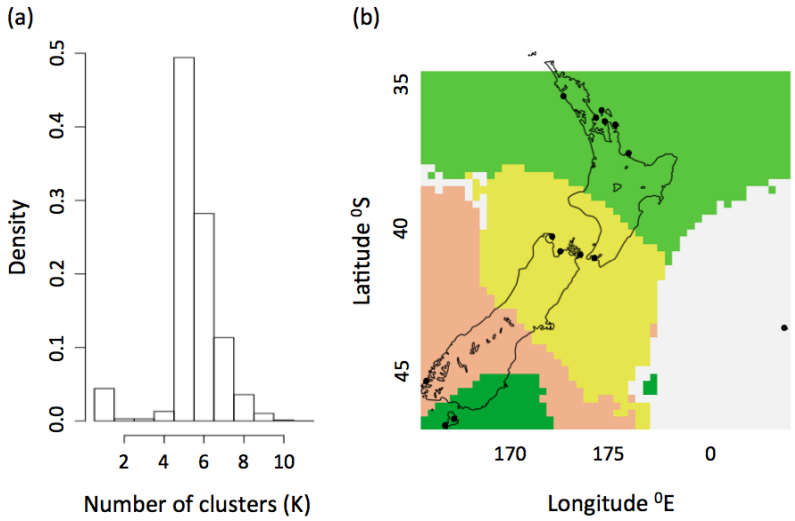

Figure 3.7 Spatial Bayesian analysis (Geneland) results for *Pecten novaezelandiae* using 10 loci: (a) posterior density distribution of the number of clusters (k=5), (b) map of population membership for k=5.

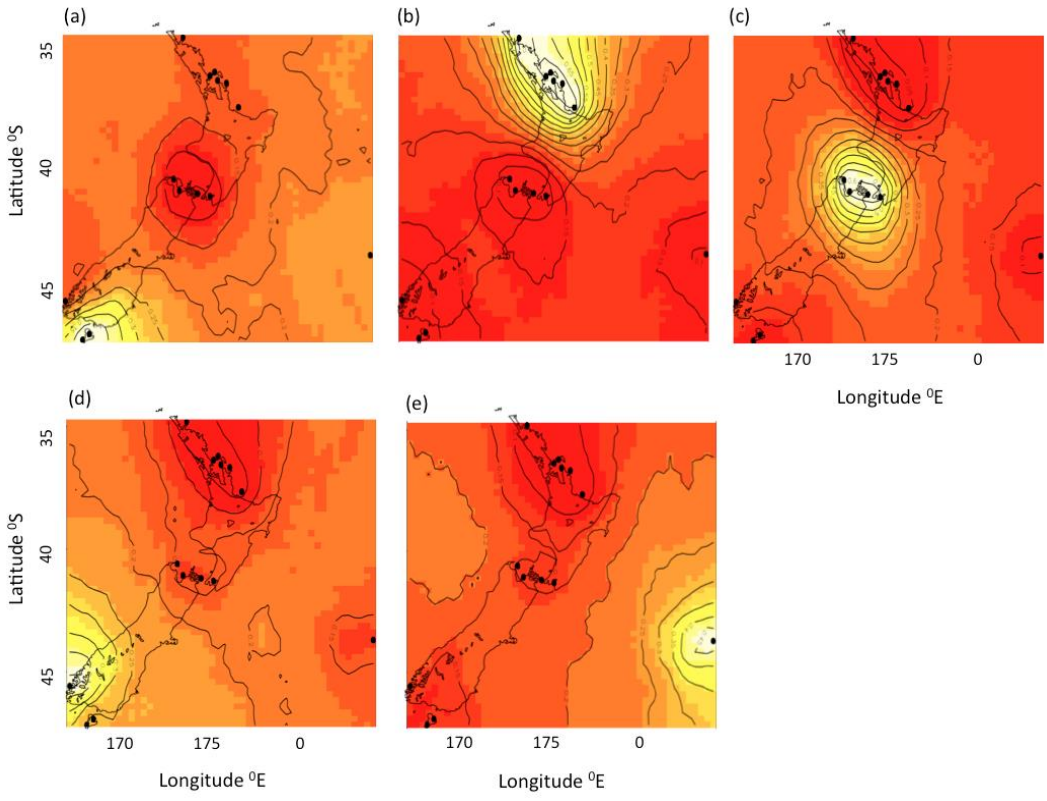

Figure 3.8 Spatial Bayesian analysis (Geneland) results for *Pecten novaezelandiae* using 10 loci: (a-e) assignment of individuals to clusters for K=1 to K=5, respectively. The highest population membership values are in light yellow and level curves indicate spatial changes in assignment values.

Mantel tests showed a weak but significant isolation by distance signal when using all populations in the mainland (R^2=0.315, p<0.01; Figure 3.9), when excluding STE12 (R^2=0.435, p<0.01) and when using only the north and central groups (R^2=0.151, p=0.01). A similar trend was observed when using R_{ST} (results not shown) excluding CHA (R^2=0.289, p<0.01) and excluding STE12 (R^2=0.393, p<0.01). However, when using only the north and central groups the result was not significant (R^2=0.015, p=0.110).

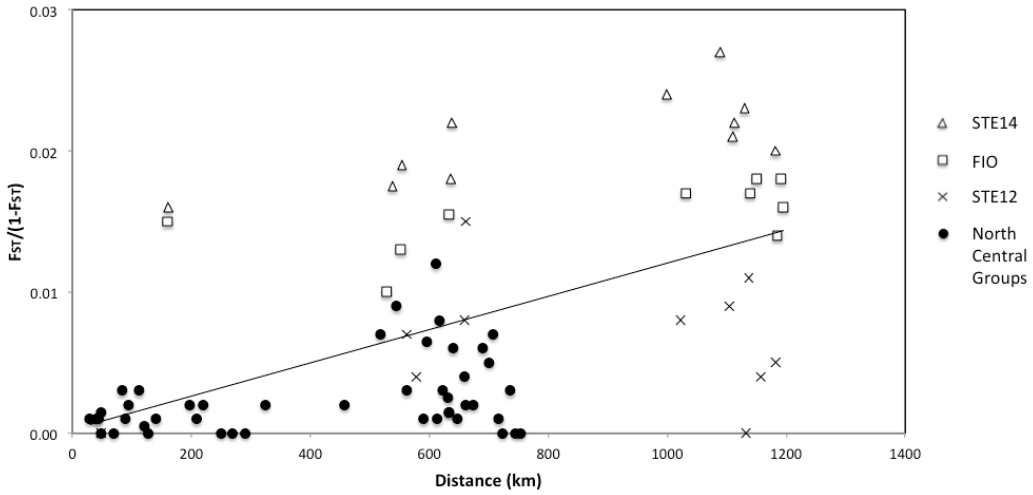

Figure 3.9 Scatterplot of Mantel tests using F_{ST} for all the mainland populations (R^2=0.324, p<0.01), when excluding STE12 (n=10) R^2=0.461 (p<0.01) and when just the north and central groups were included R^2=0.148 (p=0.05). STE14: Stewart Is, Port Pegasus; FIO: Fiordland; STE12: Stewart Is, Paterson Inlet; North Central Groups: remaining populations.

Linear regression analysis showed that allelic richness (A_R) and private allelic richness (PA_R) were significantly negatively related to latitude (p<0.001 in both cases; Figure 3.10).

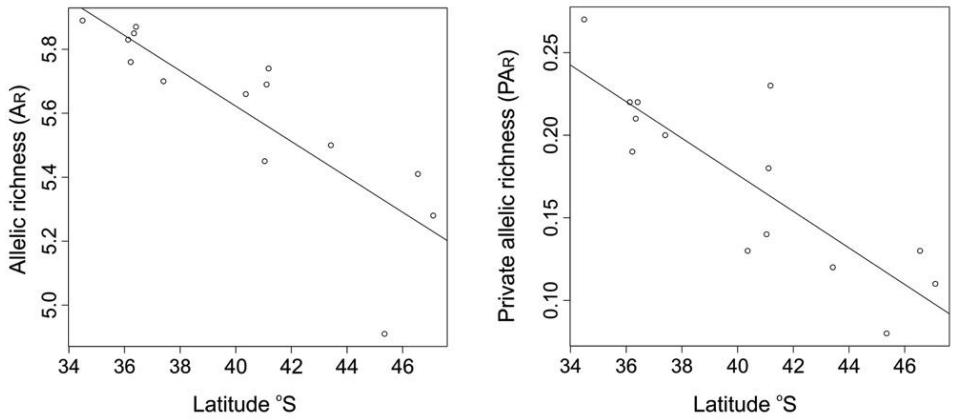

Figure 3.10 Linear regression analyses of allelic richness, A_R (R^2=0.688, p=0.0001) and private allelic richness, PA_R (R^2= 0.683, p=0.0002) as a function of latitude.

Estimates of migration

Assignment analysis detected a low number (9) of first generation (F0) migrants for all regions (Table 3.7). Populations in the northern region were not likely to receive F0 migrants while CHA was likely to receive the most F0 migrants (4). The low number of all F0 migrants was probably an underestimation due to low levels of differentiation because migrant individuals will have very similar genotypes to the individuals from the original locality. The region with the highest level of correct assignment was the north (at 85%), while the region with the lowest level was the Chatham Islands (CHA) at 17.3%. There was a southwards increase in the percentage of individuals recruited from regions other than the collection site and the Chatham Islands was the region with the highest percentage at 82.7% (Table 3.8).

Table 3.7 Number of first generation (F0) migrants detected for *Pecten novaezelandiae* at each sampled region.

		Source of F0 migrants				
		North	Central	South	CHA	Total F0 migrants
Receiving region	North					
	Central	2			1	3
	South	1			1	2
	CHA	2	2			4

Table 3.8 Percentage of individuals of *Pecten novaezelandiae* collected from each sampling region, assigned to each sampled potential source region. "Total other regions" is the percentage of individuals recruited from regions other than the collection site.

		Assigned region					Total other regions
		North	Central	South	CHA	Unassigned	
Region	North	***85.0***	13.8	0.8	0.2	0.2	14.8
	Central	51.3	***46.7***	1.2	0.8		53.3
	South	43.0	20.4	***36.6***			63.4
	CHA	58.2	20.4	4.1	***17.3***		82.7

Discussion

In this chapter, the factors that shape the genetic variability and patterns of genetic structure of *Pecten novaezelandiae* were examined. Populations within regions appeared to be well connected with little evidence of genetic differentiation, but some level of population structure were found among regions. A significant isolation by distance signal and a degree of differentiation from north to south was apparent, but conflicted with some evidence of panmixia. The observed patterns could be associated with the geographic distance among regions, the prevailing oceanographic processes and the comparatively young evolutionary age of *P. novaezelandiae*.

Population genetic structure

Overall, population genetic differentiation was low but there were significant differences between north and central regions, and populations in the south. A multi-taxon genetic break just south of the Cook Strait at 42ºS latitude has been observed for many coastal marine species in New Zealand (Apte & Gardner 2002; Ayers & Waters 2005; Goldstien *et al.* 2006; Ross *et al.* 2009; Gardner *et al.* 2010; Veale & Lavery 2011). However, the populations of *Pecten novaezelandiae* sampled were not continuous along the coast and I was unable to obtain samples from the southern margin of the 42ºS parallel so it was not possible to test for a similar pattern of genetic break. There may still be undetected population subdivision and a finer differentiation scale in populations that were not

sampled. Additionally, the detection of patterns of genetic structure is dependent on the genetic markers used. Although unlikely, it is possible that the microsatellites were unable to detect a finer population structure, which could potentially be revealed by molecular markers with higher resolution such as single nucleotide polymorphisms (SNPs).

The southern region showed the highest differentiation levels from the remaining populations and higher levels of larval retention could be contributing to this structure. Chiswell & Rickard (2011) estimated eddy diffusivity to be higher in the south of New Zealand and although the Subtropical Front flows mainly to the south turning into Cook Strait, it is weak and highly variable. Therefore, eddies in these areas may be promoting larval retention and therefore preventing larvae exchange with other populations. Also, the population in the fiords (FIO) showed the lowest levels of genetic diversity (A_R and PA_R) and high differentiation from the remaining populations. This distinct pattern of the New Zealand fiords has been observed in other studies for species with a broad distribution in New Zealand (Mladenov et al. 1997) and differentiation between fiords has also been observed elsewhere (Perrin *et al.* 2004) reflecting the unusual conditions of this habitat type with a semi-closed estuarine circulation.

The Chatham Islands were not very differentiated from other populations and had similarities with the mainland populations. Although the Chatham Islands are approximately 660 km southeast of the North Island, the subtropical convergence flowing eastward may be facilitating larval transport. This indicates that larvae of *Pecten novaezelandiae* have the potential to disperse over large distances and are strongly influenced by ocean currents. A similar pattern of differentiation was observed in the bivalve *Austrovenus stutchburyi* with similar larval duration (Ross *et al.* 2012) and also in the blue mussels *Mytilus galloprovincialis* (Westfall 2011). However, *Paphies subtriangulata*, also with similar pelagic larval duration shows significant differentiation from the mainland (Hannan 2014). These different patterns of genetic differentiation across multiple species likely reflect the influence of the life history and the evolutionary age of each species (*Austrovenus stutchburyi* – approx. 5Ma, *Mytilus galloprovincialis* and *Pecten novaezelandiae* – approx. 1Ma, *Paphies subtriangulata* – approx. 20Ma; Beu & Maxwell 1990).

Fossil records in New Zealand document the origin of the genus *Pecten* as a result of succession of populations in the middle to late Pleistocene, approximately 1 Ma ago (Beu

2010). The recent evolutionary history of *Pecten novaezelandiae* could help explain the differences on genetic differentiation observed between *P. novaezelandiae* and other species in New Zealand. For example, the bivalve *Paphies subtriangulata* (Hannan 2014) is also a broadcast spawner with a similar pelagic larval duration but its older evolutionary history which dates approximately 23-16 Ma on fossil records (Fleming 1979) might help explain the stronger population structure patterns observed, particularly between the mainland and the Chatham Islands. Other species showing a genetic break at about 42° S latitude such *Perna canaliculus* and *Patiriella regularis* have a reported divergence time between North and South populations of approximately 1.3 Ma ago (Apte & Gardner 2002; Ayers & Waters 2005). On the other hand, North and South lineages of the intertidal limpets *Cellana ornata*, *Cellana radians* and *Cellana flava* diverged more recently, approximately 200 000 to 300 000 years ago (Goldstien *et al.* 2006). These divergence periods, correspond to stages of hydrographic change across the Cook Strait region (Lewis *et al.* 1994) that could have shaped the currently observed structure in some evolutionary older species in New Zealand. In addition, it is known that microsatellites can reveal the influence of both historical and contemporary processes in shaping genetic structure, for example of the North American brook trout (Pilgrim *et al.* 2012), and they also revealed a stepping-stone model of colonization with decline of allelic richness in the Eurasian marine invader *Mnemiopsis leidyi* (Reusch *et al.* 2010).

A loss of genetic diversity in the populations located at the edge of colonization is predicted as a consequence of the species expansion, owing to a smaller amount of genetic variation that is represented in the sink populations (Shirk *et al.* 2014). An increase in F_{ST} values towards the edges is also expected as a result of the founder events that happen as colonization advances (Gaggiotti *et al.* 2009). However, results showed a decrease in genetic diversity (A_R and PA_R) and an increase in differentiation (F_{ST} values) towards the south. These results are in agreement with the recent evolutionary history of *Pecten novaezelandiae* and suggest that a possible route of colonization occurred from the north of New Zealand reflecting the species' recent expansion. In addition, the low levels of differentiation detected across the distribution range of the species might also reflect a recent range expansion and insufficient time to reach migration-drift equilibrium. Nevertheless, there is no molecular information regarding the time that lineages diverged

and the use of mitochondrial DNA (mtDNA) could potentially add more information and increase the support in examining the phylogeographic patterns of the species.

The hierarchical genetic structure observed for *P. novaezelandiae* can also be the result of local adaptation during colonization towards the south. For example, rapid population growth and local adaptation of individuals to a new habitat can result in a successful monopolisation of resources, giving these individuals a strong priority effect (De Meester *et al.* 2002; Orsini *et al.* 2013) and these patterns of differentiation can last thousands of generations (Boileau *et al.* 1992). Therefore, in areas with high population densities, locally adapted individuals of *P. novaezelandiae* could be favoured over immigrants, maintaining population genetic subdivision even when levels of migration are high. Also, it has been shown for other scallop species, such as *Argopecten irradians* and *Pecten maximus*, that populations at higher latitudes spawn earlier in the season and over longer periods of time (Shumway & Parsons 2006). This could also favour individuals locally adapted to environmental conditions over immigrants coming from northern New Zealand.

The non-parametric clustering analysis (AWclust) indicated a similar ancestor for all populations sampled (k=1). In contrast, the Bayesian analysis (Structure) suggested the presence of two clusters and a north-south cline of proportions of clusters. Structure analysis can be confounded by a significant signal of isolation by distance, which is known to cause Bayesian methods to overestimate genetic structure (Frantz *et al.* 2009). In addition, it has been shown that the earlier Structure models perform well at levels of genetic differentiation of $0.02 < F_{ST} < 0.10$ but fail at lower values (Duchesne & Turgeon 2012). As the highest F_{ST} value in this study was 0.027 and the majority of comparisons were below 0.01, it is possible that Structure failed to detect population genetic structure.

On the other hand, the spatial Bayesian analysis (Geneland) indicated the presence the 5 groups (K=5). The cluster probability provided strong support to the north and central clusters but the probability was below 0.5 for the groups Fiordland, Stewart Island and Chatham Islands. In general, Geneland results supported the F_{ST} and R_{ST} estimates suggesting limited dispersal between these 5 groups and a low but significant genetic structure. Different methods are expected to perform better under some particular scenarios and Geneland is known to be a more sensitive approach for species with very low levels of genetic differentiation (Guillot 2008). In addition, by accounting for correlation of allele frequencies across populations this model assumes that present time populations result from

the separation of an ancestral population which might give more clues about the on going evolutionary processes shaping the genetic structure of *P. novaezelandiae*.

Mantel tests showed a significant isolation by distance signal among samples overall and a weak but significant signal among samples in the north and central group, indicating that geographic distance may be an important factor explaining the population genetic structure of *P. novaezelandiae*. However, the Mantel test model is not a comprehensive description because sampling was not continuous along the coast but based on the hotspots of distribution of scallops. Therefore, these results might be biased, reflecting the hierarchical structure and the latitudinal genetic diversity gradient observed. The genetic signal of isolation by distance may be driven by colonization/extinction events and genetic drift during the species' recent range expansion and the genetic differentiation of the southern populations rather than by equilibrium conditions between dispersal and genetic drift.

Patterns of migration

In general, patterns of migration supported the observed differentiation between regions. Simulations suggest that the northern group persists mainly through self-recruitment. It has been shown that the pelagic larval duration can vary within scallop species depending on temperature (Beaumont & Barnes 1992). Therefore, populations in the north of New Zealand may have a shorter pelagic larval duration and shorter potential to disperse, which could potentially explain the higher levels of self-recruitment. Estimates of migration also suggest that the northern region is a possible important source of larvae as all other regions had a high percentage of individuals that were recruited from the north group. However, it is important to consider the limitations of these results, which might also be reflecting the hierarchical genetic structure observed.

The exchange of migrants between the mainland populations and the Chatham Islands was both recent and frequent historically. Migration was detected in both directions, however over the long-term it was mainly unidirectional with a high percentage of individuals assigned to localities on the mainland (82.7%). This substantial exchange of individuals facilitated by larval transport flowing eastward may be one of the factors explaining the low level of differentiation found between the Chatham Islands and the mainland populations.

Genetic diversity

Levels of genetic diversity in *Pecten novaezelandiae* are similar to other scallop species (Pitcher *et al.* 2002; Kenchington *et al.* 2006; Zhan *et al.* 2009; Arias *et al.* 2010; Hemond & Wilbur 2011; Marín *et al.* 2012) and might reflect scallops' high fecundity and ability to produce a large number of eggs resulting in large population sizes. Null alleles are frequently observed in other bivalve species (Hedgecock *et al.* 2004; Kenchington *et al.* 2006; Marín *et al.* 2012; Wei *et al.* 2013a). Similarly, they were observed for *P. novaezelandiae*, but it is unlikely that they affected the estimation of population differentiation as 1) there was no pattern or trend of null allele frequency as a function of either population or locus, 2) results from this study are consistent with other marine bivalves studies (e.g. Kenchington *et al.* 2006), 3) simulations suggest that F_{ST} values are unbiased when there is high gene flow, high effective population size (Ne) and moderate frequencies of null alleles (Chapuis & Estoup 2007).

The highest value of F_{IS}, observed for HAU, indicates that this is the population with the highest inbreeding rate. A possible explanation for the homozygote excess in HAU is that this population has been recently found and exploited by the fishing industry and a recent population size contraction from the resulting exploitation might have had effects on the genetic structure of this population. In contrast, the populations at Stewart Island that had the lowest values of F_{IS} might be experiencing an increase in heterozygosity due to a reduction in scallop exploitation in the region. In Paterson Inlet in particular, all commercial fishing has been prohibited since 1994 and recreational fishing is more restricted than in other areas to allow scallops stocks to regenerate; fishing is permitted only in Big Glory Bay, with a limit of 10 scallops of minimum 100 mm shell length per diver (Carbines & Michael 2007; Ministry of Primary Industries 2014). Interestingly, no strong evidence was found for inbreeding in the populations that recently have been described as depleted such as Tasman Bay, Golden Bay and Chatham Islands (Ministry of Primary Industries 2013b).

Conclusions

The observed geographic patterns of genetic variation of the New Zealand scallop reflect the life history of the species and the effects of ocean currents on promoting larval

mixing/retention. Larvae of *P. novaezelandiae* have the potential for extensive dispersal and are highly influenced by changes in the prevailing ocean currents that can limit connectivity. As a consequence, patterns of genetic structure could change over time. Temporal analyses as well as the integrated use of oceanographic approaches could be particularly informative (White *et al.* 2010). In addition, environmental variables can also cause non-random gene flow and therefore influence patterns of genetic structure (refer to Chapter 4).

Populations in the southern margin of the scallops' distribution, such as Fiordland and Stewart Island, were significantly different, which may reflect how ecologically distinct these locations are. Since these populations have atypical genetic characteristics, they are less likely to maintain their evolutionary potential and should be managed accordingly (Johannesson & André 2006). Furthermore, the northern region appears to be playing an important role as a source of larvae and has the highest levels of genetic diversity therefore is of particular importance for management and conservation.

CHAPTER 4

Seascape genetics of *Pecten novaezelandiae*: linking environmental and genetic variation

Introduction

Population genetic studies of marine species can be challenging because samples can be difficult to collect, neutral genetic markers can be difficult to develop, and data often do not follow traditional theoretical models (Selkoe *et al.* 2008). Consequently, it can be hard to identify clear geographic patterns for marine species (White *et al.* 2010). It has been recognized that the interactions between organisms and their environment play a crucial role in shaping spatial genetic structure. Independent of the geographic distance among populations, genetic differentiation between pairs of populations can increase with environmental differences as a result of the interactions between organisms and their environment (Wang & Summers 2010; Wang & Bradburd 2014). The environmental variables that might explain the genetic patterns of differentiation can be continuous, such as salinity variation, or discrete, such as sediment type; they can also describe abiotic factors such as sea surface temperature or biotic factors as chlorophyll *a* concentration. One of the main goals of population genetic studies is therefore to understand the processes responsible for shaping the spatial genetic patterns of species. Seascape genetics is a multidisciplinary approach that supplements the genetic data with environmental variability to assess how marine environmental features may contribute to the genetic structure of organisms (Liggins *et al.* 2013). Complementing traditional population genetics techniques with environmental information can increase the explanatory power of population genetic studies and also elucidate about the role of environmental features in shaping the patterns of genetic structure.

Seascape genetic studies typically use neutral genetic markers to understand associations between environmental factors and neutral genetic variation (Wei *et al.* 2013b; D'Aloia *et al.* 2014). In this case, since there is no selection, the occurrence of new alleles is dependent on neutral population processes such as gene flow, genetic drift and mutation (Liggins *et al.* 2013). Therefore, if a particular environmental factor explains the genetic variation of a species, this environmental feature might be promoting and/or preventing gene flow among population. However, tests for selection generally have low power (Slatkin 1994, 1996), it is unclear how many studies that used genetic markers assumed to be neutral have been influenced by selection (Hudson & Turelli 2003; Yang & Nielsen 2008) and it is debatable whether any locus is ever absolutely neutral (Liggins *et al.* 2013). Nonetheless, coding

genes under selection can obscure the processes of genetic drift and migration among populations, so neutral markers such as microsatellites are ideal for inferring demographic processes such as isolation or migration and changes in population size (Riginos & Liggins 2013).

Organisms with a pelagic larval stage are particularly influenced by environmental variability and their dispersion and successful recruitment is highly dependent on the prevailing environmental conditions (White *et al.* 2010). The use of multidisciplinary tools to investigate these processes has been recognized to be particularly important for marine species, increasing the power that describes the drivers of genetic patterns in species that often exhibit a relatively weak genetic signal (Selkoe *et al.* 2008). Our understanding of how environmental factors affect the maintenance of genetic structure and species evolution is still very limited, and multidisciplinary studies that integrate genetics with other tools to understand which and how environmental factors influence genetic patterns are scarce. Examples include the population structure of the Atlantic herring *Clupea harengus* is affected by salinity at spawning sites (Gaggiotti *et al.* 2009), kelp cover predicts genetic structure of the three temperate reef species *Paralabrax clathratus, Kelletia kelletii* and *Panulirus interruptus* (Selkoe *et al.* 2010), sea surface temperature explains the genetic variation of the New Zealand greenshell mussel *Perna canaliculus* (Wei *et al.* 2013b) and environmental gradients (using chlorophyll *a* concentration as a proxy) affect the genetic structure of the anemonefish *Amphiprion bicinctus* in the Red Sea (Nanninga *et al.* 2014).

Extending from subtropical to subantarctic waters, the New Zealand marine environment is very complex and its different habitats are characterised by a wide range of environmental factors (Shears *et al.* 2008). New Zealand is therefore ideal to investigate how environmental factors affect the spatial genetic patterns of marine species. However, only a limited number of seascape genetic studies have been conducted in New Zealand (e.g. Wei *et al.* 2013b; Constable 2014; Hannan 2014). As the endemic scallop *Pecten novaezelandiae* is distributed throughout New Zealand's North, South, Stewart and Chatham Islands (Shumway & Parsons 2006), all of which encompass a wide range of environments, it is an ideal species to investigate the correlation between genetic and environmental variability. The first conducted study on the population genetic structure of the New Zealand scallop (*Pecten novaezelandiae*) is presented in Chapter 3. The low

genetic signal detected across the scallop's distribution range highlights the importance of using a variety of approaches in marine population connectivity studies, especially because the statistical power to detect genetic structure in marine species can be low (Selkoe *et al.* 2008).

Although there is a paucity of marine environmental data for seascape genetic analyses, there has been an increase on local and global datasets that have become available to the public. To investigate the influence of environmental factors on the genetic variation of *Pecten novaezelandiae*, different environmental datasets were used for this study. The Marine Environmental Classification (MEC) system is an ecosystem-based spatial framework developed for marine management applications and is composed of a number of data layers with information on the New Zealand marine physical environment (Snelder *et al.* 2005). The benthic-optimised marine environment classification (BOMEC) scheme was specifically developed to assess the impacts of bottom trawling on benthic organisms in New Zealand (Boyer *et al.* 2005; Pinkerton & Richardson 2005). Additional data layers covering a global scale now exist, some of which address gaps in the New Zealand specific data. The MODIS instrument from NASA, operating on Aqua spacecraft, views the entire surface of the Earth and acquires data every one to two days. The Ocean Color Data Processing System (OCDPS) produces and distributes the ocean colour data (Thomas & Franz 2005).

The use of different analytical methods can increase confidence that the environmental variables are truly associated with the genetic variation. Therefore, to test the null hypothesis that none of the geospatial or environmental variables explain significant genetic variation in *Pecten novaezelandiae* in terms of F_{ST} values, F'_{ST} values and allelic frequencies, two statistical methodologies were employed: (1) a generalised linear model (GLZ), which involves multiple regression analysis between a dependent variable and a number of predictor variables following Wei *et al.* (2013b) and (2) a biological environmental stepwise (BEST) analysis that tests for the relationship between resemblance matrices of dependent and predictor variables following Wei *et al.* (2013b). This is one of the few studies to explore the associations between New Zealand's environment features and population genetics of marine organisms (but see Wei *et al.* 2013b; Constable 2014; Hannan 2014). This study aimed to identify environmental variables that determine the

population genetic structure of the New Zealand scallop *Pecten novaezelandiae*, bringing us one step closer to understanding the factors that shape genetic structure of populations.

Materials and methods

Data collection

Multilocus microsatellite genetic data were obtained for 952 individuals of *Pecten novaezelandiae* collected from 14 sites around New Zealand as described in Chapter 3 (Figure 4.1). Three geospatial variables were obtained from Google Maps for each site: (1) latitude (Lat), (2) longitude (Lon) and (3) index of geographic distance (Geo_dist) calculated as the sum of all shortest possible coastal distances (km) between all pairs of populations (a low value indicates a population's proximity to all other populations, whereas a high value indicates its isolation, e.g. Wei *et al.* (2013b). Thirteen site-specific environmental variables (Table 4.1a) were obtained from the New Zealand Marine Environment Classification (MEC) scheme (New Zealand Ministry for the Environment 2005). These data are from the exclusive economic zone (EEZ) with a spatial resolution of 1 km and are drawn from multiple years between 1983 and 2000. The environmental variables salinity (Boyer *et al.* 2005), suspended particulate matter and dissolved organic matter (Pinkerton & Richardson 2005) were obtained from the Benthic-optimised Marine Environment Classification (BOMEC) scheme (Leathwick *et al.* 2012; Table 4.1b). The open source Geographic Information System software QGIS 2.4 (QGIS Development Team 2014) was used to obtain site-specific data for each of the 14 locations.

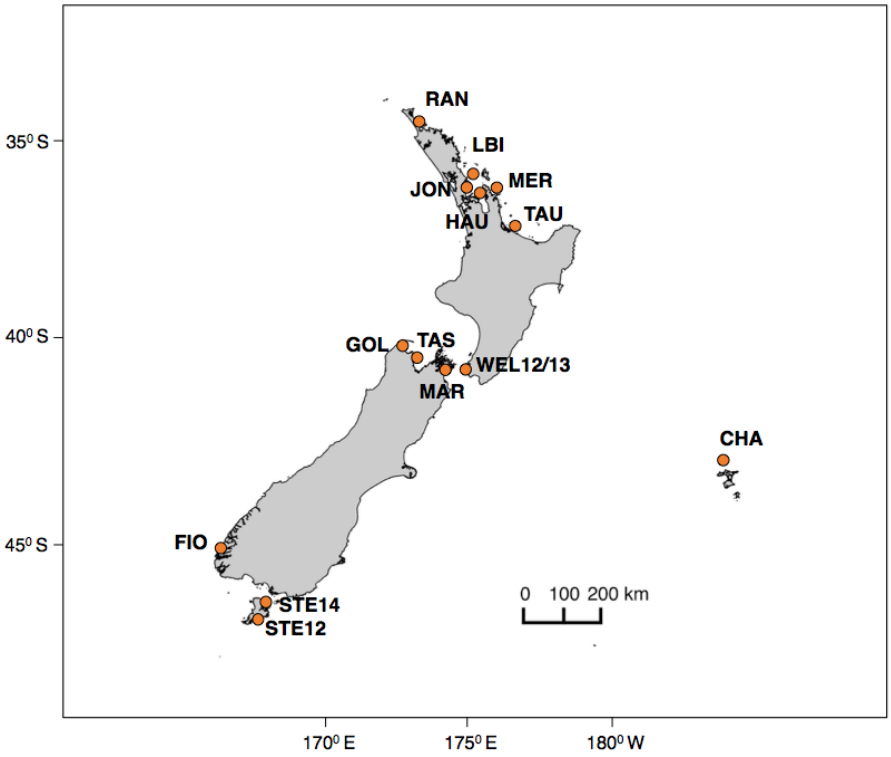

Figure 4.1 Map of sampling sites of *Pecten novaezelandiae* collected from New Zealand. Locations abbreviations as per Table 3.1.

The variables chlorophyll *a* (Chl_a) and total suspended sediment (TSS) were obtained from the ocean colour satellite data MODIS project for multiple years between 2002 and 2014 (NASA 2014; Table 4.1c). Chlorophyll *a* and total suspended sediment data were not available for the populations MAR, FIO, STE12 and CHA, which highlights that the marine environmental data available for seascape genetic studies are still limited.

Table 4.1 Environmental variables (name), abbreviation, description and units from (a) the Marine Environment Classification (MEC), (b) the Benthic-optimised Marine Environment Classification (BOMEC) and (c) data obtained from the MODIS project.

	Name	Abbreviation	Description	Units
(a)	Depth	Depth	Bathymetry grid (1 km resolution)	m
	Annual mean solar radiation	Rad_mean	Mean extra atmospheric solar radiation modified by mean annual cloud cover	Wm^{-2}
	Winter solar radiation	Rad_wint	Extra atmospheric solar radiation in June, modified by mean annual cloud cover	Wm^{-2}
	Wintertime sea surface temperature	SSTwint	Mean of daily data from early September when SST is typically lowest	^{o}C
	Annual amplitude of sea surface temperature	SSTanamp	Smoothed annual amplitude of SST	^{o}C
	Spatial gradient annual mean sea surface temperature	SSTgrad	Smoothed magnitude of the spatial gradient of annual mean SST	$^{o}C\ km^{-1}$
	Summertime sea surface temperature anomaly	SSTanom	Spatial anomalies with scales between 20 and 450 km in late February when SST is typically highest	^{o}C
	Mean orbital velocity	Orb_v_mean	Orbital velocity at the bed for the mean significant wave height calculated from a 20-year wave hindcast	m/s
	Extreme orbital velocity	Orb_v_95	Orbital velocity at the bed for the 95th percentile significant wave height calculated from a 20-year wave hindcast	m/s
	Tidal current	Tidal	Depth averaged maximum tidal current	m/s
	Sediment type (categorical variable)	Sed	Sediment type as a categorical variable	na
	Seabed rate of change of slope (profile)	Bed_prof	The rate of change of slope for each cell	$0.01m^{-1}$
	Freshwater fraction	FW	Proportion of fresh water based on river inputs	proportion
(b)	Salinity	Sal	World Ocean Atlas	psu
	Dissolved organic matter	DOM	Remote sensed	Arbitrary units
	Suspended particulate matter	SPM	Remote sensed	Arbitrary units
(c)	Chlorophyll *a*	Chl_a	Near surface concentration	mg chl-a m^{-3}
	Total suspended sediment	TSS	Total gravimetric suspended sediment	gm^{-3}

Correlation of variables

The software package Statistica 12.0 was used to test for independence of the environmental variables. A Pearson correlation test and a principal component analysis (PCA) were performed and a subset of environmental variables that were correlated at the 0.05 level was removed from further analysis. The three geospatial variables and the following six independent environmental variables were used for the seascape analysis: spatial gradient annual mean sea surface temperature (SSTgrad; $^{o}C\ km^{-1}$), mean orbital velocity (Orb_v_mean; m/s), tidal current (Tidal; m/s), freshwater fraction (FW; proportion), dissolved organic matter (DOM; arbitrary units) and suspended particulate matter (SPM; arbitrary units).

Estimates of population genetic diversity

Analyses were based on 952 individuals from 14 locations, as described in chapter 3 (WEL12 and WEL13 were treated as one location). Pairwise F_{ST} values (Weir & Cockerham 1984) were calculated across 10 microsatellite markers using the software GenePop on the web (Rousset 2008). Modified pairwise phi-statistics (F'_{ST}) were calculated using the software GenoDive 2.0b25 (Meirmans & Van Tienderen 2004; Meirmans 2006), as detailed in chapter 3. Mean multilocus F_{ST} and F'_{ST} values were averaged across locations following Wei *et al.* (2013b).

Generalized Linear Model analyses

The generalized linear model (GLZ) was calculated using the software Statistica 12.0. Akaike information criterion (AIC) was used to rank the models (best fit model with the lowest AIC score) at the significance level of $p<0.05$. The analyses were run for all variables and then repeated using only geospatial or only environmental variables to determine their relative importance in explaining genetic variation, following Wei *et al.* (2013b). Analyses were done for all 14 locations and also excluding the 3 locations in the south, as they were outliers and it might be difficult to assess the meaningfulness of the results (FIO and STE14 were the most genetically differentiated and the sample size of STE12 was only n=10).

BEST analyses

Allele frequencies at each location were calculated using the software GenePop on the web (Rousset 2008). Following Wei *et al.* (2013b), to examine the association between allele frequencies and environmental/geospatial variables, the BEST routine was implemented in Primer v.6 (Clarke & Gorley 2006). First, the analyses were run for all variables and then repeated using only geospatial or only environmental variables to determine their relative importance in explaining genetic variation. As for the GLZ, BEST analyses were done for all 14 locations and also for only 11 locations (excluding the 3 locations in the south). A Bray-Curtis resemblance matrix was employed for the allele frequencies and a Euclidean distance resemblance matrix was employed for the environmental/geospatial variables. To test for correlation between the two matrices the BIOENV routine was implemented using the Spearman correlation coefficient method (r_s). Models were considered significant at $p<0.05$ after 1,000 permutations. In addition, the association between allele frequencies and environmental/geospatial variables was also investigated for each locus for all 14 locations using the BEST routine to test for locus-specific responses.

Results

Correlation of variables

Pearson correlation analyses and PCA showed that the environmental variables FW, DOM and SPM were independent of all other variables. The variables Rad_mean, Rad_wint, SSTwint, SSTanamp, Sed, Sal, Chl_a and TSS were correlated with latitude whilst the variables Depth and Sed were correlated with longitude (Table 4.2; Figure 4.2). Therefore, the environmental variables SSTgrad, Orb_v_mean, Tidal, FW, DOM and SPM were used in the GLZ and BEST analyses.

Table 4.2 Correlations between variables as defined by Pearson's correlation test. Significantly correlated variables at $p<0.05$ are in bold. Abbreviations as per Table 4.1.

	Lat	Lon	Geo_dist	Depth	Rad_mean	Rad_wint	SSTwint	SSTanamp	SSTgrad	SSTanom	Orb_v_mean
Lat	1.000	0.253	-0.525	0.337	**0.969**	**0.993**	**0.953**	**0.742**	0.006	-0.077	-0.422
Lon	0.253	1.000	-0.254	**-0.587**	0.437	0.349	0.424	0.207	0.312	0.289	0.090
Geo_dist	-0.525	-0.254	1.000	-0.013	**-0.650**	**-0.551**	-0.382	**-0.591**	-0.347	0.254	0.361
Depth	0.337	**-0.587**	-0.013	1.000	0.163	0.246	0.182	0.274	-0.213	-0.147	-0.425
Rad_mean	**0.969**	0.437	**-0.650**	0.163	1.000	**0.987**	**0.938**	**0.761**	0.105	-0.053	-0.373
Rad_wint	**0.993**	0.349	**-0.551**	0.246	**0.987**	1.000	**0.962**	**0.746**	0.038	-0.058	-0.401
SSTwint	**0.953**	0.424	-0.382	0.182	**0.938**	**0.962**	1.000	**0.632**	0.029	0.013	-0.245
SSTanamp	**0.742**	0.207	**-0.591**	0.274	**0.761**	**0.746**	**0.632**	1.000	-0.403	0.405	-0.406
SSTgrad	0.006	0.312	-0.347	-0.213	0.105	0.038	0.029	-0.403	1.000	**-0.696**	-0.180
SSTanom	-0.077	0.289	0.254	-0.148	-0.053	-0.058	0.013	0.405	**-0.696**	1.000	0.161
Orb_v_mean	-0.423	0.090	0.361	-0.425	-0.373	-0.401	-0.245	-0.406	-0.180	0.161	1.000
Orb_v_95	-0.340	0.110	0.135	-0.499	-0.270	-0.313	-0.201	-0.330	-0.093	0.030	**0.876**
Tidal	0.409	-0.029	-0.102	0.169	0.370	0.414	0.276	**0.585**	-0.445	0.191	-0.408
Sed	**0.656**	**0.541**	**-0.615**	-0.088	**0.762**	**0.692**	**0.709**	**0.625**	0.040	0.168	0.163
Bed_prof	0.267	-0.026	-0.293	0.124	0.249	0.266	0.099	0.371	0.052	-0.040	**-0.889**
FW	0.032	0.242	-0.062	-0.376	0.108	0.064	0.103	-0.025	0.103	0.007	0.409
Sal	**0.972**	0.234	-0.380	0.320	**0.922**	**0.965**	**0.966**	**0.709**	-0.096	0.011	-0.356
DOM	0.320	0.235	-0.518	-0.015	0.381	0.325	0.240	0.412	0.114	0.001	-0.285
SPM	-0.359	0.125	0.118	-0.310	-0.314	-0.341	-0.390	-0.162	-0.005	0.211	-0.109
Chl_a	**-0.635**	-0.456	0.432	-0.001	**-0.676**	**-0.660**	**-0.623**	**-0.663**	0.132	-0.299	0.320
TSS	**-0.634**	-0.456	0.434	0.007	**-0.675**	**-0.659**	**-0.621**	**-0.658**	0.128	-0.290	0.314

Table 4.2 (cont)

	Orb_v_95	Tidal	Sed	Bed_prof	FW	Sal	DOM	SPM	Chl_a	TSS
Lat	-0.340	0.409	**0.656**	0.267	0.032	**0.972**	0.320	-0.359	**-0.635**	**-0.634**
Lon	0.110	-0.029	**0.541**	-0.026	0.242	0.234	0.235	0.125	-0.456	-0.456
Geo_dist	0.135	-0.102	**-0.615**	-0.293	-0.062	-0.380	-0.518	0.118	0.432	0.434
Depth	-0.499	0.169	-0.088	0.124	-0.376	0.320	-0.015	-0.310	-0.001	0.007
Rad_mean	-0.270	0.370	**0.762**	0.249	0.108	**0.922**	0.381	-0.314	**-0.676**	**-0.675**
Rad_wint	-0.313	0.414	**0.692**	0.266	0.064	**0.965**	0.325	-0.341	**-0.660**	**-0.659**
SSTwint	-0.201	0.276	**0.709**	0.099	0.103	**0.966**	0.240	-0.390	**-0.623**	**-0.621**
SSTanamp	-0.330	**0.585**	**0.625**	0.371	-0.025	**0.709**	0.412	-0.162	**-0.663**	**-0.658**
SSTgrad	-0.093	-0.445	0.040	0.052	0.103	-0.096	0.114	-0.005	0.132	0.128
SSTanom	0.030	0.191	0.168	-0.040	0.007	0.011	0.001	0.2110	-0.299	-0.290
Orb_v_mean	**0.876**	-0.408	0.1628	**-0.890**	0.409	-0.356	-0.285	-0.109	0.320	0.314
Orb_v_95	1.000	-0.397	0.125	**-0.676**	0.113	-0.319	-0.255	-0.048	0.074	0.063
Tidal	-0.397	1.000	0.043	**0.546**	-0.094	0.395	0.267	0.092	-0.346	-0.349
Sed	0.125	0.043	1.000	-0.280	0.464	**0.631**	0.407	-0.338	-0.437	-0.436
Bed_prof	**-0.676**	**0.546**	-0.280	1.000	-0.458	0.190	0.261	0.249	-0.360	-0.358
FW	0.113	-0.094	0.464	-0.458	1.000	0.067	0.198	-0.206	0.383	0.382
Sal	-0.319	0.395	**0.631**	0.190	0.067	1.000	0.232	-0.406	**-0.589**	**-0.586**
DOM	-0.255	0.267	0.407	0.261	0.198	0.232	1.000	0.212	-0.196	-0.197
SPM	-0.048	0.092	-0.338	0.249	-0.206	-0.406	0.212	1.000	-0.275	-0.277
Chl_a	0.074	-0.346	-0.437	-0.360	0.383	**-0.589**	-0.196	-0.275	1.000	**0.999**
TSS	0.063	-0.349	-0.436	-0.358	0.382	**-0.586**	-0.197	-0.277	**0.999**	1.000

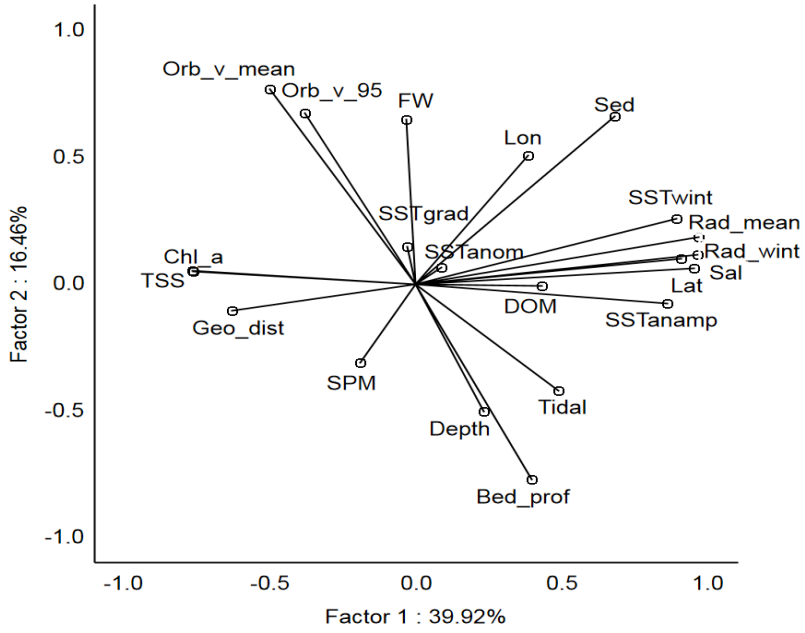

Figure 4.2 Principal component analysis (PCA) of both the geospatial and environmental variables. Abbreviations as per Table 4.1.

Generalized Linear Models

The pairwise F_{ST} values for all comparisons ranged from 0 to 0.027 while the F'_{ST} values ranged from 0 to 0.082. Mean F_{ST} values ranged from 0.004 at HAU to 0.019 at STE14 and mean F'_{ST} values ranged from -0.001 at STE12 to 0.052 at STE14.

Generalized linear models based on data from all 14 locations showed that the top ten best fitting models were all significant at $p<0.01$ when testing variation in both F_{ST} and F'_{ST} values against variation in all 9 geospatial and environmental variables. All the variables were included in the models, however only the variables Lon, Geo_dist, Tidal, FW and SPM were significant at $p<0.05$ for the test of all effects (Table 4.3).

Generalized linear model analyses based on data from 11 locations (excluding south) showed that the top 9 best fitting models were significant at $p<0.05$ when testing variation in F_{ST} values against variation in all 9 geospatial and environmental variables. All variables were included in these models but only Lon appeared in all the models and Tidal was significant at $p<0.05$ for the test of all effects. When testing variation in F'_{ST} values against variation in all 9 geospatial and environmental variables, the top ten best fitting models

were all significant at p<0.05, all the variables were included in the models and all were significant at p<0.05 for the test of all effects (Table 4.3).

Table 4.3 Results of the top ten best fitting models of generalized linear model analyses (GLZ routine in STATISTICA v12) testing for the contribution of all 9 geospatial and environmental variables to explain variation in F_{ST} and F'_{ST} for *Pecten novaezelandiae*. The checkmarks (✓) indicate which variables were included in each model. [1]p-value of each model; [2]p-value of the test of all effects, significant values at p<0.05 are in bold.

F_{ST} based on all 14 locations									
p-value[1]	Lat	Lon	Geo_ dist	SST grad	Orb_v_ mean	Tidal	FW	DOM	SPM
<0.001		✓	✓			✓	✓		✓
<0.001		✓	✓			✓	✓	✓	✓
<0.001		✓	✓	✓		✓	✓		✓
<0.001		✓	✓		✓	✓	✓		✓
<0.001		✓	✓	✓		✓	✓	✓	✓
<0.001		✓	✓		✓	✓	✓	✓	✓
<0.001			✓	✓		✓	✓		✓
<0.001			✓			✓	✓		✓
<0.001	✓	✓	✓			✓	✓		✓
<0.001		✓	✓	✓	✓	✓	✓		✓
p-value[2]	0.824	0.065	**0.004**	0.339	0.429	**0.029**	**<0.001**	0.183	**<0.001**
F'_{ST} based on all 14 locations									
p-value[1]	Lat	Lon	Geo_ dist	SST grad	Orb_v_ mean	Tidal	FW	DOM	SPM
<0.001		✓					✓	✓	✓
<0.001	✓	✓					✓	✓	✓
<0.001	✓	✓				✓	✓	✓	✓
<0.001		✓				✓	✓	✓	✓
<0.001		✓	✓				✓	✓	✓
<0.001	✓	✓		✓		✓	✓	✓	✓
<0.001		✓		✓			✓	✓	✓
<0.001		✓			✓		✓	✓	✓
<0.001		✓		✓		✓	✓	✓	✓
<0.001	✓	✓	✓				✓	✓	✓
p-value[2]	0.136	**0.014**	0.491	0.243	0.410	**0.025**	**0.016**	0.085	**0.001**

Table 4.3 (Cont.)

F_{ST} based on 11 locations (Excluding south)									
p-value[1]	Lat	Lon	Geo_ dist	SST grad	Orb_v_ mean	Tidal	FW	DOM	SPM
0.014		✓							
0.032		✓				✓			
0.039		✓						✓	
0.042		✓							✓
0.043		✓		✓					
0.044		✓					✓		
0.045		✓			✓				
0.048		✓	✓						
0.049	✓	✓							
0.051		✓				✓		✓	
p-value[2]	0.083	0.059	0.088	0.107	0.393	**0.035**	0.920	0.843	0.461
F'_{ST} based on 11 locations (Excluding south)									
p-value[1]	Lat	Lon	Geo_ dist	SST grad	Orb_v_ mean	Tidal	FW	DOM	SPM
0.002	✓	✓	✓	✓	✓	✓	✓	✓	✓
0.007		✓							
0.015		✓				✓			
0.023		✓		✓					
0.023		✓							✓
0.025		✓						✓	
0.027	✓	✓							
0.027		✓					✓		
0.027		✓			✓				
0.028		✓	✓						
p-value[2]	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**

When generalized linear models were run for only 3 geospatial variables based on data from all 14 locations, the top six best fitting models were significant at $p<0.01$ when testing variation in F_{ST} values and included all the geospatial variables. When testing variation in F'_{ST} values against variation in geospatial variables, the top two best fitting models were significant at $p<0.05$ and included only the variables Lat and Geo_dist. Generalized linear model analyses based on data from 11 locations showed that the top three best fitting models were significant at $p<0.05$ when testing variation in F_{ST} values against variation in geospatial variables and included all geospatial variables. When testing variation in F'_{ST} values against variation in geospatial variables, the top five best fitting models were

significant at p<0.05 and also included all geospatial variables. However, none of the geospatial variables were significant for the test of all effects for any scenario (Table 4.4).

Table 4.4 Results of the top ten best fitting models of generalized linear model analyses (GLZ routine in STATISTICA v12) testing for the contribution of 3 geospatial variables to explain variation in F_{ST} and F'_{ST} for *Pecten novaezelandiae*. The checkmarks (✓) indicate which variables were included in each model. [1]p-value of each model; [2]p-value of the test of all effects.

14 locations				11 locations (Excluding south)			
F_{ST}				F_{ST}			
p-value[1]	Lat	Lon	Geo_ dist	p-value[1]	Lat	Lon	Geo_ dist
0.002	✓		✓	0.014		✓	
0.001			✓	0.048		✓	✓
0.002	✓			0.049	✓	✓	
0.004	✓	✓	✓	0.061	✓		✓
0.005		✓	✓	0.096	✓	✓	✓
0.007	✓	✓		0.145	✓		
0.728		✓		0.251			✓
p-value[2]	0.125	0.639	0.091	p-value[2]	0.614	0.389	0.575
F'_{ST}				F'_{ST}			
p-value[1]	Lat	Lon	Geo_ dist	p-value[1]	Lat	Lon	Geo_ dist
0.021			✓	0.007		✓	
0.036	✓			0.027	✓	✓	
0.057	✓		✓	0.028		✓	✓
0.067		✓	✓	0.037	✓		✓
0.106	✓	✓		0.041	✓	✓	✓
0.123	✓	✓	✓	0.095			✓
0.526		✓		0.197	✓		
p-value[2]	0.558	0.809	0.313	p-value[2]	0.314	0.209	0.323

When generalized linear models were run for only 6 environmental variables based on data from all 14 locations, the top ten best fitting models were all significant at p<0.01 when testing variation in F_{ST} values against variation in environmental variables. All the environmental variables were included in the models, but only Tidal, FW, DOM and SPM were significant at p<0.05 for the test of all effects. The top ten best fitting models were also all significant at p<0.01 when testing variation in F'_{ST} values against variation in

environmenal variables. All the environmental variables were included in the models, but only SPM was significant at p<0.05 for the test of all effects. Generalized linear model analyses based on data from 11 locations showed that none of the models were significant when testing variation in both F_{ST} and F'_{ST} values against variation in environmental variables and none of the variables was significant for the test of all effects (Table 4.5).

Table 4.5 Results of the top ten best fitting models of generalized linear model analyses (GLZ routine in STATISTICA v12) testing for the contribution of 6 environmental variables to explain variation in F_{ST} and F'_{ST} for *Pecten novaezelandiae*. The checkmarks (✓) indicate which variables were included in each model. [1]p-value of each model; [2]p-value of the test of all effects, significant values at p<0.05 are in bold.

F_{ST} based on all 14 locations						
p-value[1]	SST grad	Orb_v_mean	Tidal	FW	DOM	SPM
<0.001	✓		✓	✓	✓	✓
<0.001				✓	✓	✓
<0.001			✓	✓	✓	✓
<0.001		✓		✓	✓	✓
<0.001	✓			✓	✓	✓
<0.001	✓	✓	✓	✓	✓	✓
<0.001		✓	✓	✓	✓	✓
<0.001	✓	✓		✓	✓	✓
<0.001	✓	✓	✓		✓	✓
<0.001		✓	✓		✓	✓
p-value[2]	0.060	0.604	**0.039**	**0.024**	**0.005**	**<0.001**
F'_{ST} based on all 14 locations						
p-value[1]	SST grad	Orb_v_mean	Tidal	FW	DOM	SPM
<0.001				✓	✓	✓
<0.001		✓		✓	✓	✓
<0.001	✓			✓	✓	✓
<0.001		✓			✓	✓
<0.001			✓	✓	✓	✓
<0.001	✓		✓	✓	✓	✓
<0.001	✓	✓		✓	✓	✓
<0.001		✓	✓	✓	✓	✓
<0.001		✓	✓		✓	✓
<0.001	✓	✓			✓	✓
p-value[2]	0.253	0.578	0.366	0.148	0.076	**<0.001**

Table 4.5 (Cont.)

F_{ST} based on 11 locations (Excluding south)						
p-value[1]	SST grad	Orb_v_mean	Tidal	FW	DOM	SPM
0.470			✓			
0.757	✓					
0.758				✓		
0.817		✓				
0.860					✓	
0.992						✓
0.488	✓		✓			
0.739			✓	✓		
0.769			✓		✓	
0.769		✓	✓			
p-value[2]	0.291	0.872	0.214	0.993	0.668	0.676
F'_{ST} based on 11 locations (Excluding south)						
p-value[1]	SST grad	Orb_v_mean	Tidal	FW	DOM	SPM
0.274					✓	
0.354						✓
0.441			✓			
0.567				✓		
0.765	✓					
0.982		✓				
0.423	✓		✓			
0.483			✓		✓	
0.499			✓			✓
0.507	✓				✓	
p-value[2]	0.206	0.953	0.185	0.746	0.831	0.554

BEST analyses

BEST analyses based on data from all 14 locations and 9 geospatial and environmental variables showed that the top two best fitting models were significant at $p<0.05$ and both included the variables Lat, Tidal, FW, DOM and SPM ($r_s=0.588$). The remaining top eight best fitting models had similar Spearman's Rho value (0.587 and 0.586) and the variables Lat and SPM were included in all models. The top ten best fitting models of BEST analyses based on data from 11 locations had low, non-significant Spearman's Rho values ranging from 0.340 to 0.335, but the variables Lon and SPM were included in all models (Table 4.6).

Table 4.6 Results of the ten best fitting models with respective Spearman's Rho (r_s) values from the BEST analyses testing for the contribution of all 9 geospatial and environmental variables to explain variation in allele frequencies for *Pecten novaezelandiae*. The checkmarks (✓) indicate which variables were included in each model.

All 14 locations										
Rank	rs	Lat	Lon	Geo_ dist	SST grad	Orb_v_mean	Tidal	FW	DOM	SPM
1	0.588	✓			✓		✓	✓	✓	✓
2	0.588	✓					✓	✓	✓	✓
3	0.587	✓						✓		✓
4	0.587	✓			✓			✓		✓
5	0.587	✓			✓		✓	✓		✓
6	0.587	✓						✓	✓	✓
7	0.587	✓			✓			✓	✓	✓
8	0.587	✓					✓	✓		✓
9	0.586	✓					✓		✓	✓
10	0.586	✓			✓		✓		✓	✓
11 locations (Excluding south)										
Rank	r_s	Lat	Lon	Geo_ dist	SST grad	Orb_v_mean	Tidal	FW	DOM	SPM
1	0.340		✓					✓		✓
2	0.340		✓		✓			✓		✓
3	0.338		✓				✓		✓	✓
4	0.338		✓		✓		✓		✓	✓
5	0.337		✓					✓	✓	✓
6	0.337		✓		✓			✓	✓	✓
7	0.336		✓		✓		✓			✓
8	0.336		✓							✓
9	0.336		✓		✓					✓
10	0.335		✓				✓			✓

When only the 3 geospatial variables were analysed, BEST analyses based on data from all 14 locations showed that the two best fitting models were significant at $p<0.01$ with $r_s=0.560$ and included the variables Lat and Geo_dist. The remaining five best fitting models had very similar Spearman's Rho values ranging from 0.559 to 0.499 and included all the geospatial variables. BEST analyses based on data from 11 locations showed that the seven best fitting models were not significant and had low Spearman's Rho values ranging from 0.312 to 0.236 and all the variables were included in the models (Table 4.7).

Table 4.7 Results of the ten best fitting models with respective Spearman's Rho (r_s) values from the BEST analyses testing for the contribution of 3 geospatial variables to explain variation in allele frequencies for *Pecten novaezelandiae*. The checkmarks (✓) indicate which variables were included in each model.

All 14 locations				
Rank	r_s	Lat	Lon	Geo_dist
1	0.560			✓
2	0.560	✓		✓
3	0.559		✓	✓
4	0.559	✓	✓	✓
5	0.558	✓		
6	0.501		✓	
7	0.499	✓	✓	
11 locations (Excluding south)				
Rank	r_s	Lat	Lon	Geo_dist
1	0.312		✓	
2	0.306	✓	✓	
3	0.289			✓
4	0.289	✓		✓
5	0.285		✓	✓
6	0.285	✓	✓	✓
7	0.236	✓		

When only the 6 environmental variables were analysed, BEST analyses based on data from all 14 locations showed that the ten best fitting models were not significant and had low Spearman's Rho values ranging from 0.327 to 0.234. The variable SPM was included in all the models and the variable FW was included in the eight best fitting models. BEST analyses based on data from 11 locations also showed that the ten best fitting models were not significant and had low Spearman's Rho values ranging from 0.324 to 0.296. The variables FW, DOM and SPM were included in the majority of the models (Table 4.8).

Table 4.8 Results of the ten best fitting models with respective Spearman's Rho (r_s) values from the BEST analyses testing for the contribution of 6 environmental variables to explain variation in allele frequencies for *Pecten novaezelandiae*. The checkmarks (✓) indicate which variables were included in each model.

All 14 locations							
Rank	r_s	SST grad	Orb_v_mean	Tidal	FW	DOM	SPM
1	0.327	✓			✓		✓
2	0.326				✓		✓
3	0.322				✓	✓	✓
4	0.322	✓			✓	✓	✓
5	0.296	✓		✓	✓		✓
6	0.295			✓	✓		✓
7	0.291			✓	✓	✓	✓
8	0.291	✓		✓	✓	✓	✓
9	0.235						✓
10	0.234	✓					✓
11 locations (Excluding south)							
Rank	r_s	SST grad	Orb_v_mean	Tidal	FW	DOM	SPM
1	0.324				✓	✓	✓
2	0.322				✓	✓	
3	0.322	✓			✓	✓	✓
4	0.320	✓			✓	✓	
5	0.320				✓		✓
6	0.320	✓			✓		✓
7	0.317	✓				✓	
8	0.299					✓	✓
9	0.298					✓	
10	0.296	✓				✓	✓

BEST analyses of locus-specific data showed that Spearman's Rho values ranged from 0.265 in *Pnova*_33 ($p>0.05$) to 0.572 in *Pnova*_04 ($p<0.05$) suggesting that genetic variation at some loci (as *Pnova*_04, *Pnova*_09 and *Pnova*_10) may be more affected by environmental variation than genetic variation at other loci. The variable Lat occurred 10 times in the top ten models for 7 loci, the variable Lon occurred 10 times for 2 loci and SPM occurred 10 times in the top ten models for 6 loci. Overall these results support the BEST analyses across all loci and suggest that individual locus effects are probably not occurring (Table 4.9).

Table 4.9 Results of the BEST analyses testing for the contribution of 9 geospatial and environmental variables to explain variation in allele frequencies for each locus for *Pecten novaezelandiae* for all 14 locations. Top part of table represents the best fitting model for each locus; the checkmarks (✓) indicate which variables were included in the model. Bottom part of table indicates the number of times that each variable was included in the top ten best fitting models.

Locus	r_s	p-value	Lat	Lon	Geo_ dist	SST grad	Orb_v_mean	Tidal	FW	DOM	SPM
*Pnova*_01	0.421	0.149						✓	✓	✓	✓
*Pnova*_02	0.536	0.087	✓					✓		✓	✓
*Pnova*_04	0.572	**0.030**	✓	✓					✓		✓
*Pnova*_05	0.320	0.417						✓	✓	✓	
*Pnova*_09	0.532	**0.003**	✓	✓					✓	✓	✓
*Pnova*_10	0.497	**0.034**	✓							✓	
*Pnova*_27	0.484	0.056	✓			✓		✓	✓	✓	✓
*Pnova*_28	0.365	0.322	✓								
*Pnova*_32	0.445	0.180	✓					✓			✓
*Pnova*_33	0.265	0.443				✓			✓	✓	
*Pnova*_01	-	-	0	0	0	5	0	4	8	6	10
*Pnova*_02	-	-	10	0	0	4	0	7	3	5	10
*Pnova*_04	-	-	**10**	**10**	**0**	**5**	**0**	**6**	**8**	**6**	**10**
*Pnova*_05	-	-	0	0	0	4	0	8	6	5	0
*Pnova*_09	-	-	**10**	**10**	**0**	**5**	**0**	**4**	**8**	**4**	**10**
*Pnova*_10	-	-	**10**	**0**	**0**	**5**	**0**	**2**	**6**	**6**	**0**
*Pnova*_27	-	-	10	0	0	5	0	4	8	6	10
*Pnova*_28	-	-	10	0	0	5	0	4	2	6	0
*Pnova*_32	-	-	10	0	0	5	0	6	2	4	10
*Pnova*_33	-	-	1	4	4	4	4	3	6	4	0

In summary, the main variables driving the genetic structure were longitude (Lon), freshwater fraction (FW) and suspended particulate matter (SPM). The variables latitude (Lat), index of geographic distance (Geo_dist), tidal current (Tidal), sea surface temperature (SSTgrad) and dissolved organic matter (DOM) also explained the genetic structure according to some of the models (Table 4.10).

Table 4.10 Summary of GLZ and BEST results with important variables explaining genetic variation as determined by the number of times they were included in the models, model p-values, test of all effects p-values and significance of r_s coefficients.

Test	Analysis	Important variables
F_{ST} 14 locations	GLZ	Lon, Geo_dist, Tidal, FW, DOM, SPM
F'_{ST} 14 locations	GLZ	Lon, Tidal, FW, DOM, SPM
F_{ST} 11 locations	GLZ	Lon, Tidal
F'_{ST} 11 locations	GLZ	All 9 variables
14 locations	BEST	Lat, FW, SPM
11 locations	BEST	Lon, FW, DOM, SPM

Discussion

In chapter 3, a low but significant level of population genetic structure of *Pecten novaezelandiae* was found between regions. While a degree of differentiation from north to south was apparent, it also conflicted with some evidence of panmixia. Seascape genetics can be a valuable tool for understanding these conflicting patterns of genetic differentiation and their association with the geographic and environmental variation (Riginos & Liggins 2013). In this study, analyses showed that different combinations of environmental variables explain the genetic structure observed for *P. novaezelandiae*. In general, the main variables driving the genetic structure were longitude (Lon), freshwater fraction (FW) and suspended particulate matter (SPM). While the variables latitude (Lat), index of geographic

distance (Geo_dist), tidal current (Tidal) and dissolved organic matter (DOM) explained the genetic structure according to some of the models, there was no evidence that spatial gradient annual mean sea surface temperature (SSTgrad) or mean orbital velocity (Orb_v_mean) were associated with the patterns of genetic differentiation observed.

Results showed that longitude explains genetic variation in terms of F_{ST} and F'_{ST} values for all 14 locations and allelic frequencies for 11 locations. Because sampling was based on the species distribution and was not continuous along the coast, samples were obtained from three groups of longitude values: a western group with values ranging from +166º (FIO) to +168º (STE14), a central group ranging from +172º (GOL) to +176º (TAU), and at the east the Chatham Islands at -176º (see Figure 4.1). The most differentiated populations were in the western group (FIO and STE14), so the results of seascape analyses might be biased by the distribution of the samples and reflect their differentiation. This might also be the case for the correlation of latitude with genetic variation, which was observed for allele frequencies when including all 14 locations. As the southern group (FIO and STE14) was the most differentiated, the results might reflect this hierarchical structure.

For most of the models, freshwater discharge was correlated with genetic variation in *Pecten novaezelandiae*. A significant association between genetic differentiation and salinity has been observed for the herring *Clupea harengus* (Jørgensen *et al.* 2005). Also, it has been observed a significant decrease in survivorship with the exposure to freshwater for the bivalve *Paphies australis* (McLeod & Wing 2008) and more recently a correlation of genetic variation with the volume of freshwater entering the estuary (Hannan 2014). Biochemical genetic variation at the leucine aminopeptidase (LAP) locus has also been associated with salinity variation in *Mytilus edulis* in the U.S.A. (Hilbish 1985) and in *Mytilus galloprovincialis* in New Zealand (Gardner & Palmer 1998). Although the present study does not test for causation, these results support the evidence that freshwater discharge can contribute to the population genetic variation of *P. novaezelandiae*.

There was strong evidence supporting the correlation of genetic variation (F_{ST}, F'_{ST} and allelic frequencies) with levels of suspended particulate matter, except for F_{ST} values when excluding the 3 locations in the south, which was probably due to lower levels of genetic variation among locations. Models that had significant correlation of genetic variation with levels of suspended particulate matter also showed some levels of correlation with

dissolved organic matter, except for BEST analyses using 14 locations. Given that coastal areas are generally influenced by similar sources of suspended particulate matter and dissolved organic matter (D'Sa *et al.* 2007) it is not unreasonable to expect similar results.

It is known that bivalves' response to different concentrations of suspended particulate matter differs substantially among species. Bricelj & Malouf (1984) suggested that bivalves such as clams and scallops that regulate ingestion primarily by reducing clearance rates are more susceptible to high concentrations of suspended sediment than mussels and oysters, which control ingestion mainly by increasing pseudofaecal production. However, studies suggest that intermediate strategies may occur and the ability to cope with different levels of suspended particulate matter may also vary within a species (Navarro & Iglesias 1993). It has been shown that prolonged exposure to suspended particulate matter can affect both the feeding behaviour and growth rate of the scallop *Pecten maximus*. Although elevated suspended particulate matter did not have any short-term effects on survival of the scallops, significantly lower growth rates were observed under both low and high levels of suspended particulate matter (Szostek *et al.* 2013). Higher concentrations of suspended particulate matter can affect, for example, feeding and respiration of *Pecten novaezelandiae* (by gill-clogging) and might further modify their genetic variation by favouring locally adapted individuals. Therefore, different levels of suspended particulate matter among locations can be one of the factors contributing to population genetic structure of *P. novaezelandiae*.

According to some of the GLZ models, genetic variation was correlated with the index of geographic distance between locations. These results are in agreement with the significant isolation by distance signal detected in chapter 3 suggesting that the distance between locations is an important explanatory variable. The pattern of isolation by distance, where all populations are connected by continuous migration but gene flow is higher between nearby populations, has been shown for other bivalves such as the sea scallop *Placopecten magellanicus* (Kenchington *et al.* 2006) and the softshell clam *Mya arenaria* (St-Onge *et al.* 2013). However, for *Pecten novaezelandiae* it appears that the level of genetic differentiation is not a simple function of the geographic distance between populations. For example, it is not evident that the distance between the Chatham Islands and the mainland acts as an important barrier to larval dispersal. Other environmental or geospatial factors beyond the ones tested in this study could be playing an important role in

explaining genetic variation. For example, the subtropical convergence flowing eastward might be facilitating gene flow and thus minimising the impact of geographic distance between the Chatham Islands and the mainland New Zealand.

Tidal current was one of the environmental factors explaining the genetic structure according to some of the models. In the Coromandel fishery for example, scallops are more common in depths of 10 to 30 m (Ministry of Primary Industries 2013a), so the flow of tidal currents could still represent a selective agent for *P. novaezelandiae*. The littorine snail *Littorina saxatilis* shows strong evidence for selection at a single locus (allozyme locus *Aat*; EC. 2.6.1.1). The enzyme aspartate aminotransferase plays an important role in amino acid metabolism and while Aat^{120} is most frequent in high shore areas of Northern Europe, Aat^{100} is more common in low shore areas (Johannesson & Johannesson 1989; Johannesson *et al.* 1995). There is also considerable evidence for adaptive variation associated with distinct intertidal microhabitats at the glucose phosphate isomerase locus (Gpi) and the mannose phosphate isomerase (Mpi) locus in the northern acorn barnacle *Semibalanus balanoides* (Rand *et al.* 2002).

Sea surface temperature has been identified as one important explanatory factor for the observed genetic variation in other species (Wei *et al.* 2013b; Constable 2014; Hannan 2014) and it is one important environmental factor triggering spawning in scallops (Shumway & Parsons 2006). In this study, a few models related SSTgrad with genetic variation, and for locus-specific data this variable was included 4 to 5 times in the top ten best-fitting models. Although there was not strong support for a correlation between temperature and genetic variation of *P. novaezelandiae*, these results may be masked by the significant importance of other environmental factors.

In general, for the BEST analyses, correlations with the geospatial variables for both scenarios (for all locations and excluding south) were higher compared to correlations with environmental variables only. This suggests that geospatial variables might be an important factor determining the large-scale population genetic structure of *Pecten novaezelandiae*. However, as suggested by GLZ and BEST analyses, other environmental factors such as levels of suspended particulate matter and freshwater input could also be affecting larval settlement, feeding behaviour and growth rate of the New Zealand scallop, and therefore contributing to an increase in genetic differentiation among populations.

Other unknown factors could also be limiting larval dispersal between populations but are undetected in this study. For example, Talman *et al.* (2004) showed that survival of juvenile *Pecten novaezelandiae* was affected by the ambient scallop density and that adult scallop predation increased with a smaller number of other species such as sponges and ascidians. In addition, ocean currents and hydrodynamic forces such as eddies and current discontinuities can strongly affect gene flow and population structure (White *et al.* 2010). This study provides valuable information not only for a better understanding of population genetics of *P. novaezelandiae* but also for identifying common environmental factors affecting population genetic structure of multiple species. Although the mechanisms behind local adaptation are unknown, studies like this one provide important insights on the processes shaping marine population structure and form a basis for identifying suitable management strategies across species.

Conclusions

In general, results of this study suggest that a combination of variables might be influencing the population genetic structure of *Pecten novaezelandiae*. Although several population genetic studies highlight the importance of geographic distance between populations, for *Pecten novaezelandiae* it appears that the level of genetic differentiation is not a simple function of this geospatial variable. There were strong evidences that levels of suspended particulate matter can be one of the factors contributing to population genetic structure of *P. novaezelandiae*.

Coastal marine environments often experience a large variation in levels of suspended particulate matter that can be driven by oceanographic cycles, wave action and high rainfall resulting in increased river output (Hall 1994). The increase of input of sediments into coastal areas can also be associated with the development of coastal regions and land use such as farming or forestry. This increase in suspended sediment can greatly alter the structure and function of coastal ecosystems including decreasing photosynthetic output and smothering of plants and animals (Thrush *et al.* 2004). As both ecosystems are highly linked, it is very important to account for these effects on marine ecosystems when planning land management and conservation practices (Stoms *et al.* 2005).

As for most seascape genetic studies to date, the current study is not able to test for causation. Other techniques such as direct observation of dispersal and reproduction or functional genomics would be required to evaluate the link between genetic variation and a particular spatial or environmental factor (Liggins *et al.* 2013). Another limitation of this study is that extreme events and temporal variation of the environmental data are not specifically represented in the averaged mean and these environmental oscillations can highly influence gene flow and the genetic structure of organisms. While more environmental and genetic data have become available for seascape genetic studies, studies are still scarce and patchy. Therefore, interpretations of results are still limited. Nevertheless, the application of seascape genetics is a valuable tool, particularly for marine species exhibiting a weak genetic signal, which is the case of *Pecten novaezelandiae*. By identifying previously unknown environmental factors that can be driving genetic variation, the emerging field of seascape genetics provides essential clues for further research guidelines.

CHAPTER 5

Spatial and temporal patterns of dispersal of *Pecten novaezelandiae* in the Coromandel fishery: implications for management

Introduction

Abundance and distribution of highly fecund marine species with a pelagic larval stage can vary greatly in space and time. The causes of variation in larval dispersal are difficult to assess and contrasting results are commonly reported across space, time and taxa (Levin 2006; Gardner *et al.* 2010). The use of different tools that provide independent estimates of population genetic structure is a powerful approach to understand larval dispersal and marine connectivity. Using only one sampling scale in population genetic studies may not detect some important factors influencing gene flow (Anderson *et al.* 2010). Although employing different strategies cannot exclude all sources of noise, they increase precision of estimating the factors that shape population genetic structure.

Complex genetic patterns can arise even in marine species that do not have obvious barriers to gene flow. As a result, some broadcast spawning marine invertebrates can exhibit small-scale spatial genetic structure (e.g. Wood & Gardner 2007; Zhan *et al.* 2009; Owen & Rawson 2013). Restricted dispersal of larvae can be the result of (1) high levels of self-recruitment, (2) high mortality rates, and/or (3) fine scales of larval transport (reviewed in Pineda *et al.* 2007). However, the distance that larvae can travel, their place and timing of final settlement, and their subsequent successful reproduction depend on many interdependent factors such as biological features (e.g. larval behaviour), local hydrodynamic characteristics such as eddies and gyres, and the habitat availability at settlement locations (reviewed in Swearer *et al.* 2002).

Temporally variable genetic structure is sometimes observed among some marine invertebrates (e.g. Owen & Rawson 2013; Yednock & Neigel 2014) and can potentially influence interpretations about spatial patterns of differentiation (Toonen & Grosberg 2011). Unexpected temporal patterns can be determined by a large variance in reproductive success rates. The hypothesis of Sweepstakes Reproductive Success (SRS), postulates that very fecund marine animals with high early mortality rates have high variance in individual reproductive success and therefore only a small number of adults contribute to the next generation (Hedgecock 1982). As a result, juveniles are expected to exhibit reduced genetic diversity, higher relatedness and smaller effective population sizes. In addition, SRS can greatly contribute to the patterns of genetic differentiation and can also result in chaotic genetic patchiness (Johnson & Black 1982; Pujolar *et al.* 2006; Hogan *et al.* 2010;

Hedgecock & Pudovkin 2011; Broquet *et al.* 2013). A lack of temporal stability can also be the result of stochastic factors, such as variation in oceanic currents, which can affect the movement of larvae and consequently the genetic patterns (Sotka *et al.* 2004; Selkoe & Toonen 2006; Pringle & Wares 2007). Nonetheless, in most studies, only spatial patterns of genetic structure are examined and the possibility for temporal genetic variation in scallops has been rarely addressed (Lewis & Thorpe 1994; Owen & Rawson 2013).

One of the main goals for fisheries management is to avoid depletion of fish stocks and a crucial prerequisite is to match biologically relevant processes with management action (Reiss *et al.* 2009). Therefore, understanding population dynamics and patterns of connectivity is vital for the delimitation of spatial management areas with meaningful biological units. Marine species may reside in "source" or "sink" habitats, where populations occurring in "sink" habitats only make a small contribution of juveniles to the spawning stock and populations in "source" habitats contribute an excess of individuals that sustains populations both in source and sink habitats (Pulliam 1988). These source-sink dynamics have been observed for several marine species (e.g. Lipcius *et al.* 1997; Chiswell & Booth 2008; Barson *et al.* 2009; Drake & Griffen 2013; Thomas & Bell 2013) and it has important implications for fisheries management. Exploiting a source population can markedly reduce productivity of a sink population and for example, marine protected areas could provide a continuous source of recruitment and bring important environmental and economic benefits (Tuck & Possingham 2000).

It has been demonstrated for some scallop species that populations separated by only a few tens to hundreds of kilometres show genetic differentiation. For example, individuals of the Zhikong Scallop (*Chlamys farreri*) collected from different marine gyres showed significant genetic differentiation (Zhan *et al.* 2009) and the genetic structure of the Atlantic sea scallop (*Placopecten magellanicus*) coincides with the ocean current structure of the Eastern Maine Coastal Current (Owen & Rawson 2013). This information on population dynamics of species at fine spatial scales is crucial when delineating meaningful management units because separate stocks may correspond to geographic areas that are smaller than expected for marine species.

The New Zealand endemic scallop *Pecten novaezelandiae* supports very important fisheries, particularly in the Coromandel region. The Coromandel scallop fishery encompasses the area between Cape Rodney in the north and Town Point in the south

(Ministry of Primary Industries 2013a). Scallops occur in dense aggregations or "beds" in the region and although they are not completely sedentary, Morrison (1999) found that adults rarely move more than 10 m. Although scallops are managed as one single stock in the Coromandel (Ministry of Primary Industries 2013a), there is no previous information on the genetic connectivity between these "beds". The Coromandel region is a key marine environment in New Zealand, supporting large wild fisheries and at the same time being on the edge of New Zealand's largest city (Auckland, 1.2 million population). The Coromandel fishery area encompasses the Hauraki Gulf, a semi-enclosed area of north-eastern New Zealand, and an open coastal environment both characterized by complex hydrodynamics. The East Auckland Current (EAUC) flowing southeast influences the physical oceanography (Zeldis *et al.* 2004) and nutrient supply (Zeldis 2004) of both environments, the Gulf and the open coast. Depending on the predominant currents and gyre dynamics, gene flow between scallop aggregations or self-recruitment within aggregations may be facilitated. Therefore, understanding patterns of dispersal of scallops in the region is essential for an effective management and provides important knowledge about the processes that influence source-sink dynamics of populations.

In chapter 3, the first genetic structure study of *Pecten novaezelandiae* was conducted, encompassing the full distributional range of the species. The present chapter aimed to estimate the spatial and temporal patterns of genetic differentiation of *Pecten novaezelandiae* in the Coromandel fishery region using 10 microsatellite markers and a hydrodynamic modelling approach to track the dispersal path of larvae released at three locations. Temporal analysis combined with a geographic analysis of genetic structure allows inferences on whether genetic variation among populations is due to self-recruitment or sporadic recruitment from another genetically distinct source population. This study also aimed to identify source-sink relationships. If a model of source–sink dynamics occurs, an asymmetrical dispersal between two populations is expected, with individuals predominantly dispersing from the source to the sink population. However, the processes that result in source-sink dynamics are not well understood. Therefore, this study aimed to provide insight into the processes that shape recruitment of populations, with particular applications to the Coromandel scallop fishery.

Materials and methods

Sampling

A total of 592 individual scallops, *Pecten novaezelandiae*, were collected from the Coromandel region of northern New Zealand for this study. Data were analysed in two groups: a spatial analysis using 5 locations sampled in 2012 (Figure 5.1a, Table 5.1a) and a temporal analysis from 3 locations using a reduced data set of samples from 2012 (chapter 3) and additional samples from the same locations collected in 2014 (Figure 5.1b, Table 5.1b). Therefore, a subset of larger scallops collected in 2012 and smaller scallops collected in 2014 were used to discern individuals derived from different recruitment seasons to test for the temporal stability of patterns of genetic structure.

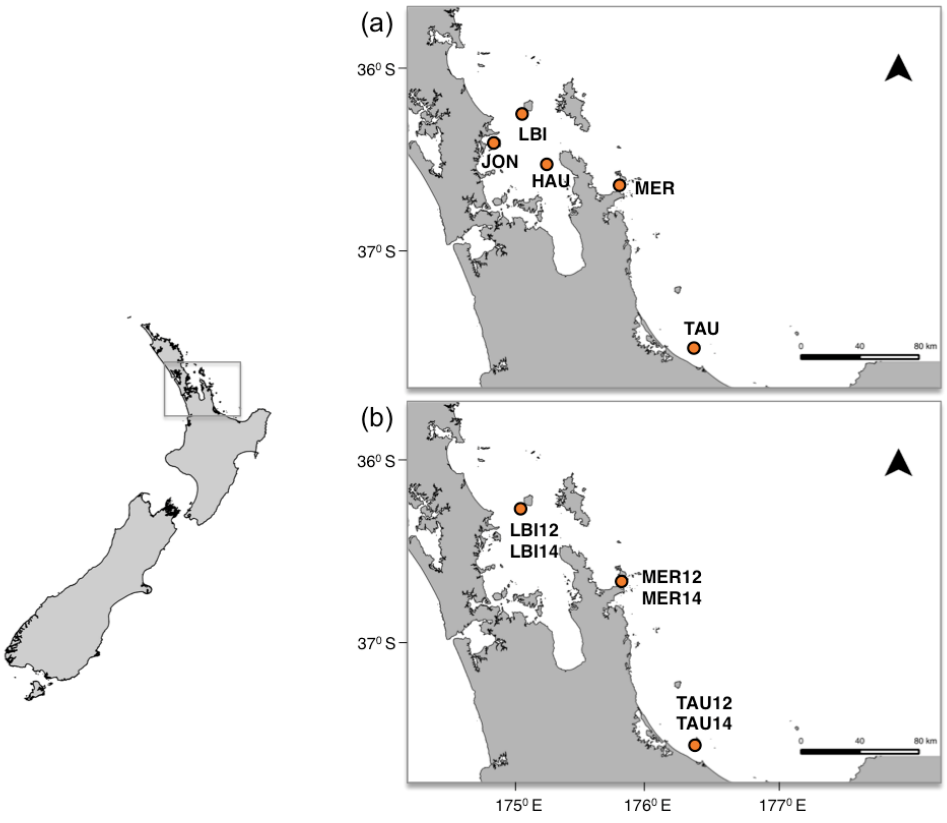

Figure 5.1 Map of sampling sites in the Coromandel region: (a) for the spatial analyses individuals of *Pecten novaezelandiae* were collected in 2012 and (b) for the temporal analyses a subset of individuals collected in 2012 and additional samples collected in 2014 was used. Locations abbreviations as per Table 5.1.

All the individuals were measured (left shell length) and size structure was analysed using the software R 3.1.0 (R Core Team 2014). Individuals were genotyped for 10 loci (detailed laboratory protocols are described in Chapters 2 and 3) and the additional 192 samples collected in 2014 were analysed as per Chapters 2 and 3.

Table 5.1 Collecting site descriptions for the (a) spatial and (b) temporal analyses of *Pecten novaezelandiae* in the Coromandel region with sample sizes (N), mean depth (m), dates and geospatial coordinates.

(a)

Code	Site Description	N	Depth (m)	Date collected	Latitude	Longitude
LBI	Little Barrier Is	95	15	1/05/2012	-36° 13' 51.0"	+175° 4' 17.40"
JON	Jones Bay	40	10	15/11/2012	-36° 22' 53.6"	+174° 48' 59.48"
HAU	Hauraki Gulf	99	43	28/11/2012	-36° 34' 9.60"	+175° 14' 6.57"
MER	Mercury Is	69	15	1/05/2012	-36° 41' 3.60"	+175° 43' 33.60"
TAU	Tauranga	99	22	3/05/2012	-37° 40' 14.4"	+176° 24' 10.80"
Total		402				

(b)

Code	Site Description	N	Depth (m)	Date collected	Latitude	Longitude
LBI12	Little Barrier Is	63	15	1/05/2012	-36° 13' 51.0"	+175° 4' 17.40"
LBI14	Little Barrier Is	64	16	6/07/2014	-36° 12' 40.0"	+175° 2' 32.00"
MER12	Mercury Is	60	15	1/05/2012	-36° 41' 3.60"	+175° 43' 33.60"
MER14	Mercury Is	60	23	6/07/2014	-36° 40' 25.0"	+175° 42' 22.00"
TAU12	Tauranga	70	22	3/05/2012	-37° 40' 14.4"	+176° 24' 10.80"
TAU14	Tauranga	66	25	6/07/2014	-37° 37' 57.0"	+176° 20' 14.00"
Total		383				

Analysis of genetic diversity

Genotyping artefacts were assessed using the software Micro-Checker v.2.2.0.3 (Van Oosterhout *et al.* 2004). Analyses of departure from Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium (LD) were performed using the software GenePop on the web using the Markov chain method and Fisher´s exact test (Rousset 2008). False discovery rate (FDR) control (Verhoeven *et al.* 2005) was applied to p-values in all statistical analyses that included multiple comparisons.

The software Lositan (Antao *et al.* 2008) was used to perform an outlier analysis with 50,000 simulations and a confidence interval (CI) of 0.95 under the infinite alleles model (IAM) for a sample size of 50.

The software HP-Rare (Kalinowski 2005) was used to quantify genetic diversity as allelic richness (A_R) and private allelic richness (P_{AR}) with a rarefaction sample size of 60 genes for the spatial analyses and 112 genes for the temporal analyses. GenAlEx 6.5 (Peakall & Smouse 2012) was used to quantify the number of private alleles per site (Pa), observed (H_O) and expected (H_E) heterozygosity and the fixation index (F_{IS}).

Population structure

The software GenePop on the web (Rousset 2008) was used to calculate pairwise F_{ST} values (adapted by Weir & Cockerham, 1984). An exact G-test (Goudet *et al.* 1996) was also calculated using the G log likelihood ratio with 10,000 dememorization steps, 1,000 batches and 10,000 iterations per batch for each pair. All p-values were corrected using the False Discovery Rate (FDR) (Verhoeven *et al.* 2005) at $p < 0.05$.

The neighbour joining (NJ) method (Saitou & Nei 1987) was used to generate a population tree using the software PopTreeW (Takezaki *et al.* 2014) based on F_{ST} values with 1000 bootstrap replicates. A principal components analysis (PCoA) was performed in GenAlEx 6.5 (Peakall & Smouse 2006) to test for variation among locations using co-dominant genetic distance.

A non-parametric analysis was conducted in the software package AWclust (Gao & Starmer 2008) to evaluate population genetic structure among locations, following the approach of Gruber et al. (2013) and Wei et al. (2013a). As a comparison, a Bayesian cluster analysis was also performed in Structure 2.3.4 (Pritchard *et al.* 2000) using 100,000 interactions, a burn-in length of 10,000, 'admixture' model, 'correlated allele frequencies' and sampling regions were used as 'prior' for k=1 through k=5 for the spatial analyses and through k=6 for the temporal analyses. Results were evaluated using the software Structure Harvester (Earl & VonHoldt 2012) and the appropriate number of clusters was determined by the log probability (L(K)) and ΔK across multiple runs according to Evanno et al. (2005).

An Analysis of Molecular Variation (AMOVA) was performed in GenAlEx 6.5 (Peakall & Smouse 2012) using 999 permutations. For the spatial analyses, the 5 locations were

grouped into 3 regions (1: LBI, HAU, 2: JON, 3: MER, TAU) and 4 regions (1: LBI, 2: HAU, 3: JON, 4: MER, TAU) to test for the significance of the PCoA and the neighbour joining analysis. For the temporal analyses, the 6 locations were grouped in 2 regions for a temporal test between years using all locations (1: LBI12, MER12, TAU12, 2: LBI14, MER14, TAU14) and for a temporal test between years for locations MER and TAU (1: MER12, TAU12, 2: MER14, TAU14).

Estimates of migration

The Bayesian program Geneclass 2 (Piry *et al.* 2004) was used to identify first-generation migrants as well as the proportion of individuals recruiting to a location, using the Markov chain Monte Carlo (MCMC) and the algorithm of Paetkau et al. (2004). The likelihood ratio 'L_home/L_max' was used with a 0.01 rejection level and a simulated population size of 10,000 individuals per site. This approach selects an individual's genotype from the location in which it was sampled over the highest likelihood observed for this genotype in any location (Paetkau *et al.* 2004). The individuals were assigned to the location with the highest probability.

Relatedness

To test whether scallop samples from 2014 had a greater number of relatives than the samples from 2012, the mean population relatedness (r) (Queller and Goodnight 1989) was calculated in GenAlEx 6.5 (Peakall & Smouse 2006) across all locations using 999 bootstrap permutations for significance. The measure r is calculated based on the genetic similarity between two individuals in relation to the similarity between random individuals in a reference population (Pamilo 1990).

Oceanographic model

The online marine connectivity interface ConnIe2 (CSIRO 2014) was used to investigate the advection of propagules by oceanic currents in the Coromandel region. ConnIe2 was developed using OFAM (Ocean Forecasting Australia Model) which, in turn, was developed using the Modular Ocean Model (MOM4) code as part of the BLUElink Project. This three-dimensional nonlinear hydrodynamic model has a spatial resolution of 0.1 degrees (~10 km), so a finer spatial resolution would be necessary for simulations in the

inner part of the Hauraki Gulf. Consequently, connectivity was estimated for the open coastal environment using the embedded particle-tracking module under three different scenarios: particles released from Little Barrier Island (LBI), from Mercury Island (MER) and from Tauranga (TAU). The behavioural trait of diel vertical migration was incorporated (Kaartvedt *et al.* 1987), particles were released in early summer (the main dispersal period of *P. novaezelandiae* in the Coromandel region) and tracked for a larval duration of 25 days (the approximate pelagic larval duration), and results were averaged across ten years (1997-2007), the latest data available.

Results

Of the 592 scallops analysed, 402 were employed in the spatial analyses and 383 were employed in the temporal analyses. For the spatial analyses all individuals were > 65 mm in shell length and classified as mature (Williams & Babcock 2005). The average size of all individuals was 99.31 ± 6.70 mm (Figure 5.2a) and at this length they are likely to have recruited 1.5 years prior to collection (i.e., 2010-2011). For the temporal analyses, all individuals were > 70 mm in shell length and classified as mature (Williams & Babcock 2005) with an average size of 96.57 ± 7.67 mm. The average size of individuals collected in 2012 was 101.36 ± 5.53 mm. Individuals collected in 2014 had an average size of 91.42 ± 6.18 mm and at this length they are likely to have recruited in 2012-2013 (Figures 5.2b and 5.3).

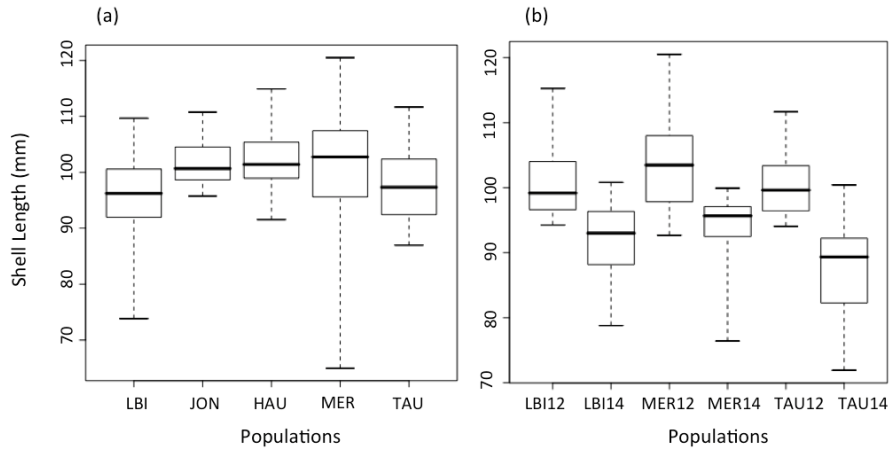

Figure 5.2 Size structure of individuals of *Pecten novaezelandiae* collected in the Coromandel region for the (a) spatial and (b) temporal studies. Dashed lines represent the maximum and minimum size at each site, while the bars represent the 25th and 75th

quartile of size ranges, with the median indicated within each bar. Location abbreviations as per Table 5.1

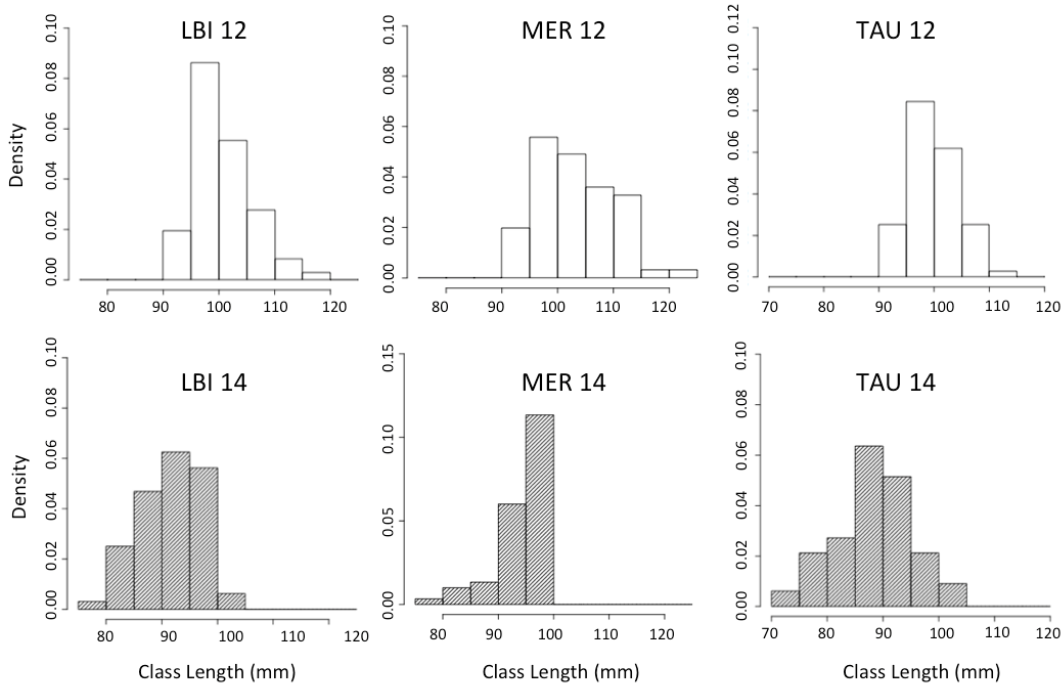

Figure 5.3 Length-frequency histograms of *Pecten novaezelandiae* collected in 2012 and 2014 in the Coromandel region for the temporal analyses. Location abbreviations as per Table 5.1.

Genetic diversity

For the spatial analyses, Micro-Checker analyses identified putative null alleles at *Pnova_01*, *Pnova_02*, *Pnova_05*, *Pnova_10*, *Pnova_27* and *Pnova_33* due to homozygote excess and no long allele dropout was detected. After FDR correction for multiple tests, *Pnova_10* was identified as being significantly out of HWE at all locations and *Pnova_27* at more than half of the locations. There was no evidence of significant linkage disequilibrium between locus pairs. Lositan analyses identified all 10 loci as neutral markers. Allelic richness ranged from 9.78 at TAU to 10.07 at MER. Private allelic richness ranged from 0.48 at TAU to 0.65 at HAU. In total there were 33 private alleles across all locations; LBI had the greatest number (9). The observed heterozygosity ranged from 0.564 at HAU to 0.662 at MER, and expected heterozygosity ranged from 0.658 at TAU to 0.671 at HAU. Location MER had the lowest value of F_{IS} (0.006) and HAU had

the highest value (0.146). All locations showed significant departures from HWE expectations after FDR correction, except MER (Table 5.2a).

For the temporal analyses, putative null alleles were identified at *Pnova_01*, *Pnova_02*, *Pnova_10*, *Pnova_27, Pnova_28* and *Pnova_33*. After FDR correction for multiple tests, *Pnova_10* and *Pnova_27* were identified as being significantly out of HWE at more than half of the locations. There was no evidence of significant linkage disequilibrium between locus pairs. All 10 loci were identified as neutral markers. Allelic richness ranged from 10.73 at MER14 to 11.54 at MER12. Private allelic richness ranged from 0.11 at TAU14 to 0.65 at MER12. In total there were 25 private alleles across all locations; MER12 and TAU12 had the highest number (7 each). Overall, there were lower levels of allelic richness and private allelic richness as well as higher values of F_{IS} in samples collected in 2014 than those collected in 2012. All locations showed significant departure from HWE expectations after FDR correction, except MER12 (Table 5.2b).

Table 5.2 Genetic variation in *P. novaezelandiae* in the Coromandel region for locations used for (a) the spatial study and (b) the temporal study. Allelic richness (A_R), private allelic richness (PA_R), number of private alleles per site (Pa), observed heterozygosity (H_O), expected heterozygosity (H_E) and fixation index (F_{IS}). F_{IS} values in bold show significant departure from HWE expectations after FDR correction ($p<0.05$). Locations abbreviations as per Table 5.1.

	Location	A_R	PA_R	Pa	H_O	H_E	F_{IS}
(a)	**LBI**	10.00	0.55	9	0.605	0.665	**0.088**
	JON	9.79	0.51	5	0.596	0.668	**0.115**
	HAU	9.94	0.65	6	0.564	0.671	**0.146**
	MER	10.07	0.56	6	0.662	0.670	0.006
	TAU	9.78	0.48	7	0.596	0.658	**0.083**
(b)	**LBI12**	11.39	0.33	5	0.608	0.660	**0.071**
	LBI14	10.93	0.32	4	0.579	0.660	**0.129**
	MER12	11.54	0.65	7	0.666	0.670	0.002
	MER14	10.73	0.12	1	0.556	0.646	**0.139**
	TAU12	11.29	0.45	7	0.593	0.651	**0.068**
	TAU14	10.74	0.11	1	0.599	0.671	**0.096**

Population structure

For the spatial study, F_{ST} values for all comparisons ranged from 0.0004 to 0.0033. Of the 10 comparisons, 3 were significant after FDR correction for multiple comparisons (Table 5.3). For the temporal study, F_{ST} values for all comparisons ranged from 0 to 0.0048. Of the 15 comparisons, 5 were significant after FDR correction for multiple comparisons. Interestingly, locations MER12-MER14 and TAU12-TAU14 were significantly different but not the locations LBI12-LBI14 (Table 5.4).

Table 5.3 Pairwise F_{ST} values for *Pecten novaezelandiae* for the spatial study are below the diagonal and p-values are above the diagonal. Significant values are in bold after FDR testing ($p<0.05$). Locations abbreviations as per Table 5.1.

Code	LBI	JON	HAU	MER	TAU
LBI		**0.0018**	0.2370	0.2194	0.2752
JON	**0.0022**		**0.0000**	0.0430	0.0361
HAU	0.0008	**0.0021**		0.0730	**0.0098**
MER	0.0032	0.0024	0.0005		0.3998
TAU	0.0013	0.0033	**0.0022**	0.0004	

Table 5.4 Pairwise F_{ST} values for *Pecten novaezelandiae* for the temporal study are below the diagonal and p-values are above the diagonal. Significant values are in bold after FDR testing ($p<0.05$). Locations abbreviations as per Table 5.1.

Code	LBI12	LBI14	MER12	MER14	TAU12	TAU14
LBI12		0.1862	0.3279	0.2563	0.0627	**0.0256**
LBI14	0.0000		0.0939	0.0337	0.2210	0.0457
MER12	0.0007	0.0025		**0.0198**	0.2319	0.0501
MER14	0.0000	0.0025	**0.0048**		**0.0152**	**0.0057**
TAU12	0.0029	0.0010	0.0007	**0.0030**		**0.0135**
TAU14	**0.0017**	0.0015	0.0015	**0.0008**	**0.0005**	

For the spatial analyses, the NJ tree showed locations MER and TAU grouped together with 44% support and the locations JON and LBI grouped separately (Figure 5.4a). For the temporal analyses, the locations TAU12 and MER12 were grouped together (48% bootstrap) as well as locations LBI12 and MER14 (54% bootstrap). The location LBI14 was grouped separately (Figure 5.4b).

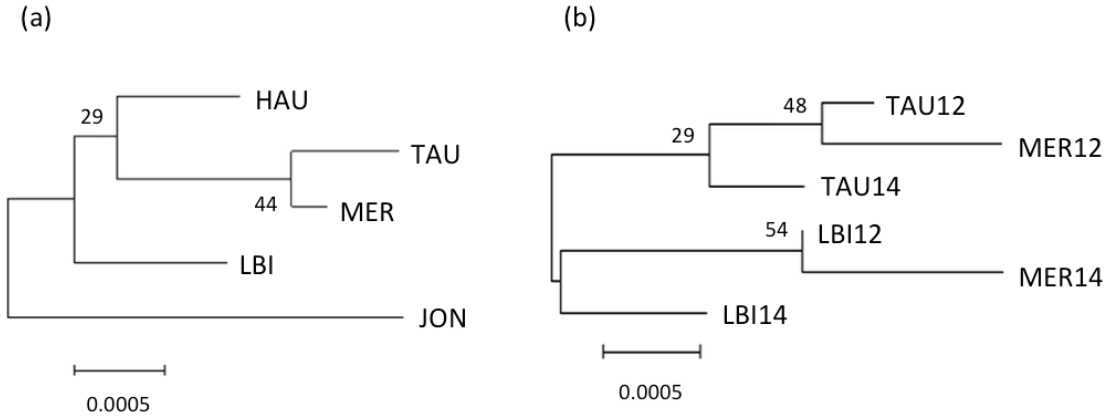

Figure 5.4 Neighbour joining population tree for *Pecten novaezelandiae* based on F_{ST} values for (a) the spatial study and (b) the temporal study. Location abbreviations as per Table 5.1.

The principal components analysis (PCoA) for the spatial study showed that Axis 1 explained 63.96% of the variation and Axis 2 explained 23.25%. The analysis grouped the locations TAU and MER together (Figure 5.5a). For the temporal analyses, the PCoA showed that Axis 1 explained 60.93% of the variation and Axis 2 explained 25.47%. The analysis grouped the locations TAU12 and MER12 on the left side of the axis, with the remaining locations on the right side of the axis (Figure 5.5b).

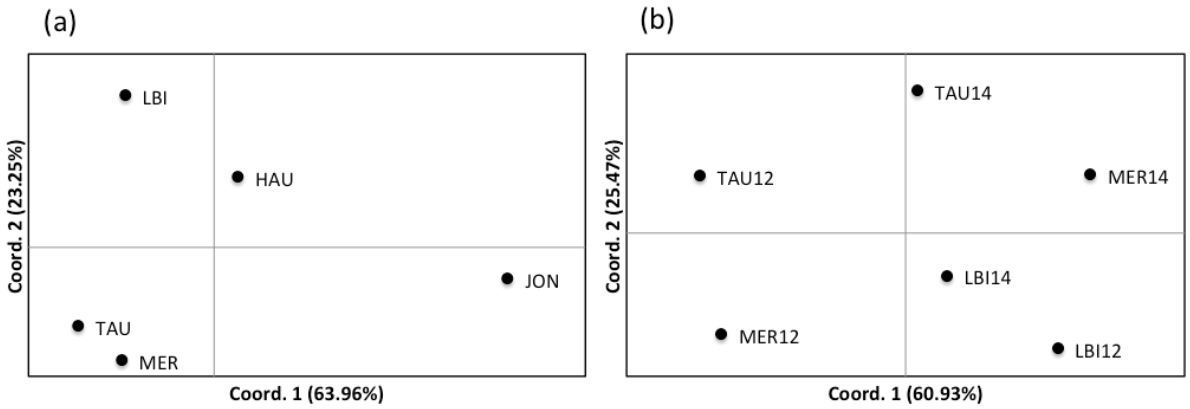

Figure 5.5 Principal components analysis (PCoA) for *Pecten novaezelandiae* using pairwise genetic distance for (a) the spatial and (b) the temporal study. Locations abbreviations as per Table 5.1.

For the spatial study, the non-parametric analysis (AWclust) showed a large gap value at k=3, with some degree of overlap of confidence intervals (Figures 5.6a and 5.7). For the temporal study, the largest gap value of AWclust analyses was at k=6, with extensive overlap of confidence intervals (Figures 5.6b and 5.8).

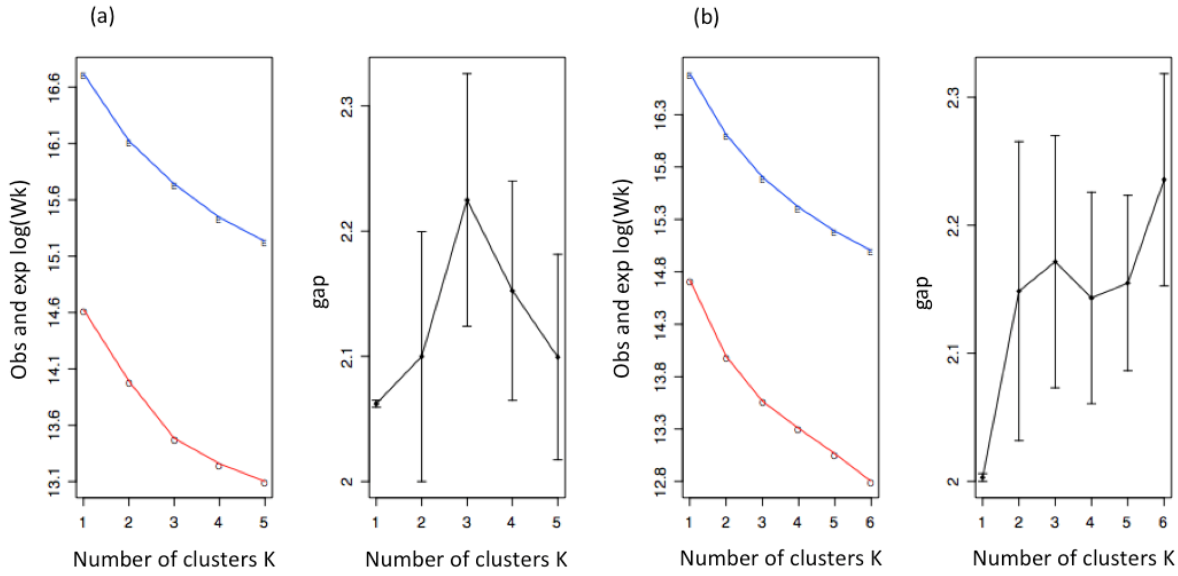

Figure 5.6 AWclust analyses for *Pecten novaezelandiae* for (a) the spatial study and (b) the temporal study.

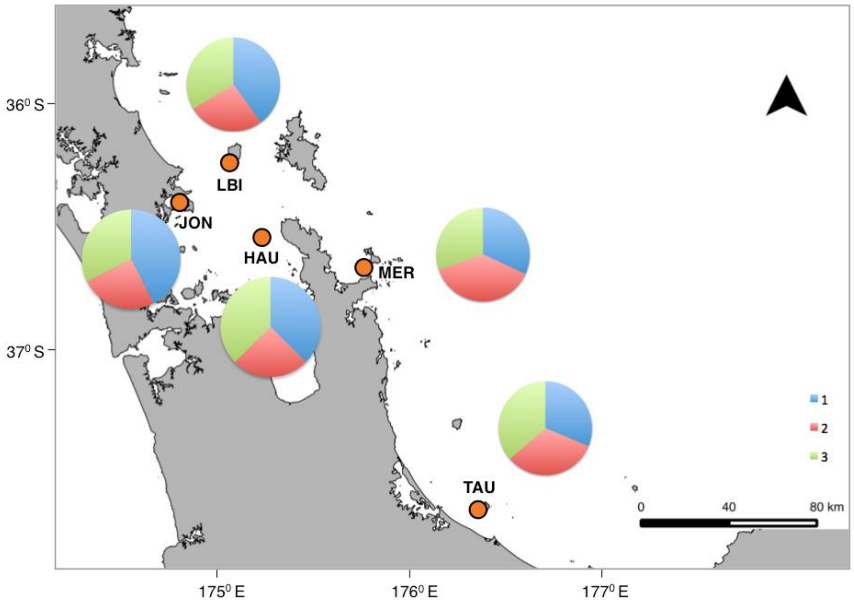

Figure 5.7 AWclust analysis results for *Pecten novaezelandiae* for the spatial study. Each colour represents an estimated portion of K=3 clusters. Locations abbreviations as per Table 5.1.

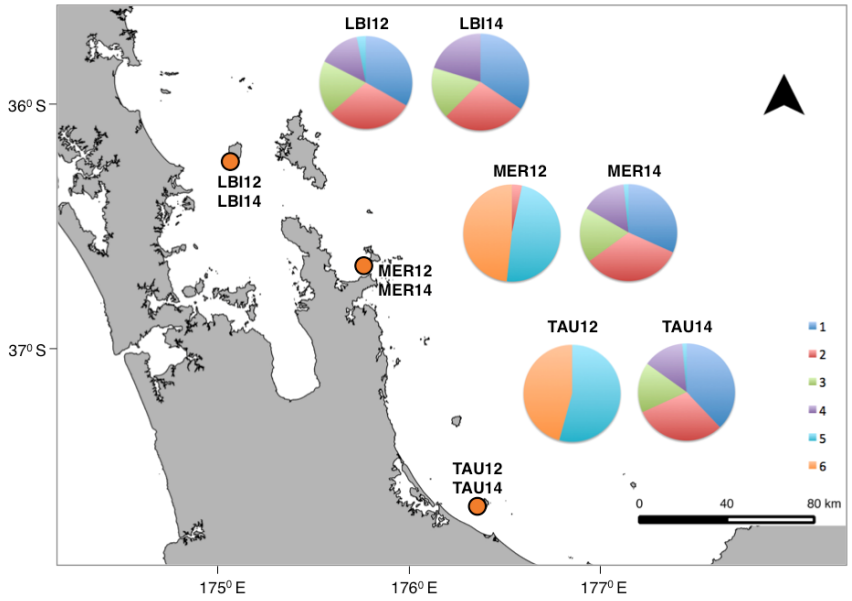

Figure 5.8 AWclust analysis results for *Pecten novaezelandiae* for the temporal study. Each colour represents an estimated portion of K=6 clusters. Locations abbreviations as per Table 5.1.

The Bayesian analysis (Structure) showed the greatest value of ΔK for 4 clusters for the spatial study (Table 5.5a) and 2 clusters for the temporal study (Table 5.5b). However, the

maximum log-likelihood of K showed the greatest value of 1 cluster (no structure, panmixia) for both studies and the bar plot did not show any trend of proportions of clusters (results not shown).

Table 5.5 Evanno table (Evanno *et al.* 2005) output for (a) the spatial study and (b) the temporal study of genetic structure of *Pecten novaezelandiae.*

(a)

K	Reps	Mean LnP(K)	Stdev LnP(K)	Ln'(K)	|Ln''(K)|	Delta K
1	5	-14452.900000	0.484768	—	—	—
2	5	-14669.660000	93.725226	-216.760000	41.400000	0.441717
3	5	-14927.820000	199.987517	-258.160000	67.060000	0.335321
4	5	-15118.920000	148.555737	-191.100000	419.060000	2.820894
5	5	-15729.080000	485.813531	-610.160000	—	—

(b)

K	Reps	Mean LnP(K)	Stdev LnP(K)	Ln'(K)	|Ln''(K)|	Delta K
1	5	-12477.500000	1.614001	—	—	—
2	5	-12532.900000	26.360861	-55.400000	59.760000	2.266997
3	5	-12648.060000	72.634172	-115.160000	69.660000	0.959053
4	5	-12693.560000	123.017511	-45.500000	192.760000	1.566931
5	5	-12931.820000	209.378478	-238.260000	6.280000	0.029994
6	5	-13163.800000	325.368875	-231.980000	—	—

The analyses of molecular variance (AMOVA) for the spatial study using 3 regions showed that 0.3% of the variation was explained among regions and the models were significant at $p<0.01$ (Table 5.6). AMOVA analysis using 4 regions showed that 0.4% of the variation was explained among regions and the models were significant at $p<0.01$ (Table 5.7).

Table 5.6 Analysis of molecular variance (AMOVA) for the spatial study of *P. novaezelandiae* using 3 regions.

Source of variation	Degrees of Freedom	Sum of Squares	Estimated Variance	% Variation	Differentiation Indices	Significance
Among Regions	2	13.94	0.011	0.3%	F_{RT} = 0.003	0.002
Among Locations	2	9.16	0.004	0.1%	F_{SR} = 0.001	0.133
Among Individuals	397	1557.23	0.512	15.0%	F_{ST} = 0.004	0.001
Within Locations	402	1165.00	2.898	84.6%	F_{IS} = 0.150	0.001
Total	803	2745.34	3.425	100.0%	F_{IT} = 0.154	0.001

Table 5.7 Analysis of molecular variance (AMOVA) for the spatial study of *P. novaezelandiae* using 4 regions.

Source of variation	Degrees of Freedom	Sum of Squares	Estimated Variance	% Variation	Differentiation Indices	Significance
Among Regions	3	19.35	0.014	0.4%	F_{RT} = 0.004	0.001
Among Locations	1	3.75	0.000	0.0%	F_{SR} = 0.000	0.544
Among Individuals	397	1557.23	0.512	15.0%	F_{ST} = 0.004	0.001
Within Locations	402	1165.00	2.898	84.6%	F_{IS} = 0.150	0.001
Total	803	2745.34	3.425	100.0%	F_{IT} = 0.154	0.001

For the temporal study, AMOVA analysis using all locations grouped in 2 regions (between years) showed that 0.02% of the variation was explained among regions and the model was not significant (Table 5.8). AMOVA analysis using locations MER and TAU grouped in 2 regions (between years) showed that 0.23% of the variation was explained among regions and the model was significant at $p<0.05$ (Table 5.9).

Table 5.8 Analysis of molecular variance (AMOVA) for the temporal study of *P. novaezelandiae* using all locations grouped in 2 regions (between years).

Source of variation	Degrees of Freedom	Sum of Squares	Estimated Variance	% Variation	Differentiation Indices	Significance
Among Regions	1	4.72	0.001	0.02%	F_{RT} = 0.000	0.319
Among Locations	4	17.70	0.004	0.13%	F_{SR} = 0.001	0.086
Among Individuals	377	1455.59	0.473	13.94%	F_{ST} = 0.002	0.042
Within Locations	383	1116.50	2.915	85.91%	F_{IS} = 0.140	0.001
Total	765	2594.50	3.393	100.0%	F_{IT} = 0.141	0.001

Table 5.9 Analysis of molecular variance (AMOVA) for the temporal study of *P. novaezelandiae* using locations MER and TAU grouped in 2 regions (between years).

Source of variation	Degrees of Freedom	Sum of Squares	Estimated Variance	% Variation	Differentiation Indices	Significance
Among Regions	1	5.88	0.008	0.23%	F_{RT} = 0.002	0.026
Among Locations	2	7.77	0.000	0.01%	F_{SR} = 0.000	0.406
Among Individuals	252	966.93	0.452	13.31%	F_{ST} = 0.002	0.022
Within Locations	256	751.00	2.934	86.45%	F_{IS} = 0.133	0.001
Total	511	1731.50	3.394	100.00%	F_{IT} = 0.136	0.001

Estimates of migration

First-generation of migrants analysis detected a low number of migrants for all locations, for both the spatial and temporal studies (6 and 11 first-generation migrants, respectively; Tables 5.10, 5.12). This low number was probably an underestimation of first-generation migrants due to low levels of differentiation between locations as a result of very similar genotypes between migrants and individuals from the original locality. For the spatial study, the location with the highest level of correct assignment was HAU (75.8%), while

the location with the lowest level was TAU (26.3%). These locations also had the lowest (HAU) and highest (TAU) percentage of individuals recruited from locations other than the collection site (Table 5.11).

Table 5.10 Number of first generation (F0) migrants detected for *Pecten novaezelandiae* at each sampled location for the spatial study in Coromandel. Locations abbreviations as per Table 5.1.

		Source of F_0 migrants					
		LBI	JON	HAU	MER	TAU	Total F_0 migrants
Receiving location	LBI						0
	JON				2		2
	HAU		1		1		2
	MER						0
	TAU	1	1				2

Table 5.11 Percentage of individuals of *Pecten novaezelandiae* collected from each sampling location, assigned to each sampled potential source location for the spatial study in the Coromandel. "Total other regions" is the percentage of individuals recruited from regions other than the collection site. Location abbreviations as per Table 5.1.

		Assigned location						Total other location
		LBI	JON	HAU	MER	TAU	Unassigned	
Location	LBI	***55.8***	6.3	28.4	4.2	5.3		44.2
	JON	20.0	***50.0***	20.0	7.5	2.5		50.0
	HAU	10.1	6.1	***75.8***	4.0	4.0		24.2
	MER	15.7	10.0	28.6	***40.0***	5.7		60.0
	TAU	23.2	10.1	34.3	5.1	***26.3***	1.0	72.7

Table 5.12 Number of first generation (F0) migrants detected for *Pecten novaezelandiae* at each sampled location for the temporal study in the Coromandel. Location abbreviations as per Table 5.1.

		Source of F0 migrants						
		LBI12	LBI14	MER12	MER14	TAU12	TAU14	Total F0 migrants
Receiving location	LBI12				1		1	2
	LBI14							0
	MER12					1		1
	MER14	1		1		1		3
	TAU12						1	1
	TAU14	1		2	1			4

For the temporal study, the location with the highest level of correct assignment was LBI12 (71.4%), while the location with the lowest level was LBI14 (40.6%). These locations also had the lowest (LBI12) and highest (LBI14) percentage of individuals recruited from locations other than the collection site (Table 5.13).

Table 5.13 Percentage of individuals of *Pecten novaezelandiae* collected from each sampling location, assigned to each sampled potential source location for the temporal study in the Coromandel. "Total other regions" is the percentage of individuals recruited from regions other than the collection site. Location abbreviations as per Table 5.1.

		Assigned location							Total other location
		LBI12	LBI14	MER12	MER14	TAU12	TAU14	Unassigned	
Location	LBI12	***71.4***	1.6	9.5	3.2	0.0	14.3		28.6
	LBI14	31.2	***40.6***	12.5	7.8	1.6	6.3		59.4
	MER12	13.3	1.7	***65.0***	6.7	5.0	8.3		35.0
	MER14	20.0	3.3	21.7	***45.0***	1.7	8.3		55.0
	TAU12	27.1	2.9	10.0	4.3	***48.6***	7.1		51.4
	TAU14	12.1	6.1	15.2	9.1	4.5	***53.0***		47.0

Relatedness

Overall, mean relatedness ranged from -0.019 in TAU14 to 0.017 in MER14. All locations had the means within the upper and lower 95% confidence intervals of randomly generated values (Figure 5.9) and no location was significantly different from random.

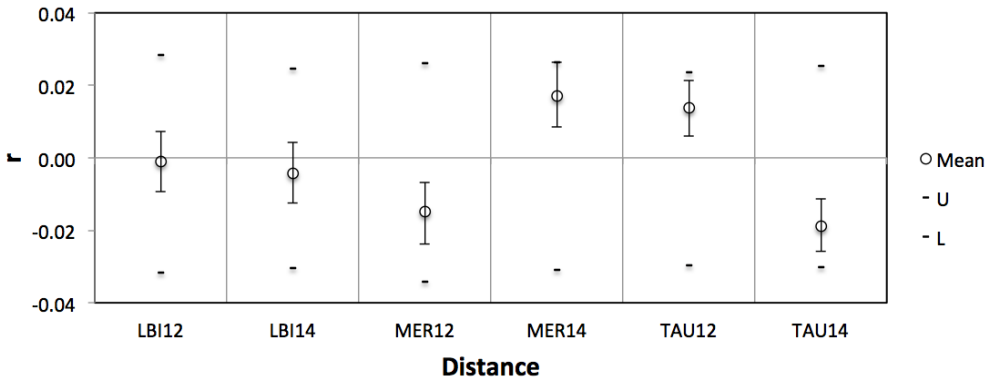

Figure 5.9 Mean values of observed relatedness for *Pecten novaezelandiae* for the temporal study. Upper and lower error bars represent the 95% confidence interval about the mean values as determined by 1000 bootstraps resampling. Upper (U) and lower (L) confidence limits represent the 95% confidence interval for the null hypothesis of 'No Difference' across the locations as determined by 999 permutations. Location abbreviations as per Table 5.1.

Oceanographic model

The connectivity estimation showed a clear pattern of oceanic currents flowing predominantly southeast for all scenarios. The highest percentage of propagules (20%) dispersed less than a few tens of kilometres for scenario (a) when particles were released at Little Barrier Island (Figure 5.10a). However, for scenarios (b) and (c) when particles were released at Mercury Island and Tauranga, the edge of the 20% dispersal kernel was not evident (Figure 5.10b, c). The dispersal kernel of low probability (the blue area) extended a few hundred kilometres from the release point of particles for all scenarios (illustrated in Figure 5.10a-c).

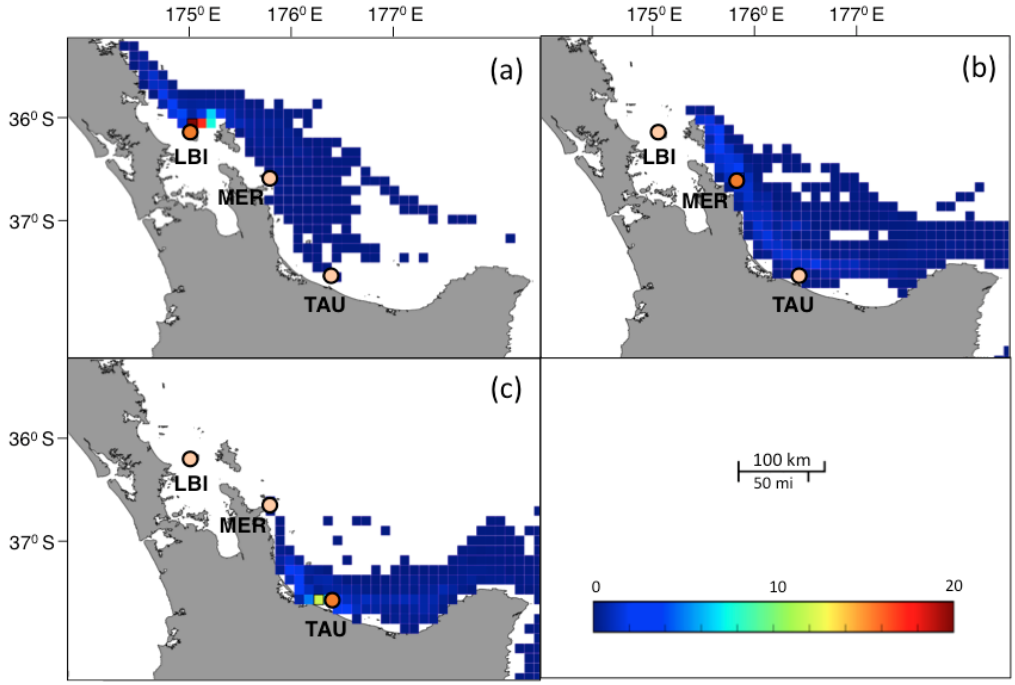

Figure 5.10 Probability distributions of particles released at (a) Little Barrier Island (LBI), (b) Mercury Island (MER) and (c) Tauranga (TAU). Maps show results of particles with diel vertical migration run for 25 days and released in early summer. Results are averaged across ten years (1997-2007). The colour bar indicates final position probability (%). Location abbreviations as per Table 5.1.

Discussion

Information on spatial and temporal genetic structure is critical for identifying meaningful fisheries management units. Failure to incorporate this information can result in reduced productivity, local reduction of populations or even extinction of local populations (Worm *et al.* 2006). Therefore, studies like this one are important to understand the spatial and temporal dynamics of larval recruitment for informing fisheries management. This study shows small but significant spatial and temporal genetic differentiation in the Coromandel region, suggesting that the sampled locations did not form a single panmictic unit with free gene flow. The levels of genetic variation are consistent with the findings of chapter 3, as very low genetic differentiation was found within regional clusters and levels of differentiation were lower at a smaller spatial scale.

Genetic diversity

Levels of genetic diversity for both spatial and temporal studies were in agreement with Chapter 3 and with other scallop species (Kenchington *et al.* 2006; Zhan *et al.* 2009; Arias *et al.* 2010; Hemond & Wilbur 2011; Marín *et al.* 2012). Genetic diversity in terms of allelic richness showed a decrease from 2012 to 2014 and this trend was also observed for measures of private allelic richness. In addition, there was a temporal increase in inbreeding rates (F_{IS}) for all locations.

A possible explanation for these observations is that these locations correspond to three very important fishing beds (LBI, MER and TAU corresponding to fishery areas of "Barrier", "Mercury" and "Plenty", respectively; Ministry of Primary Industries 2013), so the effects of fishing can be reflected in the temporal genetic pattern. Other studies have shown a significant loss of genetic diversity in overfished populations (Hauser *et al.* 2002; Pinsky & Palumbi 2014) indicating that not only can very small populations suffer significant loss of genetic diversity but also many abundant marine species may have their evolutionary potential impacted by overfishing. On the other hand, a rapid decrease in genetic diversity, particularly for the locations MER and TAU, can be related to changes in larval source as a result of stochastic oceanographic conditions or to temporal variability in recruitment success.

Population structure

The different analyses of population structure showed evidence of a low but significant genetic spatial and temporal structure in the Coromandel region. The clustering analyses were unable to identify clear patterns of genetic structure, which is not surprising given the low levels of genetic differentiation. Although pairwise F_{ST} values were very low (0.0004 to 0.0048), neighbor joining analysis, PCoA and AMOVA supported the F_{ST} values. In addition, even low migration rates that suggest demographic independence can coincide with very small F_{ST} values (Waples *et al.* 2008).

This study provided evidence of moderate levels of self-recruitment of *Pecten novaezelandiae* at Little Barrier Island (LBI). For the temporal study, estimates of migration detected a high percentage of individuals self-assigned to LBI12 (71.4%), while

the location LBI14 had a high percentage of individuals assigned to both LBI12 and LBI14 (71.8%). In addition, the oceanographic model supported the results of estimates of migration since the first scenario (particles released in LBI) produced the highest probability values of particle dispersal (20%) at less than a few tens of kilometres from LBI. This dispersal kernel of higher probability was not observed in the two other scenarios (particles released in MER and TAU), which is also in agreement with estimates of migration suggesting that these locations have lower levels of self-recruitment as a result of the predominant ocean currents.

This study also suggested moderate to high levels of self-recruitment for locations JON and HAU as indicated by estimates of migration. These observations are in agreement with the prevailing ocean currents in the region. Although a high-resolution hydrodynamic model more suitable for simulations in the inner part of the Hauraki Gulf was not available for this study, ocean currents are expected to become slower in the inner part of the Gulf (Zeldis *et al.* 2004) and consequently to reduce further the potential for larval dispersal. As a comparison, there is evidence of potential of gene flow between locations MER and TAU, where ocean currents are expected to be faster (i.e., provide more connectivity). These locations were not differentiated, as they had the lowest pairwise F_{ST} value and similar genetic diversity and temporal structure. As the simulation results show for the temporal study, ocean currents outside the Hauraki Gulf can facilitate gene flow between locations MER and TAU.

Interestingly, the location HAU had the highest levels of self-recruitment (75.8%) and also a high percentage of individuals from other locations were recruited from HAU (between 20% in JON and 34.3% in TAU). It is unclear if these patterns represent accurate gene flow estimates or if they are an artefact of the analysis. Studies suggest that assignment tests can be very useful for population studies and a good indicator of gene flow between populations but their accuracy is highly dependent on the levels of population differentiation. For example, Berry *et al.* (2004) showed that assignment methods were 100% accurate for low to moderate levels of genetic differentiation (F_{ST}~0.07) but the accuracy was reduced to ~78% for populations with lower levels of genetic subdivision (F_{ST}=0.04). Therefore, results from this study need to be interpreted with caution because of the limitations of assignment tests in measuring dispersal of *P. novaezelandiae*, which has little population differentiation in the Coromandel region. Although population

differentiation was low, both assignment tests and the PCoA analysis supported the observed levels of differentiation between locations. In addition, for the temporal analysis, the patterns of migration were also in agreement with the oceanographic model, providing some confidence that assignment tests can reasonably represent dispersal levels across sampled locations. If this is true, the location HAU can coincide with an important source population. Lastly, it has been shown for *Pecten novaezelandiae* that adults in deeper beds (28-40 m) spawn first (Tunbridge 1968). As the sampled location HAU coincides with the deepest bed of scallops in the Coromandel region, adults in this population can be spawning earlier in the season and therefore are more likely to occupy habitats at settlement locations early in the season.

The temporal stability in LBI, moderate self-recruitment and the oceanographic model (first scenario particles released in LBI) represent evidence that this location might be a source population. A temporally stable genetic structure in an area indicates either a consistent source of recruits or a consistent system of retention (Larson & Julian 1999). As locations north of LBI were not sampled for this study, the former cannot be tested. However, the oceanographic model showed a clear pattern of oceanic currents flowing southeast indicating that possibly locations north of LBI can also be a source of recruits. In addition, the temporally stable genetic structure is possibly also related to a consistent system of retention, as indicated by the oceanographic model, assignment tests and mean relatedness values.

For the locations MER and TAU, the high percentage of individuals (60% and 72.7% for MER and TAU, respectively) was recruited from locations other than the collection site and assignment tests for the temporal study and the oceanographic model suggest that these locations are sink populations. In addition, the lack of temporal stability indicates temporal changes in larval source at these two locations, which can be the result of a combination of processes such as 1) stochastic oceanographic conditions, 2) low levels of self-recruitment and 3) temporal variability in recruitment success.

Temporal instability patterns of genetic structure as a result of variable source of recruits have been observed for other marine species (Barber *et al.* 2002; Robainas-Barcia *et al.* 2008; Hogan *et al.* 2010; Kesäniemi *et al.* 2014; Yednock & Neigel 2014). Ocean currents can greatly affect the movement of pelagic larvae even at small scales (Pringle & Wares 2007; Wood & Gardner 2007) and the population genetic structure of some marine species

can correspond with ocean circulation (White *et al.* 2010). For example, a small-scale genetic structure has been observed for the Zhikong scallop *Chlamys farreri* and locations separated by strong marine currents or within different marine gyres showed significant genetic differentiation (Zhan *et al.* 2009). Changes in larval source can also be the result of low levels of self-recruitment. For example, Saenz-Agudelo *et al.* (2012) showed that the coral reef fish *Amphiprion polymnus* had lower levels of self-recruitment at the scale of individual sites, which was related to higher levels of connectivity between these sites. This is in agreement with the results of this study, as the locations MER and TAU had the lowest levels of self-recruitment and highest potential for gene flow. Since migrants' recruitment is greater than local self-recruitment, a change in recruits migrating from a different genetic source could contribute to a lack of temporal stability in these locations. Finally, variance in reproductive success in which only a few individuals contribute to the next generation has been shown to affect the temporal genetic structure in some marine species (Flowers *et al.* 2002; Christie *et al.* 2010; Underwood *et al.* 2012; Pusack *et al.* 2014). The small-scale spatial and temporal genetic structure observed for the Atlantic sea scallop (*Placopecten magellanicus*) was possibly explained by inter-annual differences in larval supply or reproductive success (Owen & Rawson 2013). Although the variance in reproductive success cannot be tested in this study, it can be one of the processes influencing the genetic structure of *Pecten novaezelandiae* and can also help explain the significant between-year differences in allele frequencies found for locations MER and TAU.

Fisheries management implications

The expected relationships between locations sampled in the Coromandel region are summarised in Figure 5.11. The sampled locations MER and TAU coincide with the very productive fishing areas of "Mercury" and "Plenty", respectively, that have high levels of annual recruitment, particularly the Mercury Islands (Ministry of Primary Industries 2013). The results of this study suggest that oceanographic mechanisms in these regions do not facilitate high levels of self-recruitment, which implies that larvae recruiting to these areas are mostly coming from other sources.

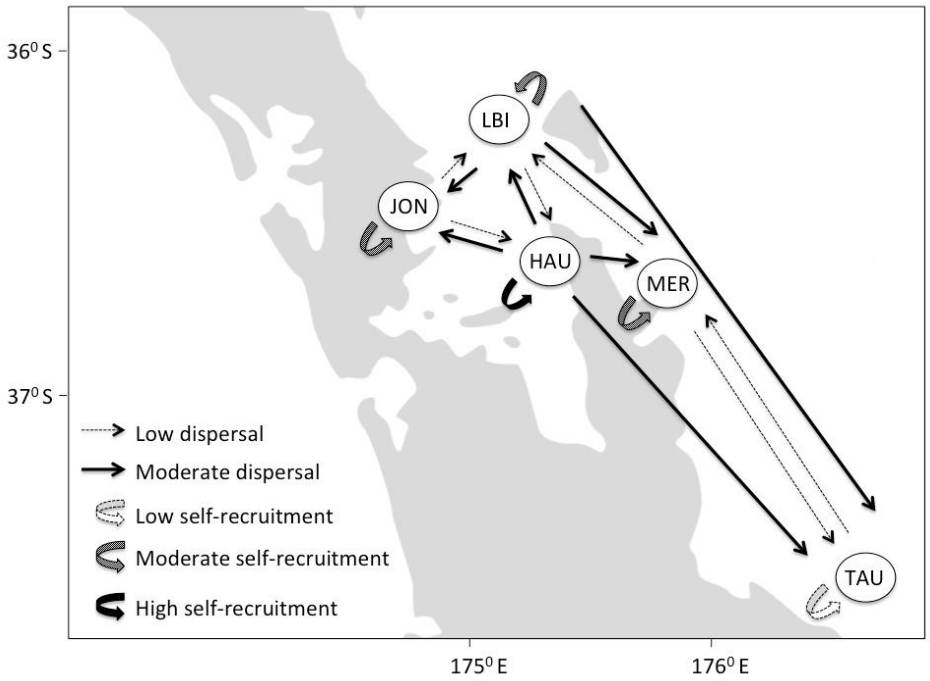

Figure 5.11 Expected relationships between locations sampled in Coromandel with estimated levels of larval dispersal and self-recruitment (low, moderate and high) indicated by the arrows. Circles are locations sampled, site abbreviations as per Table 5.1.

The genetic analyses and the oceanographic model suggest that the location LBI can be one of the sources of larvae recruiting to MER and TAU. This location (LBI) coincides with the very productive fishery area of Little Barrier Is (Ministry of Primary Industries 2013a). In addition, the genetic data also showed a stronger pattern of a source population for the location HAU. This location coincides with a recently found fishery area with good densities of scallops at 45-50 m depth that supported a large proportion of fishing in 2011 and 2012 (Ministry of Primary Industries 2013a). Therefore, as important source populations, management of these fisheries should be cautious. However, as levels of genetic differentiation between locations were very low, there are limitations in the assignment analyses and these results should be interpreted with caution. A high-resolution hydrodynamic model more suitable for simulations in the inner part of the Hauraki Gulf would help deciphering the complex nature of larval dispersal of *Pecten novaezelandiae*. Also, other source/sink populations can potentially be present in the region but were not sampled and are not represented in this study.

The source-sink population dynamics detected in this study have important implications for fisheries management. For example, adults in the sink populations (MER and TAU) are less likely to contribute to the larval pool and an attempt to restock these populations would probably not be as successful as restocking source populations. Restocking of populations through translocation from sink to source populations has been successfully attempted for the Tasmanian rock lobster *Jasus edwardsii* (Gardner & Van Putten 2008). Translocations can complement the management of marine resources but the creation of marine protected areas (MPAs) capable of both self-recruitment and exporting larvae to other unprotected and exploited areas is also an important tool for fisheries management. Comparing to no spatial management, strategically placed MPAs can for example substantially increase profits (Rassweiler *et al.* 2012) and also abundance and size of organisms (Pande *et al.* 2008).

This study shows complex spatial and temporal genetic patterns of *P. novaezelandiae* in the Coromandel region. The physical oceanographic characteristics likely play a significant role in generating these patterns of differentiation, which highlights how important it is to incorporate multidisciplinary approaches to understand marine population dynamics. However, this has yet to be widely applied in New Zealand and there is still a lack of empirical data using multidisciplinary tools that support connectivity patterns. This study provided important information for management and conservation applications of the New Zealand scallop. Patterns of dispersal and population dynamics have important effects on the genetic composition and resilience of populations. This study is the first step towards a better understanding of patterns of marine connectivity and dynamics of populations.

CHAPTER 6

General discussion

The New Zealand marine environment is a very complex and diverse system, which represents a major management and conservation challenge (Gordon *et al.* 2010). At the same time, it is an ideal system for studying the processes shaping the genetic structure of marine species. The increasing exploitation of marine resources and human-induced environmental changes pose a threat to the world's oceans and information on the genetic structure and population dynamics of species is increasingly important for the effective management and conservation of marine resources. Population genetics integrated with ecological data is a powerful approach to address questions about population structure and dynamics of marine organisms.

The general aims of this thesis were to investigate the genetic structure of *Pecten novaezelandiae* and its relationship with environmental variation around New Zealand, and also to examine spatial and temporal patterns of dispersal of *P. novaezelandiae* in the Coromandel fishery region. For this first study of population genetics of *P. novaezelandiae*, a multidisciplinary approach was used with genetic markers (specifically developed for this study), environmental data and hydrodynamic modelling. Little is known about population dynamics of the New Zealand scallop, and species inhabiting estuarine and sandy open coast habitats in general (Gardner *et al.* 2010; Constable 2014; Hannan 2014). Therefore, this study provides important information for management of *P. novaezelandiae*, contributes to a broader understanding of the patterns of gene flow in the New Zealand marine environment and brings important information about the processes shaping the patterns of population genetic structure.

In this general discussion the major findings of this study are first reviewed, with chapters 2, 3, 4 and 5 being addressed separately. Evolutionary consequences that arise from this research are discussed and implications for the management of *P. novaezelandiae* throughout its distribution range and in particular in the Coromandel fishery are then presented. Finally, the contributions of this study to the field of marine population genetics and future research needs are discussed.

Major findings

Microsatellite markers were specifically developed for *P. novaezelandiae* for this study (Chapter 2). Some loci showed significant deviation from Hardy-Weinberg equilibrium

(HWE) and evidence of null alleles. Null alleles are frequently observed in bivalves (Hedgecock *et al.* 2004; Kenchington *et al.* 2006; Marín *et al.* 2012; Wei *et al.* 2013a) possibly causing departures from Hardy-Weinberg equilibrium (HWE) and the underestimation of heterozygote frequency. However, other factors such as spatial/temporal population structure could also contribute to deviation from HWE. In addition, results from this study are consistent with studies of other marine bivalves and simulations suggest that F_{ST} values are unbiased when there is high gene flow, high effective population size (Ne) and moderate frequencies of null alleles (Chapuis & Estoup 2007), so null alleles are unlikely to significantly influence the conclusions of this study.

Low levels of genetic differentiation were detected for *Pecten novaezelandiae* across New Zealand (Chapter 3), which is expected given the large reproductive potential, the pelagic larval duration and the recent evolutionary history of this species. In general, population genetic structure was weak but there were significant differences between north, central and the southern New Zealand. The null hypothesis of panmixia was rejected since there was some evidence of genetic structure and an apparent hierarchical degree of differentiation from north to south.

The patterns of genetic variation of *P. novaezelandiae* across New Zealand were associated with a combination of environmental variables (Chapter 4). Although the geographic distance between populations was an important variable explaining the genetic variation, it appears that levels of genetic differentiation are not a simple function of distance. Evidence suggests that freshwater discharge and suspended particulate matter might be important factors contributing to the genetic structure of *P. novaezelandiae* in New Zealand.

Complex spatial and temporal patterns of genetic structure were observed for *P. novaezelandiae* in the Coromandel fishery region (Chapter 5). While low levels of genetic structure were detected, temporal instability patterns suggested a variable source of recruits. There was evidence of source-sink population dynamics, where populations in source habitats appeared to sustain populations both in source and sink habitats. Therefore, the null hypothesis of panmixia in the Coromandel fishery region was rejected.

Evolutionary consequences

With a growing realisation that fisheries can induce evolutionary responses in the life history of harvested species (Kuparinen & Merilä 2007), the importance of considering evolutionary processes in fisheries management and conservation is increasingly evident. Species are often distributed into spatially discrete 'populations' that form the basic units on which evolutionary forces, such as drift, gene flow, mutation and selection act over time. These forces determine the allelic composition of and variation between populations, and therefore different patterns of genetic variation can emerge within a species' range (Hedgecock *et al.* 2007). A full understanding of these evolutionary processes will allow fisheries management to adapt and prevent/reduce fisheries-induced impacts on productivity while maintaining the potential for evolutionary change in the future.

Complex historical and contemporary processes determine the population genetic structure of *P. novaezelandiae*. The patterns of genetic variation observed for *P. novaezelandiae* throughout New Zealand reflect a hierarchical degree of differentiation from north to south and also a latitudinal genetic diversity gradient. These patterns might be reflecting a recent colonisation event southwards and insufficient time to reach migration-drift equilibrium. The low level of genetic differentiation observed between the Chatham Islands and mainland New Zealand suggests that larvae of *P. novaezelandiae* have a high dispersal potential, which might be preventing population subdivision. On the other hand, significant differences were observed between populations in the south of New Zealand, in habitats where other species also have shown significant genetic differentiation (e.g. Mladenov *et al.* 1997; reviewed in Gardner *et al.* 2010).

Population genetic studies are largely based on the use of neutral genetic markers, where gene flow and genetic drift are considered the main forces driving population genetic structure of organisms. Such neutral processes are likely to be shaping the genetic structure of *P. novaezelandiae*, with the south of New Zealand, for example, having highly variable oceanic currents and higher eddy diffusivity, which may be preventing larval exchange with other populations (Chiswell & Rickard 2011) and therefore increasing levels of genetic differentiation. Also, although there is evidence that geographic distance between populations is an important variable explaining the genetic variation of *P. novaezelandiae*, it is not evident that the distance between the Chatham Islands and the mainland acts as an

important barrier to larval dispersal. The subtropical convergence flowing eastward might be facilitating dispersal and gene flow from mainland New Zealand to the Chatham Islands and thus could explain the lower levels of differentiation.

Local adaptation has also been proposed as an indirect mechanism structuring neutral genetic variation within and among natural populations. For example, colonization processes can influence genetic variation of *P. novaezelandiae*. Rapid population growth and local adaptation of a new habitat can result in a successful monopolisation of resources, giving these resident individuals a strong priority effect (De Meester *et al.* 2002; Orsini *et al.* 2013). Genetic differentiation arising from founder events can last thousands of generations (Boileau *et al.* 1992). Therefore, in areas with high population densities, locally adapted individuals of *P. novaezelandiae* could be favoured over immigrants, maintaining population genetic subdivision even when levels of migration are high. Also, it has been shown for other scallop species that populations at higher latitudes spawn earlier in the season and over longer periods of time (Shumway & Parsons 2006), which could also favour locally adapted individuals over immigrants coming from lower latitudes.

Freshwater discharge and suspended particulate matter were identified as important environmental factors shaping the genetic structure of *P. novaezelandiae*. As microsatellites are assumed to be neutral genetic markers (Freeland *et al.* 2011), these environmental variables can be influencing the genetic variation by neutral processes such as gene flow, genetic drift and mutation. However, it is debatable whether any locus is ever absolutely neutral (Liggins *et al.* 2013) because tests for selection generally have low power (Slatkin 1994, 1996) and it is unclear how many studies that used neutral genetic markers have been influenced by selection (Hudson & Turelli 2003; Yang & Nielsen 2008).

The association between genetic differentiation and the environmental factors ‘freshwater discharge’ and ‘suspended particulate matter’ has been shown for other marine species (Bricelj & Malouf 1984; Bacon *et al.* 1998; Gardner & Palmer 1998; Jørgensen *et al.* 2005; Hannan 2014). Exposure to suspended particulate matter has also been shown to affect both the feeding behaviour and growth rate of the scallop *Pecten maximus* (Szostek *et al.* 2013). Results from this study are in agreement with our knowledge about the biology and ecology of scallops regarding the low tolerance to variation in levels of suspended particulate matter and salinity (Shumway & Parsons 2006). It is possible that exposure to higher levels of suspended particulate matter and/or freshwater discharge are placing strong

selective pressure on *P. novaezelandiae* inhabiting such habitats, favouring locally adapted individuals, which might indirectly modify their genetic variation.

In addition, environmental features of more closed habitats such as harbours, gulfs and inlets are likely to influence larval dispersal processes and population dynamics. The Coromandel fishery area in north-eastern New Zealand encompasses the Hauraki Gulf, a semi-enclosed area and an open coastal environment, both characterised by a complex hydrodynamic environment. The physical oceanography and nutrient supply of both environments are highly influenced by the East Auckland Current (EAUC) flowing southeast (Zeldis 2004; Zeldis *et al.* 2004). This study suggests that patterns of dispersal of *P. novaezelandiae* in the region are characterized by a complex source-sink model of population dynamics. Also, the temporal decrease in genetic diversity observed can be the result of overfishing, stochastic oceanographic conditions or temporal variability in recruitment success. Genetic diversity is essential to maintain the evolutionary potential and adaptive ability of species (Allendorf *et al.* 2008). Populations with lower genetic diversity are less productive and resistant to disturbance or disease than populations with higher genetic diversity. If genetic diversity of *P. novaezelandiae* continues to decay it may lead to a long-term impact on the evolutionary potential.

Dispersal limitation, local adaptation and colonization history play an important role in shaping the genetic structure of species, both at neutral and non-neutral genetic variations (Orsini *et al.* 2013). It is likely that all these processes are driving the observed patterns of genetic structure in *P. novaezelandiae* and that complex relationships between these processes are placing strong selective pressure on scallops inhabiting specific habitats.

Fisheries management implications

Combining genetic markers with ecological information is a powerful approach to identify evolutionarily meaningful management units or stocks. This study was the first to investigate genetic variation of *P. novaezelandiae* at different geographic and temporal scales with the aim of representing the complexity of population dynamics. The findings of this study have important implications for the management of the scallop *P. novaezelandiae* throughout New Zealand and in particular, in the Coromandel scallop fishery.

Fisheries management in New Zealand

The complexity of the New Zealand marine environment is favourable to produce a variety of patterns of genetic structure. Comparing connectivity patterns among species can help establish common biogeographic barriers and provide knowledge at the ecosystem level, both of which are required for management efforts. Levels of connectivity were high between populations of *P. novaezelandiae*, but there was an evident hierarchical degree of differentiation from north to south. Similar patterns of genetic structure have been observed for other species in New Zealand (Gardner *et al.* 2010; Westfall 2011; Ross *et al.* 2012), but in this study there was not evidence of a clear barrier to gene flow for *P. novaezelandiae*.

Compared to northern New Zealand, the southern region showed higher levels of differentiation as a result of lower genetic and demographic connectivity. Management of these southern stocks should be particularly cautious because they showed lower levels of genetic diversity and separate stocks may correspond to smaller geographic areas than the quota management areas currently accounted for by the quota management system. Populations within inlets and fiords are likely to experience lower connectivity to populations in the open marine environment, resulting in higher genetic differentiation. There is also the possibility that individuals within these areas such as Fiordland and Paterson Inlet on Stewart Island are locally adapted to specific environmental conditions. This would have serious implications for stock recovery if dependent on external sources of recruits that are adapted to open coast environment conditions.

Findings from this study that freshwater discharge and suspended particulate matter might be shaping the genetic structure of *P. novaezelandiae* have important management implications. Individuals can be adapted to the local environment and a shift in conditions such as, for example, variation in oceanographic cycles and high rainfall or an increase in sediment discharge in urbanised areas or from areas of heavy logging activity, can compromise the productivity of stocks. Terrestrial and marine ecosystems are intricately linked; however, current management practices rarely consider the effects of land-sea

interactions and ignoring such interactions can result in failing to achieve management and conservation goals (Stoms *et al.* 2005).

Determining meaningful marine biogeographic patterns in New Zealand is an important step to develop effective planning units at a large spatial scale and appropriate scales and boundaries for management. In marine systems these biogeographic boundaries are intrinsically dynamic because of the complex environmental conditions and different life histories of species. The New Zealand marine environment is particularly complex with small currents and eddies, variable wind, waves and tides as well as coastal currents shaped by interactions with ocean floor topography (Ross *et al.* 2009). These characteristics represent a challenge to scientists, fisheries managers and conservationists, and have created difficulties in predicting the influence of the marine environment on population structure of species and in defining clear biogeographic provinces in the New Zealand marine environment (Shears *et al.* 2008).

As a result of higher genetic connectivity, populations in the north of New Zealand tend to show a lower degree of population differentiation compared to the southern region. However, unexpected small-scale patterns of differentiation can arise and may change over time. There was also evidence that self-recruitment may play an important role in maintaining productivity of stocks in the region. Understanding this complex dynamic at different geographic scales is essential for establishing effective management plans therefore, management implications of this study for the Coromandel scallop fishery are discussed below.

The Coromandel scallop fishery (SCA CS)

The Coromandel fishery area is characterized by a complex hydrodynamic environment. The East Auckland Current (EAUC) flowing southeast influences both the Hauraki Gulf and the open coast environment, creating complex eddies that can greatly influence population dynamics of *Pecten novaezelandiae* at small spatial scales (Chiswell & Rickard 2011). This study detected a source-sink model of population dynamics, which has important implications for fisheries management of the New Zealand scallop in the Coromandel region. Gene flow estimates between locations need to be taken with caution because of the limitations of the assignment tests (Berry *et al.* 2004). However, the

oceanographic model supported the results of assignment tests, which provides some confidence that dispersal levels in the Coromandel fishery are reasonably well represented.

Scallop populations that conform to a source-sink model may be best managed by precautionary management of the source populations. There was evidence that some of the sampled locations, which coincided with important fisheries such as 'Mercury' and 'Plenty', were sink populations. This means that adults of scallops inhabiting these sink habitats are less likely to contribute to the larval pool. On the other hand, some of the sampled locations that coincided with the very productive fishing areas 'Hauraki' and 'Barrier' appeared to sustain populations both in source and sink habitats, and therefore are likely to be source populations.

The complex dynamics of *Pecten novaezelandiae* in the Coromandel region is potentially influenced by a combination of oceanographic conditions such as the East Auckland Current (EAUC) that may be facilitating larval transport from 'Barrier' to southern populations and other environmental factors such as water depth in 'Hauraki', where individuals may spawn earlier in the season (Tunbridge 1968) and are more likely to occupy habitats at settlement locations early in the season. In addition, some populations such as 'Hauraki' may rely heavily on self-recruitment, in which case a localised precautionary management approach would be appropriate. The reliance on self-recruitment poses a risk when stocks are heavily exploited and can become depleted, since recovery and rebuilding of biomass to sustainable levels may take a long time (Worm *et al.* 2009). This recovery can be even more problematic if recruits are not adapted to local environmental conditions such as water depth in 'Hauraki'. Given this, this population is probably more vulnerable to over-exploitation.

Contribution to the field and future directions

Findings of this study bring important contributions to fisheries management of *Pecten novaezelandiae*, significant knowledge about marine connectivity in New Zealand and important findings regarding the processes that can shape population genetic structure of species. New microsatellite markers were developed for *P. novaezelandiae* and these powerful molecular markers were used in this first study of population genetics of the endemic New Zealand scallop to address important ecological questions. The

multidisciplinary approach used in this research highlights the importance of considering environmental factors in population genetic studies. In general, these findings can be applied to the management of *P. novaezelandiae* around New Zealand and in the Coromandel fishery area, and potentially to other bivalve species with similar life history characteristics and inhabiting similar habitats. Identifying common patterns among species and factors shaping those patters is crucial to our understanding of evolutionary and ecological processes as well as for management and conservation efforts. Therefore, the results of this study add to the increasing evidence that many marine species can show considerable genetic structure despite high dispersal potential, and can contributed to our understanding of evolutionary and population processes influencing marine connectivity and shaping population structure of marine species.

It has been recognised that a comprehensive understanding of population dynamics involves integration of methods that estimate dispersal over different spatial and temporal scales (Anderson *et al.* 2010). Results from this study highlight the importance of using different temporal and spatial scales in population genetic studies. Genetic differentiation can change across multiple temporal scales, which can influence interpretations about spatial patterns of differentiation (Toonen & Grosberg 2011). Population genetic studies with samples obtained over multiple years can better elucidate about the complex processes producing temporal instability. However, there are several difficulties associated with sampling marine invertebrates over multiple temporal and spatial scales.

The use of high resolution physical modelling is a helpful approach that can effectively predict the patterns of connectivity (Werner *et al.*; Gallego *et al.* 2007), helping to answer several ecological questions. Physical models are frequently combined with detailed biological variables to provide realistic estimates of dispersal. Individual-Based Coupled Physical–Biological Models (ICPBMs), which incorporate biological characteristics of species such as larval behaviour and estimates of mortality are becoming increasingly popular (Miller 2007; Reidenbach *et al.* 2009; Bolle *et al.* 2009; Berry *et al.* 2012). One of the first studies integrating oceanographic and genetic models was developed by Galindo *et al.* (2006) to predict gene flow among locations of a reef-building coral across the Caribbean Sea. ICPBMs are evolving rapidly, becoming more spatially resolved and including more biological detail (Miller 2007). This is an increasingly important tool in advancing our understanding of larval dispersal and recruitment but it has yet to be widely

applied in population genetic studies, particularly in New Zealand (but see Le Port *et al.* 2014). A particle tracking technique was used in this study as an exploratory analysis to estimate connectivity from specified source regions (Chapter 5). Unfortunately, a higher resolution model was not available for this study but a better understanding of processes shaping the population dynamics of *P. novaezelandiae* in the Coromandel fishery region and across New Zealand can be potentially achieved with an improved model.

An important finding of this research was the evidence of a source-sink model of population dynamics for *P. novaezelandiae* in the Coromandel fishery area. However, these results must be interpreted with caution since other sink/source populations may be present in the region but not sampled, and the assignment analyses have limitations given the low levels of genetic differentiation among populations (Berry *et al.* 2004). Applying a suitable hydrodynamic model for the entire Coromandel region, including the inner part of the Hauraki Gulf, would help elucidate the patterns of larval dispersal and connectivity between scallop's beds. In addition, the translocation of animals from sink to source populations can potentially be implemented as a complementary management tool for maintaining the genetic diversity of populations, which has decreased temporally (Gardner & Van Putten 2008).

To fully understand evolutionary and population dynamic processes shaping patterns of population structure in the New Zealand marine environment, it is necessary to compare studies among multiple species. Meta-analyses can significantly improve our knowledge and resolve uncertainty about common patterns of genetic structure by combining the results from multiple studies. For example, Weersing & Toonen (2009) used a meta-analysis approach to investigate the link between pelagic larval duration (PLD) and connectivity among populations, challenging the conventional view that PLD is a good predictor of the extent of gene flow in marine systems. Also, Toonen *et al.* (2011) conducted a study of 27 taxonomically and ecologically diverse species and showed the presence of four concordant barriers to dispersal within the Hawaiian Archipelago which were not detected in single-species studies. A meta-analysis of population genetic studies conducted for New Zealand marine species linking the patterns of genetic variation with environmental variation, would be the first step towards a better understanding of the processes shaping coastal population structure and therefore, defining meaningful boundaries at which to apply ecosystem-based fishery management (EBFM).

In general, the typical fisheries management approach focuses on a single target species and often ignores interactions with other species and with the ecosystem. Prioritising the ecosystem rather than the target species is the main objective of ecosystem-based fishery management (EBFM; Slocombe 1993; Pikitch *et al.* 2004). A full understanding of ecosystem processes is essential for implementing EBFM; however, data are not always available when implementing management strategies. Because fisheries systems are complex, management should embrace uncertainty and be precautionary. Management should utilise an adaptive approach, continually testing how ecosystems respond to fisheries pressure and management strategies, which has been shown to improve our understanding of ecosystem dynamics (Hughes *et al.* 2007; Silva *et al.* 2013). Finally, intensive fishing can induce changes in life-history traits, behaviour, physiology, and morphology of species, which in turn can dramatically change the monetary value of resources. Therefore it is vital to assess the impacts of fisheries induced evolution (FIE) and assess the evolutionary consequences of fishing within an ecosystem-based management approach (Laugen *et al.* 2014).

This study provides important information about the processes that influence population dynamics of species. Further development should include improving models of larval dispersal and marine connectivity by expanding the use of multidisciplinary tools in areas such as physics, statistics, larval ecology and genetics (Selkoe *et al.* 2008; Cowen & Sponaugle 2009). Successful management of *P. novaezelandiae* and other marine resources will require on-going monitoring and a good understanding of relevant ecological and evolutionary processes in the face of growing exploitation and changing environmental conditions.

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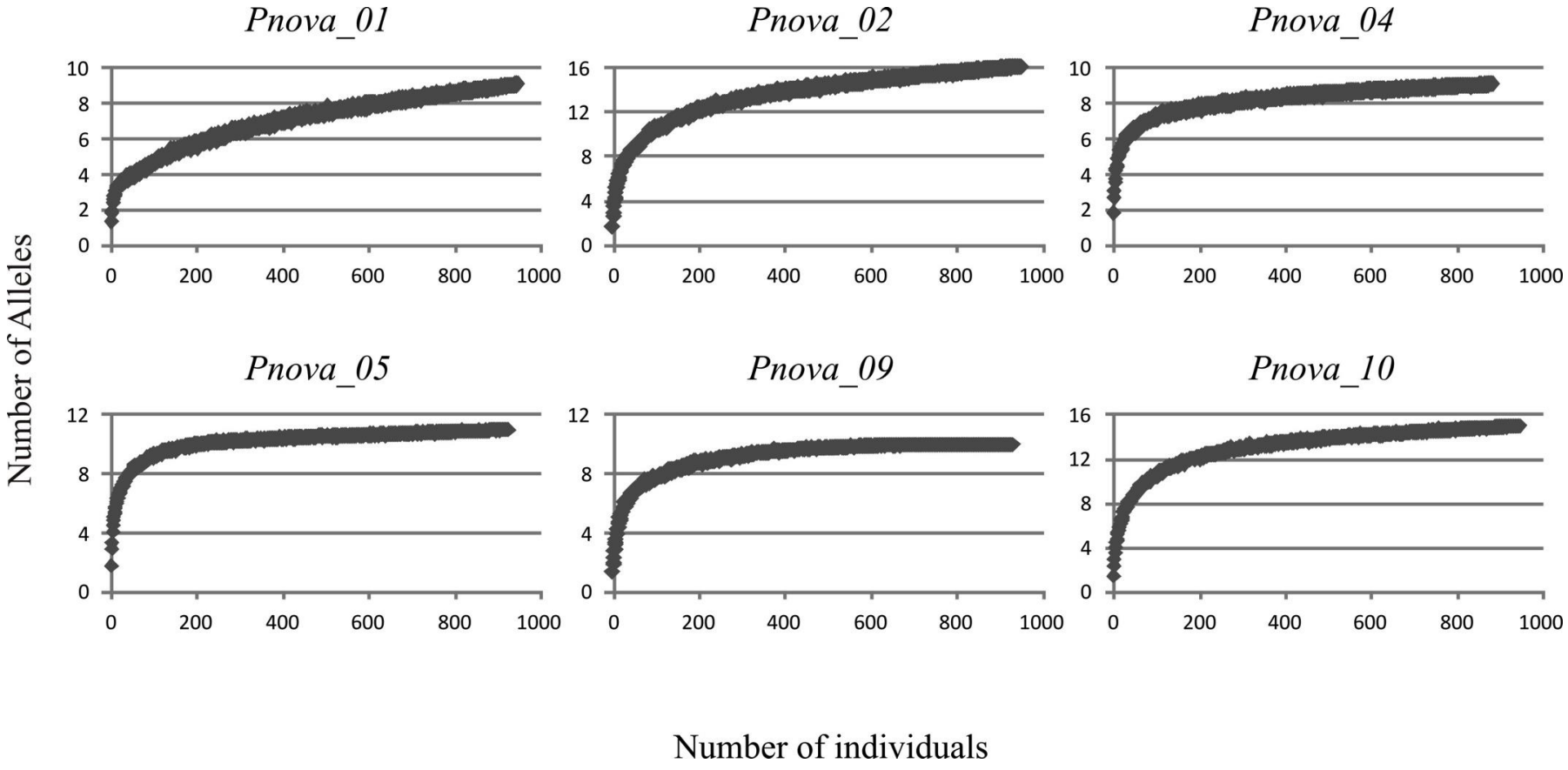
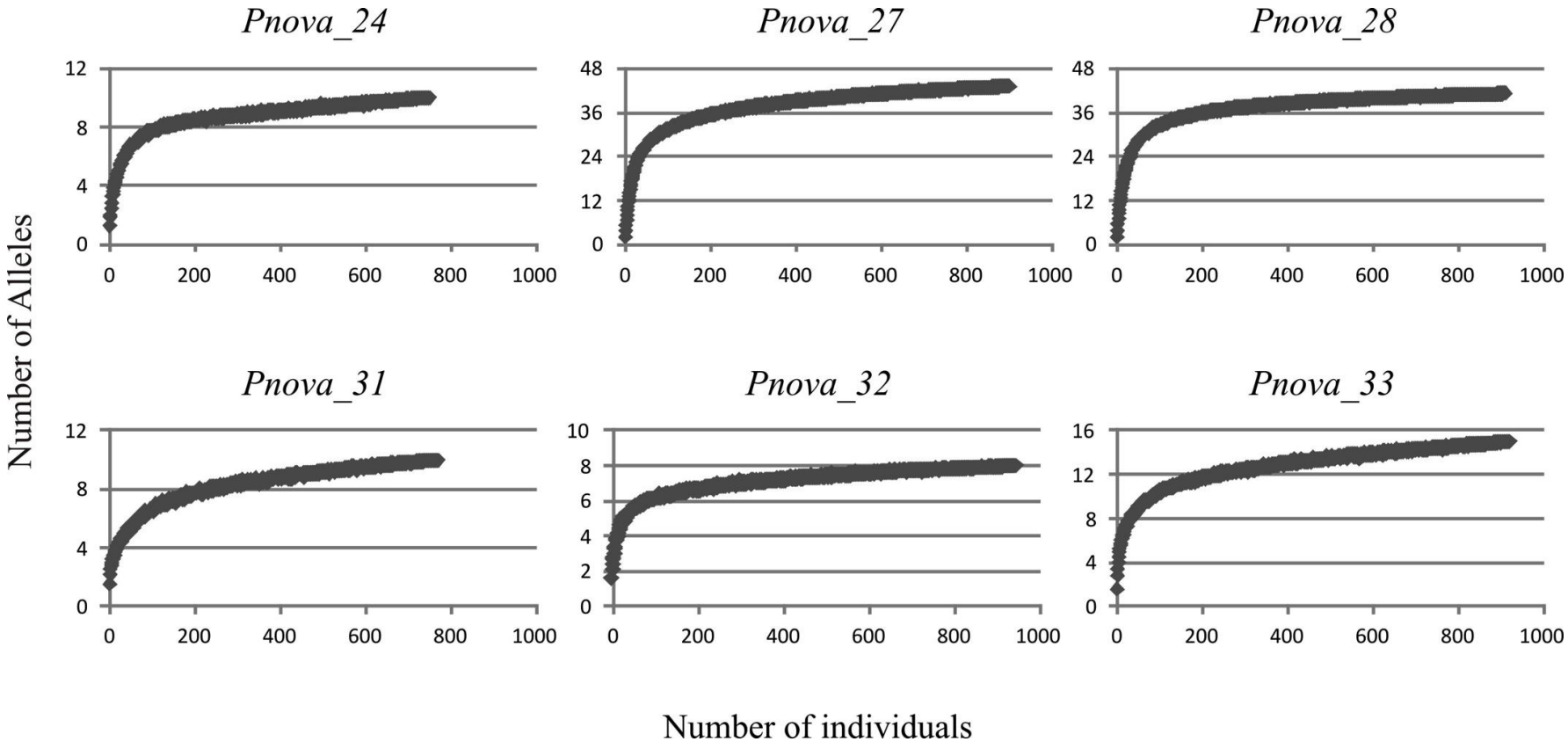
Appendices

Supplementary Table 1 PCR conditions for 12 microsatellite loci of *Pecten novaezelandiae* (Chapter 2).

Multiplex group	Locus	Repeat	Forward primer sequence (5´-3´)	Dye	Cycling conditions
1 (Pool 1)	*Pnova*_09	$(AGTT)_5$	GGCGTCCACTGACAGATAAG	VIC	
	*Pnova*_24	$(AGAC)_5$	CACTGACGAAACGTTGGTGT	PET	
2 (Pool 1)	*Pnova*_02	$(TA)_{11}$	CAGTAGCTCCTGCCCCATTA	6-FAM	94ºC (5 min)
	*Pnova*_10	$(TA)_{11}$	GGAAGGAAGCACAGCAGGTA	6-FAM	36 cycles at 94ºC (30 s)/ 61ºC (45 s) / 74ºC (60 s)
	*Pnova*_27	$(TATC)_{33}$	CAGATACGTCAGAGTGCTGATTC	NED	
3 (Pool 1)	*Pnova*_01	$(TA)_8$	GTAGCACACGCAAATGCCTA	6-FAM	74ºC (10 min)
	*Pnova*_04	$(TTGT)_7$	AATGCAGGAAGGTTTTGGTTT	PET	
	*Pnova*_28	$(CAA)_{19}$	AAGGCATATAACTCAGCTGGAA	VIC	
4 (Pool 2)	*Pnova*_05	$(ACAG)_7$	AGCGACATACAATGGGGAAG	VIC	94ºC (5 min)
	*Pnova*_31	$(TA)_{11}$	TGCGCTACAGTGTCGTTCTT	6-FAM	36 cycles at 94ºC (30 s)/ 62ºC (45 s) / 74ºC (60 s)
	*Pnova*_32	$(AT)_{11}$	GTGTCGTCTACAGCCGGAAT	NED	
	*Pnova*_33	$(AATAT)_{10}$	CTCCAGGAGTAGAGCCGATG	PET	74ºC (10 min)



Supplementary Figure 1 Allele discovery curves for *Pecten novaezelandiae* (Chapter 3).



Supplementary Figure 1 (Cont.)

Supplementary Table 2 Allele frequencies for 10 microsatellite loci of *Pecten novaezelandiae* for 15 locations (Chapter 3).

Locus	Allele	RAN	LBI	JON	HAU	MER	TAU	WEL12	WEL13	MAR	TAS	GOL	FIO	STE12	STE14	CHA
*Pnova*_01	**207**	0.000	0.011	0.000	0.000	0.000	0.000	0.007	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	217	0.000	0.000	0.013	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	221	0.143	0.101	0.050	0.121	0.123	0.051	0.075	0.135	0.198	0.115	0.094	0.206	0.200	0.281	0.087
	223	0.832	0.878	0.800	0.869	0.848	0.918	0.896	0.802	0.771	0.854	0.885	0.794	0.800	0.719	0.903
	225	0.026	0.005	0.113	0.005	0.029	0.031	0.015	0.021	0.010	0.031	0.021	0.000	0.000	0.000	0.005
	227	0.000	0.000	0.025	0.000	0.000	0.000	0.007	0.010	0.010	0.000	0.000	0.000	0.000	0.000	0.000
	229	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	231	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005
	233	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.010	0.000	0.000	0.000	0.000	0.000	0.000
*Pnova*_02	**153**	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	157	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005
	159	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.014	0.000	0.000	0.000
	161	0.005	0.000	0.000	0.010	0.007	0.000	0.000	0.032	0.000	0.010	0.021	0.000	0.000	0.052	0.010
	163	0.005	0.000	0.013	0.000	0.000	0.010	0.007	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000
	165	0.015	0.021	0.013	0.025	0.036	0.035	0.045	0.021	0.040	0.042	0.031	0.214	0.050	0.094	0.015
	167	0.250	0.266	0.295	0.197	0.239	0.288	0.239	0.191	0.250	0.250	0.188	0.257	0.150	0.208	0.245
	169	0.505	0.479	0.500	0.556	0.522	0.510	0.470	0.564	0.540	0.490	0.458	0.414	0.650	0.469	0.587
	171	0.061	0.069	0.090	0.045	0.094	0.045	0.090	0.106	0.060	0.073	0.104	0.043	0.100	0.125	0.102
	173	0.097	0.128	0.000	0.101	0.065	0.051	0.067	0.032	0.050	0.083	0.094	0.000	0.000	0.000	0.000
	175	0.031	0.016	0.064	0.035	0.014	0.030	0.060	0.043	0.050	0.042	0.073	0.043	0.000	0.052	0.031
	177	0.015	0.011	0.026	0.005	0.014	0.010	0.000	0.011	0.000	0.000	0.010	0.000	0.000	0.000	0.000
	179	0.000	0.011	0.000	0.010	0.007	0.010	0.000	0.000	0.000	0.010	0.010	0.000	0.000	0.000	0.000
	181	0.005	0.000	0.000	0.010	0.000	0.005	0.015	0.000	0.000	0.000	0.000	0.014	0.050	0.000	0.000
	183	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	185	0.005	0.000	0.000	0.000	0.000	0.005	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005

Supplementary Table 2 (cont.)

Locus	Allele	RAN	LBI	JON	HAU	MER	TAU	WEL12	WEL13	MAR	TAS	GOL	FIO	STE12	STE14	CHA
*Pnova*_04	**272**	0.000	0.000	0.000	0.000	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	276	0.137	0.131	0.163	0.148	0.104	0.117	0.185	0.159	0.288	0.192	0.211	0.157	0.000	0.125	0.087
	280	0.005	0.023	0.013	0.022	0.007	0.010	0.000	0.000	0.013	0.000	0.000	0.043	0.000	0.021	0.031
	284	0.089	0.097	0.063	0.099	0.030	0.071	0.083	0.037	0.050	0.051	0.053	0.043	0.300	0.167	0.138
	288	0.500	0.511	0.525	0.495	0.634	0.561	0.444	0.573	0.450	0.577	0.513	0.471	0.450	0.354	0.367
	292	0.211	0.193	0.200	0.192	0.179	0.199	0.269	0.220	0.125	0.154	0.171	0.214	0.200	0.323	0.316
	296	0.053	0.034	0.025	0.044	0.022	0.031	0.019	0.012	0.038	0.013	0.039	0.071	0.050	0.010	0.041
	300	0.005	0.011	0.013	0.000	0.007	0.005	0.000	0.000	0.025	0.013	0.013	0.000	0.000	0.000	0.020
	304	0.000	0.000	0.000	0.000	0.007	0.005	0.000	0.000	0.013	0.000	0.000	0.000	0.000	0.000	0.000
*Pnova*_05	**131**	0.036	0.043	0.033	0.052	0.059	0.041	0.022	0.031	0.020	0.010	0.021	0.000	0.000	0.010	0.026
	135	0.117	0.161	0.117	0.063	0.096	0.112	0.164	0.094	0.130	0.177	0.115	0.129	0.000	0.198	0.149
	139	0.168	0.140	0.167	0.092	0.154	0.168	0.104	0.198	0.080	0.167	0.125	0.100	0.200	0.156	0.180
	143	0.357	0.403	0.233	0.385	0.397	0.434	0.358	0.271	0.360	0.375	0.469	0.486	0.300	0.344	0.371
	147	0.240	0.167	0.300	0.293	0.213	0.163	0.246	0.302	0.290	0.188	0.229	0.243	0.400	0.198	0.216
	151	0.046	0.054	0.067	0.075	0.051	0.046	0.067	0.063	0.060	0.042	0.021	0.000	0.100	0.042	0.031
	155	0.020	0.016	0.033	0.011	0.029	0.015	0.022	0.010	0.010	0.031	0.010	0.014	0.000	0.031	0.010
	159	0.005	0.005	0.000	0.011	0.000	0.000	0.015	0.010	0.020	0.000	0.010	0.029	0.000	0.010	0.005
	163	0.010	0.011	0.050	0.000	0.000	0.010	0.000	0.010	0.010	0.000	0.000	0.000	0.000	0.010	0.005
	167	0.000	0.000	0.000	0.017	0.000	0.005	0.000	0.010	0.020	0.010	0.000	0.000	0.000	0.000	0.005
	171	0.000	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
*Pnova*_09	**104**	0.020	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	108	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.034	0.000
	112	0.015	0.043	0.013	0.046	0.030	0.026	0.007	0.011	0.000	0.000	0.021	0.015	0.000	0.000	0.016
	116	0.051	0.033	0.038	0.056	0.075	0.052	0.030	0.022	0.043	0.000	0.031	0.000	0.150	0.011	0.053

Supplementary Table 2 (cont.)

Locus	Allele	RAN	LBI	JON	HAU	MER	TAU	WEL12	WEL13	MAR	TAS	GOL	FIO	STE12	STE14	CHA
*Pnova*_09	**120**	0.740	0.766	0.800	0.724	0.679	0.742	0.888	0.880	0.840	0.885	0.885	0.882	0.800	0.898	0.700
	124	0.051	0.054	0.063	0.066	0.090	0.052	0.052	0.054	0.053	0.083	0.042	0.000	0.050	0.023	0.147
	128	0.092	0.087	0.063	0.082	0.082	0.098	0.015	0.011	0.000	0.021	0.010	0.015	0.000	0.000	0.063
	132	0.020	0.011	0.025	0.026	0.030	0.015	0.000	0.011	0.043	0.000	0.010	0.088	0.000	0.011	0.011
	136	0.005	0.000	0.000	0.000	0.007	0.010	0.000	0.011	0.011	0.010	0.000	0.000	0.000	0.023	0.011
	144	0.005	0.005	0.000	0.000	0.007	0.005	0.007	0.000	0.011	0.000	0.000	0.000	0.000	0.000	0.000
*Pnova*_10	**254**	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	256	0.021	0.000	0.026	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.005
	258	0.026	0.043	0.051	0.041	0.058	0.027	0.015	0.052	0.020	0.010	0.042	0.000	0.000	0.010	0.010
	260	0.067	0.092	0.090	0.107	0.101	0.048	0.112	0.094	0.120	0.156	0.177	0.338	0.188	0.188	0.179
	262	0.010	0.033	0.000	0.046	0.007	0.011	0.067	0.052	0.040	0.021	0.063	0.000	0.000	0.000	0.015
	264	0.273	0.293	0.372	0.245	0.254	0.293	0.194	0.219	0.340	0.344	0.208	0.147	0.375	0.240	0.245
	266	0.438	0.397	0.372	0.434	0.420	0.426	0.463	0.448	0.430	0.385	0.406	0.500	0.438	0.500	0.444
	268	0.108	0.109	0.064	0.097	0.138	0.138	0.112	0.115	0.050	0.052	0.063	0.015	0.000	0.042	0.061
	270	0.026	0.016	0.013	0.005	0.007	0.016	0.037	0.010	0.000	0.010	0.031	0.000	0.000	0.010	0.036
	272	0.005	0.005	0.000	0.020	0.000	0.005	0.000	0.000	0.000	0.021	0.000	0.000	0.000	0.000	0.000
	274	0.015	0.005	0.013	0.005	0.000	0.027	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005
	278	0.000	0.005	0.000	0.000	0.007	0.011	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.010	0.000
	280	0.000	0.000	0.000	0.000	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
*Pnova*_27	**151**	0.000	0.011	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	167	0.000	0.000	0.000	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	171	0.000	0.000	0.000	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	183	0.018	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	187	0.006	0.005	0.000	0.005	0.000	0.000	0.000	0.022	0.000	0.011	0.011	0.000	0.000	0.000	0.000
	191	0.006	0.011	0.028	0.016	0.000	0.011	0.008	0.011	0.010	0.000	0.000	0.000	0.000	0.011	0.000
	195	0.006	0.005	0.028	0.005	0.008	0.005	0.031	0.000	0.010	0.021	0.011	0.000	0.000	0.021	0.028
	199	0.006	0.021	0.014	0.026	0.030	0.027	0.008	0.000	0.000	0.021	0.043	0.000	0.000	0.011	0.006

Supplementary Table 2 (cont.)

Locus	Allele	RAN	LBI	JON	HAU	MER	TAU	WEL12	WEL13	MAR	TAS	GOL	FIO	STE12	STE14	CHA
Pnova_27	**203**	0.018	0.005	0.014	0.021	0.061	0.011	0.015	0.011	0.010	0.011	0.000	0.000	0.000	0.011	0.044
	207	0.029	0.032	0.014	0.032	0.023	0.049	0.069	0.022	0.063	0.011	0.043	0.086	0.050	0.021	0.050
	211	0.029	0.016	0.014	0.047	0.015	0.038	0.038	0.011	0.052	0.032	0.033	0.129	0.100	0.021	0.083
	215	0.035	0.032	0.042	0.021	0.015	0.049	0.031	0.033	0.063	0.011	0.033	0.057	0.100	0.074	0.078
	219	0.024	0.069	0.042	0.026	0.030	0.055	0.031	0.065	0.052	0.032	0.054	0.057	0.000	0.085	0.044
	223	0.012	0.053	0.014	0.032	0.061	0.066	0.054	0.054	0.052	0.064	0.011	0.057	0.150	0.128	0.050
	227	0.065	0.048	0.111	0.053	0.030	0.060	0.023	0.043	0.042	0.085	0.043	0.100	0.050	0.043	0.056
	231	0.053	0.064	0.042	0.053	0.061	0.049	0.038	0.022	0.094	0.032	0.011	0.086	0.100	0.096	0.089
	235	0.053	0.064	0.042	0.047	0.053	0.044	0.062	0.076	0.083	0.064	0.054	0.086	0.000	0.053	0.100
	239	0.059	0.059	0.042	0.037	0.053	0.071	0.054	0.022	0.021	0.074	0.054	0.057	0.050	0.064	0.061
	243	0.106	0.059	0.097	0.042	0.053	0.077	0.031	0.033	0.073	0.043	0.022	0.086	0.050	0.053	0.061
	247	0.076	0.064	0.069	0.079	0.023	0.071	0.031	0.065	0.031	0.096	0.130	0.057	0.000	0.053	0.033
	251	0.041	0.032	0.069	0.063	0.053	0.077	0.077	0.011	0.031	0.053	0.043	0.014	0.100	0.074	0.056
	255	0.041	0.016	0.014	0.074	0.076	0.049	0.023	0.043	0.073	0.043	0.065	0.071	0.000	0.074	0.056
	259	0.065	0.059	0.083	0.053	0.061	0.027	0.038	0.033	0.042	0.074	0.033	0.014	0.000	0.043	0.028
	263	0.029	0.048	0.111	0.063	0.083	0.044	0.054	0.033	0.031	0.032	0.065	0.029	0.100	0.011	0.022
	267	0.035	0.037	0.028	0.032	0.030	0.016	0.038	0.065	0.000	0.043	0.033	0.000	0.100	0.021	0.022
	271	0.035	0.043	0.014	0.026	0.023	0.033	0.038	0.043	0.021	0.053	0.000	0.000	0.000	0.011	0.006
	275	0.035	0.027	0.028	0.026	0.030	0.016	0.046	0.043	0.031	0.011	0.022	0.000	0.000	0.000	0.011
	279	0.035	0.043	0.014	0.005	0.023	0.005	0.023	0.000	0.021	0.032	0.033	0.014	0.000	0.000	0.017
	283	0.029	0.016	0.028	0.042	0.053	0.005	0.031	0.011	0.031	0.011	0.022	0.000	0.000	0.000	0.000
	287	0.024	0.005	0.000	0.011	0.000	0.005	0.015	0.076	0.021	0.032	0.022	0.000	0.000	0.011	0.000
	291	0.006	0.016	0.000	0.011	0.015	0.005	0.023	0.011	0.000	0.000	0.033	0.000	0.050	0.000	0.000
	295	0.000	0.005	0.000	0.005	0.008	0.000	0.008	0.033	0.031	0.000	0.043	0.000	0.000	0.011	0.000
	299	0.000	0.011	0.000	0.005	0.015	0.005	0.000	0.033	0.010	0.000	0.022	0.000	0.000	0.000	0.000
	303	0.006	0.005	0.000	0.000	0.000	0.000	0.008	0.022	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	307	0.012	0.000	0.000	0.011	0.000	0.000	0.008	0.033	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Supplementary Table 2 (cont.)

Locus	Allele	RAN	LBI	JON	HAU	MER	TAU	WEL12	WEL13	MAR	TAS	GOL	FIO	STE12	STE14	CHA
*Pnova*_27	**311**	0.000	0.011	0.000	0.011	0.000	0.005	0.000	0.000	0.000	0.000	0.011	0.000	0.000	0.000	0.000
	315	0.000	0.000	0.000	0.000	0.000	0.011	0.015	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	319	0.000	0.000	0.000	0.000	0.000	0.000	0.015	0.000	0.000	0.011	0.000	0.000	0.000	0.000	0.000
	323	0.000	0.011	0.000	0.000	0.000	0.000	0.000	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	327	0.000	0.000	0.000	0.000	0.000	0.005	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	339	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	343	0.000	0.000	0.000	0.000	0.000	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	379	0.000	0.000	0.000	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
*Pnova*_28	**248**	0.006	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	251	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000
	254	0.022	0.022	0.025	0.011	0.031	0.022	0.008	0.021	0.021	0.042	0.021	0.074	0.167	0.083	0.047
	257	0.011	0.000	0.013	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.026
	263	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	266	0.000	0.005	0.013	0.000	0.008	0.000	0.008	0.032	0.010	0.021	0.000	0.000	0.000	0.010	0.000
	269	0.000	0.022	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005
	272	0.000	0.000	0.000	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005
	275	0.006	0.005	0.000	0.006	0.000	0.011	0.015	0.000	0.000	0.000	0.010	0.000	0.056	0.000	0.005
	278	0.017	0.000	0.000	0.011	0.000	0.005	0.015	0.011	0.021	0.010	0.000	0.000	0.000	0.000	0.005
	281	0.034	0.027	0.063	0.011	0.015	0.005	0.038	0.021	0.010	0.021	0.010	0.000	0.000	0.010	0.010
	284	0.028	0.016	0.038	0.022	0.015	0.022	0.069	0.043	0.042	0.021	0.021	0.044	0.000	0.021	0.026
	287	0.039	0.016	0.025	0.011	0.015	0.016	0.015	0.053	0.010	0.000	0.010	0.015	0.000	0.000	0.005
	290	0.022	0.016	0.063	0.017	0.062	0.027	0.062	0.032	0.063	0.010	0.021	0.000	0.056	0.010	0.052
	293	0.051	0.032	0.088	0.034	0.031	0.022	0.069	0.085	0.063	0.052	0.010	0.088	0.000	0.052	0.052
	296	0.045	0.048	0.050	0.062	0.062	0.060	0.046	0.053	0.042	0.063	0.052	0.015	0.056	0.052	0.078
	299	0.079	0.108	0.038	0.062	0.069	0.038	0.062	0.064	0.021	0.104	0.115	0.044	0.056	0.094	0.063
	302	0.056	0.097	0.050	0.101	0.054	0.130	0.031	0.043	0.083	0.094	0.073	0.103	0.111	0.083	0.094
	305	0.056	0.054	0.038	0.079	0.069	0.103	0.077	0.106	0.063	0.052	0.115	0.074	0.000	0.083	0.089

Supplementary Table 2 (cont.)

Locus	Allele	RAN	LBI	JON	HAU	MER	TAU	WEL12	WEL13	MAR	TAS	GOL	FIO	STE12	STE14	CHA
*Pnova*_28	**308**	0.062	0.038	0.063	0.096	0.046	0.054	0.069	0.138	0.104	0.115	0.052	0.088	0.167	0.073	0.057
	311	0.056	0.081	0.013	0.062	0.046	0.065	0.077	0.053	0.073	0.073	0.031	0.044	0.111	0.073	0.068
	314	0.056	0.038	0.063	0.017	0.038	0.065	0.062	0.021	0.083	0.021	0.104	0.044	0.000	0.063	0.104
	317	0.051	0.054	0.038	0.034	0.015	0.049	0.046	0.011	0.073	0.104	0.031	0.029	0.000	0.042	0.057
	320	0.034	0.038	0.025	0.045	0.038	0.027	0.046	0.000	0.021	0.042	0.031	0.118	0.000	0.021	0.016
	323	0.034	0.027	0.063	0.017	0.054	0.011	0.023	0.032	0.031	0.000	0.063	0.044	0.000	0.042	0.031
	326	0.022	0.022	0.013	0.011	0.038	0.016	0.015	0.032	0.031	0.042	0.031	0.103	0.056	0.052	0.026
	329	0.022	0.016	0.038	0.045	0.038	0.027	0.023	0.021	0.021	0.021	0.052	0.029	0.056	0.042	0.016
	332	0.028	0.022	0.038	0.039	0.015	0.027	0.031	0.021	0.042	0.031	0.021	0.015	0.056	0.042	0.016
	335	0.017	0.022	0.000	0.011	0.023	0.027	0.031	0.021	0.021	0.031	0.010	0.000	0.000	0.010	0.010
	338	0.028	0.022	0.025	0.034	0.031	0.005	0.015	0.032	0.010	0.010	0.021	0.000	0.056	0.021	0.016
	341	0.000	0.022	0.025	0.028	0.023	0.016	0.008	0.021	0.000	0.000	0.000	0.000	0.000	0.010	0.005
	344	0.022	0.005	0.013	0.028	0.031	0.038	0.015	0.011	0.000	0.000	0.052	0.015	0.000	0.010	0.000
	347	0.006	0.032	0.025	0.028	0.015	0.011	0.015	0.000	0.010	0.000	0.010	0.000	0.000	0.000	0.005
	350	0.039	0.027	0.038	0.022	0.031	0.022	0.008	0.000	0.021	0.000	0.010	0.015	0.000	0.000	0.000
	353	0.022	0.016	0.000	0.006	0.023	0.038	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000
	356	0.022	0.016	0.013	0.011	0.031	0.022	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.005
	359	0.006	0.011	0.000	0.017	0.000	0.000	0.000	0.000	0.010	0.010	0.000	0.000	0.000	0.000	0.000
	362	0.000	0.011	0.000	0.000	0.008	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005
	365	0.000	0.005	0.000	0.017	0.015	0.000	0.000	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	368	0.000	0.005	0.013	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	377	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
*Pnova*_32	**167**	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	173	0.015	0.000	0.000	0.010	0.007	0.010	0.000	0.010	0.000	0.021	0.011	0.000	0.000	0.000	0.005
	175	0.658	0.670	0.625	0.606	0.558	0.536	0.642	0.635	0.660	0.594	0.660	0.529	0.375	0.396	0.633
	177	0.240	0.229	0.275	0.298	0.333	0.347	0.276	0.260	0.280	0.281	0.266	0.397	0.375	0.219	0.270
	179	0.041	0.043	0.025	0.025	0.036	0.051	0.030	0.042	0.020	0.073	0.021	0.015	0.000	0.052	0.026

Supplementary Table 2 (cont.)

Locus	Allele	RAN	LBI	JON	HAU	MER	TAU	WEL12	WEL13	MAR	TAS	GOL	FIO	STE12	STE14	CHA
*Pnova*_32	**181**	0.036	0.032	0.050	0.056	0.014	0.036	0.022	0.042	0.020	0.010	0.011	0.044	0.188	0.333	0.041
	183	0.000	0.027	0.025	0.005	0.051	0.015	0.022	0.010	0.020	0.021	0.032	0.000	0.063	0.000	0.026
	185	0.000	0.000	0.000	0.000	0.000	0.005	0.007	0.000	0.000	0.000	0.000	0.015	0.000	0.000	0.000
*Pnova*_33	**149**	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	154	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000
	159	0.000	0.000	0.000	0.000	0.008	0.011	0.000	0.000	0.000	0.000	0.000	0.015	0.000	0.000	0.000
	164	0.095	0.070	0.063	0.052	0.061	0.084	0.053	0.063	0.130	0.052	0.048	0.045	0.167	0.052	0.082
	169	0.211	0.279	0.213	0.222	0.159	0.216	0.250	0.250	0.190	0.333	0.310	0.212	0.222	0.260	0.296
	174	0.295	0.297	0.350	0.330	0.402	0.289	0.326	0.250	0.300	0.292	0.298	0.424	0.222	0.260	0.281
	179	0.211	0.192	0.263	0.196	0.242	0.263	0.182	0.219	0.150	0.167	0.155	0.273	0.167	0.260	0.173
	184	0.126	0.058	0.038	0.113	0.053	0.053	0.076	0.125	0.120	0.083	0.083	0.000	0.111	0.094	0.071
	189	0.021	0.058	0.075	0.036	0.015	0.047	0.076	0.073	0.020	0.031	0.060	0.030	0.056	0.031	0.020
	194	0.005	0.017	0.000	0.010	0.008	0.005	0.015	0.010	0.010	0.021	0.048	0.000	0.000	0.010	0.026
	199	0.021	0.012	0.000	0.010	0.023	0.016	0.000	0.010	0.030	0.010	0.000	0.000	0.000	0.000	0.015
	204	0.000	0.012	0.000	0.021	0.008	0.016	0.015	0.000	0.010	0.000	0.000	0.000	0.056	0.021	0.015
	209	0.011	0.006	0.000	0.005	0.000	0.000	0.000	0.000	0.040	0.010	0.000	0.000	0.000	0.000	0.020
	214	0.000	0.000	0.000	0.005	0.015	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	229	0.000	0.000	0.000	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Supplementary Table 3 Allele frequencies for 10 microsatellite loci of *Pecten novaezelandiae* for 5 locations in the Coromandel fishery (Chapter 5 – spatial study).

Locus	Allele	LBI	JON	HAU	MER	TAU
*Pnova*_01	**207**	0.011	0.000	0.000	0.000	0.000
	217	0.000	0.013	0.000	0.000	0.000
	221	0.101	0.050	0.121	0.123	0.051
	223	0.878	0.800	0.869	0.848	0.918
	225	0.005	0.113	0.005	0.029	0.031
	227	0.000	0.025	0.000	0.000	0.000
	229	0.005	0.000	0.000	0.000	0.000
	231	0.000	0.000	0.005	0.000	0.000
*Pnova*_02	**161**	0.000	0.000	0.010	0.007	0.000
	163	0.000	0.013	0.000	0.000	0.010
	165	0.021	0.013	0.025	0.036	0.035
	167	0.266	0.295	0.197	0.239	0.288
	169	0.479	0.500	0.556	0.522	0.510
	171	0.069	0.090	0.045	0.094	0.045
	173	0.128	0.000	0.101	0.065	0.051
	175	0.016	0.064	0.035	0.014	0.030
	177	0.011	0.026	0.005	0.014	0.010
	179	0.011	0.000	0.010	0.007	0.010
	181	0.000	0.000	0.010	0.000	0.005
	183	0.000	0.000	0.005	0.000	0.000
	185	0.000	0.000	0.000	0.000	0.005
*Pnova*_04	**272**	0.000	0.000	0.000	0.007	0.000
	276	0.131	0.163	0.148	0.104	0.117
	280	0.023	0.013	0.022	0.007	0.010
	284	0.097	0.063	0.099	0.030	0.071
	288	0.511	0.525	0.495	0.634	0.561
	292	0.193	0.200	0.192	0.179	0.199
	296	0.034	0.025	0.044	0.022	0.031
	300	0.011	0.013	0.000	0.007	0.005
	304	0.000	0.000	0.000	0.007	0.005
*Pnova*_05	**131**	0.043	0.033	0.052	0.059	0.041
	135	0.161	0.117	0.063	0.096	0.112
	139	0.140	0.167	0.092	0.154	0.168
	143	0.403	0.233	0.385	0.397	0.434
	147	0.167	0.300	0.293	0.213	0.163
	151	0.054	0.067	0.075	0.051	0.046
	155	0.016	0.033	0.011	0.029	0.015
	159	0.005	0.000	0.011	0.000	0.000
	163	0.011	0.050	0.000	0.000	0.010
	167	0.000	0.000	0.017	0.000	0.005

Supplementary Table 3 (Cont.)

Locus	Allele	LBI	JON	HAU	MER	TAU
*Pnova*_05	**171**	0.000	0.000	0.000	0.000	0.005
*Pnova*_09	**112**	0.043	0.013	0.046	0.030	0.026
	116	0.033	0.038	0.056	0.075	0.052
	120	0.766	0.800	0.724	0.679	0.742
	124	0.054	0.063	0.066	0.090	0.052
	128	0.087	0.063	0.082	0.082	0.098
	132	0.011	0.025	0.026	0.030	0.015
	136	0.000	0.000	0.000	0.007	0.010
	144	0.005	0.000	0.000	0.007	0.005
*Pnova*_10	**256**	0.000	0.026	0.000	0.000	0.000
	258	0.043	0.051	0.041	0.058	0.027
	260	0.092	0.090	0.107	0.101	0.048
	262	0.033	0.000	0.046	0.007	0.011
	264	0.293	0.372	0.245	0.254	0.293
	266	0.397	0.372	0.434	0.420	0.426
	268	0.109	0.064	0.097	0.138	0.138
	270	0.016	0.013	0.005	0.007	0.016
	272	0.005	0.000	0.020	0.000	0.005
	274	0.005	0.013	0.005	0.000	0.027
	278	0.005	0.000	0.000	0.007	0.011
	280	0.000	0.000	0.000	0.007	0.000
*Pnova*_27	**151**	0.011	0.000	0.005	0.000	0.000
	167	0.000	0.000	0.000	0.008	0.000
	171	0.000	0.000	0.011	0.000	0.000
	183	0.000	0.000	0.005	0.000	0.000
	187	0.005	0.000	0.005	0.000	0.000
	191	0.011	0.028	0.016	0.000	0.011
	195	0.005	0.028	0.005	0.008	0.005
	199	0.021	0.014	0.026	0.030	0.027
	203	0.005	0.014	0.021	0.061	0.011
	207	0.032	0.014	0.032	0.023	0.049
	211	0.016	0.014	0.047	0.015	0.038
	215	0.032	0.042	0.021	0.015	0.049
	219	0.069	0.042	0.026	0.030	0.055
	223	0.053	0.014	0.032	0.061	0.066
	227	0.048	0.111	0.053	0.030	0.060
	231	0.064	0.042	0.053	0.061	0.049
	235	0.064	0.042	0.047	0.053	0.044
	239	0.059	0.042	0.037	0.053	0.071
	243	0.059	0.097	0.042	0.053	0.077
	247	0.064	0.069	0.079	0.023	0.071

Supplementary Table 3 (Cont.)

Locus	Allele	LBI	JON	HAU	MER	TAU
*Pnova*_27	**251**	0.032	0.069	0.063	0.053	0.077
	255	0.016	0.014	0.074	0.076	0.049
	259	0.059	0.083	0.053	0.061	0.027
	263	0.048	0.111	0.063	0.083	0.044
	267	0.037	0.028	0.032	0.030	0.016
	271	0.043	0.014	0.026	0.023	0.033
	275	0.027	0.028	0.026	0.030	0.016
	279	0.043	0.014	0.005	0.023	0.005
	283	0.016	0.028	0.042	0.053	0.005
	287	0.005	0.000	0.011	0.000	0.005
	291	0.016	0.000	0.011	0.015	0.005
	295	0.005	0.000	0.005	0.008	0.000
	299	0.011	0.000	0.005	0.015	0.005
	303	0.005	0.000	0.000	0.000	0.000
	307	0.000	0.000	0.011	0.000	0.000
	311	0.011	0.000	0.011	0.000	0.005
	315	0.000	0.000	0.000	0.000	0.011
	323	0.011	0.000	0.000	0.000	0.000
	327	0.000	0.000	0.000	0.000	0.005
	379	0.000	0.000	0.000	0.008	0.000
*Pnova*_28	**248**	0.000	0.000	0.000	0.000	0.005
	254	0.022	0.025	0.011	0.031	0.022
	257	0.000	0.013	0.000	0.000	0.000
	266	0.005	0.013	0.000	0.008	0.000
	269	0.022	0.000	0.000	0.000	0.000
	272	0.000	0.000	0.000	0.008	0.000
	275	0.005	0.000	0.006	0.000	0.011
	278	0.000	0.000	0.011	0.000	0.005
	281	0.027	0.063	0.011	0.015	0.005
	284	0.016	0.038	0.022	0.015	0.022
	287	0.016	0.025	0.011	0.015	0.016
	290	0.016	0.063	0.017	0.062	0.027
	293	0.032	0.088	0.034	0.031	0.022
	296	0.048	0.050	0.062	0.062	0.060
	299	0.108	0.038	0.062	0.069	0.038
	302	0.097	0.050	0.101	0.054	0.130
	305	0.054	0.038	0.079	0.069	0.103
	308	0.038	0.063	0.096	0.046	0.054
	311	0.081	0.013	0.062	0.046	0.065
	314	0.038	0.063	0.017	0.038	0.065
	317	0.054	0.038	0.034	0.015	0.049

Supplementary Table 3 (Cont.)

Locus	Allele	LBI	JON	HAU	MER	TAU
*Pnova*_28	**320**	0.038	0.025	0.045	0.038	0.027
	323	0.027	0.063	0.017	0.054	0.011
	326	0.022	0.013	0.011	0.038	0.016
	329	0.016	0.038	0.045	0.038	0.027
	332	0.022	0.038	0.039	0.015	0.027
	335	0.022	0.000	0.011	0.023	0.027
	338	0.022	0.025	0.034	0.031	0.005
	341	0.022	0.025	0.028	0.023	0.016
	344	0.005	0.013	0.028	0.031	0.038
	347	0.032	0.025	0.028	0.015	0.011
	350	0.027	0.038	0.022	0.031	0.022
	353	0.016	0.000	0.006	0.023	0.038
	356	0.016	0.013	0.011	0.031	0.022
	359	0.011	0.000	0.017	0.000	0.000
	362	0.011	0.000	0.000	0.008	0.011
	365	0.005	0.000	0.017	0.015	0.000
	368	0.005	0.013	0.006	0.000	0.000
	377	0.005	0.000	0.000	0.000	0.000
*Pnova*_32	**173**	0.000	0.000	0.010	0.007	0.010
	175	0.670	0.625	0.606	0.558	0.536
	177	0.229	0.275	0.298	0.333	0.347
	179	0.043	0.025	0.025	0.036	0.051
	181	0.032	0.050	0.056	0.014	0.036
	183	0.027	0.025	0.005	0.051	0.015
	185	0.000	0.000	0.000	0.000	0.005
*Pnova*_33	**159**	0.000	0.000	0.000	0.008	0.011
	164	0.070	0.063	0.052	0.061	0.084
	169	0.279	0.213	0.222	0.159	0.216
	174	0.297	0.350	0.330	0.402	0.289
	179	0.192	0.263	0.196	0.242	0.263
	184	0.058	0.038	0.113	0.053	0.053
	189	0.058	0.075	0.036	0.015	0.047
	194	0.017	0.000	0.010	0.008	0.005
	199	0.012	0.000	0.010	0.023	0.016
	204	0.012	0.000	0.021	0.008	0.016
	209	0.006	0.000	0.005	0.000	0.000
	214	0.000	0.000	0.005	0.015	0.000
	229	0.000	0.000	0.000	0.008	0.000

Supplementary Table 4 Allele frequencies for 10 microsatellite loci of *Pecten novaezelandiae* for 6 locations in the Coromandel fishery (Chapter 5 – temporal study).

Locus	Allele	LBI	LBI14	MER	MER14	TAU	TAU14
*Pnova*_01	**219**	0.000	0.008	0.000	0.000	0.000	0.000
	221	0.095	0.056	0.133	0.102	0.057	0.154
	223	0.897	0.913	0.842	0.864	0.929	0.831
	225	0.000	0.024	0.025	0.034	0.014	0.015
	229	0.008	0.000	0.000	0.000	0.000	0.000
*Pnova*_02	**159**	0.000	0.016	0.000	0.000	0.000	0.000
	161	0.000	0.016	0.000	0.017	0.000	0.000
	163	0.000	0.000	0.000	0.000	0.014	0.000
	165	0.032	0.040	0.042	0.034	0.050	0.008
	167	0.242	0.290	0.250	0.216	0.236	0.250
	169	0.460	0.492	0.517	0.543	0.557	0.540
	171	0.073	0.040	0.100	0.086	0.029	0.081
	173	0.145	0.081	0.075	0.086	0.064	0.073
	175	0.024	0.016	0.000	0.017	0.021	0.024
	177	0.008	0.000	0.017	0.000	0.007	0.008
	179	0.016	0.000	0.000	0.000	0.007	0.016
	181	0.000	0.008	0.000	0.000	0.007	0.000
	185	0.000	0.000	0.000	0.000	0.007	0.000
*Pnova*_04	**276**	0.129	0.197	0.103	0.167	0.101	0.103
	280	0.026	0.016	0.009	0.018	0.014	0.000
	284	0.069	0.090	0.034	0.088	0.065	0.071
	288	0.552	0.451	0.638	0.561	0.558	0.540
	292	0.198	0.230	0.172	0.140	0.210	0.214
	296	0.026	0.008	0.026	0.026	0.036	0.056
	300	0.000	0.008	0.009	0.000	0.007	0.016
	304	0.000	0.000	0.009	0.000	0.007	0.000
*Pnova*_05	**131**	0.057	0.094	0.067	0.058	0.043	0.045
	135	0.131	0.102	0.108	0.133	0.116	0.136
	139	0.148	0.164	0.175	0.175	0.159	0.167
	143	0.385	0.414	0.367	0.383	0.457	0.364
	147	0.189	0.156	0.208	0.167	0.145	0.212
	151	0.049	0.031	0.050	0.067	0.043	0.030
	155	0.025	0.031	0.025	0.008	0.014	0.038
	159	0.008	0.000	0.000	0.008	0.000	0.000
	163	0.008	0.008	0.000	0.000	0.014	0.008
	167	0.000	0.000	0.000	0.000	0.007	0.000
*Pnova*_09	**112**	0.065	0.063	0.034	0.061	0.022	0.023
	116	0.032	0.031	0.060	0.044	0.065	0.054
	120	0.734	0.773	0.690	0.798	0.739	0.792
	124	0.048	0.039	0.095	0.009	0.051	0.062
	128	0.105	0.078	0.078	0.079	0.094	0.062
	132	0.008	0.008	0.026	0.009	0.022	0.000
	136	0.000	0.008	0.009	0.000	0.007	0.008
	144	0.008	0.000	0.009	0.000	0.000	0.000

Supplementary Table 4 (Cont.)

Locus	Allele	LBI	LBI14	MER	MER14	TAU	TAU14
*Pnova*_10	**256**	0.000	0.000	0.000	0.042	0.000	0.016
	258	0.049	0.047	0.050	0.100	0.022	0.070
	260	0.107	0.109	0.092	0.100	0.051	0.078
	262	0.016	0.023	0.008	0.008	0.014	0.039
	264	0.295	0.242	0.250	0.225	0.275	0.242
	266	0.410	0.406	0.425	0.383	0.435	0.422
	268	0.107	0.125	0.158	0.108	0.138	0.078
	270	0.016	0.023	0.008	0.008	0.022	0.031
	272	0.000	0.008	0.000	0.025	0.007	0.008
	274	0.000	0.016	0.000	0.000	0.036	0.000
	278	0.000	0.000	0.000	0.000	0.000	0.016
	280	0.000	0.000	0.008	0.000	0.000	0.000
*Pnova*_27	**151**	0.016	0.000	0.000	0.000	0.000	0.000
	167	0.000	0.000	0.009	0.000	0.000	0.000
	191	0.016	0.008	0.000	0.000	0.016	0.000
	195	0.008	0.033	0.009	0.035	0.008	0.016
	199	0.016	0.025	0.026	0.018	0.016	0.023
	203	0.008	0.057	0.044	0.018	0.016	0.023
	207	0.008	0.033	0.026	0.053	0.047	0.008
	211	0.016	0.016	0.009	0.044	0.047	0.047
	215	0.032	0.025	0.018	0.018	0.063	0.047
	219	0.089	0.025	0.035	0.018	0.008	0.086
	223	0.032	0.057	0.061	0.053	0.086	0.094
	227	0.048	0.041	0.035	0.088	0.047	0.055
	231	0.048	0.107	0.061	0.070	0.070	0.055
	235	0.073	0.082	0.061	0.070	0.047	0.047
	239	0.048	0.049	0.044	0.026	0.070	0.094
	243	0.056	0.066	0.061	0.088	0.086	0.055
	247	0.056	0.066	0.018	0.009	0.063	0.094
	251	0.040	0.033	0.053	0.105	0.102	0.039
	255	0.016	0.033	0.079	0.044	0.047	0.039
	259	0.089	0.057	0.061	0.053	0.023	0.055
	263	0.056	0.041	0.079	0.018	0.047	0.008
	267	0.040	0.025	0.035	0.044	0.023	0.023
	271	0.032	0.016	0.018	0.026	0.016	0.031
	275	0.016	0.000	0.035	0.035	0.016	0.016
	279	0.040	0.025	0.018	0.018	0.000	0.008
	283	0.016	0.008	0.053	0.009	0.008	0.016
	287	0.008	0.025	0.000	0.000	0.000	0.008
	291	0.016	0.016	0.018	0.009	0.000	0.000
	295	0.008	0.008	0.009	0.009	0.000	0.000
	299	0.016	0.000	0.018	0.009	0.008	0.008
	303	0.008	0.008	0.000	0.000	0.000	0.000
	307	0.000	0.000	0.000	0.009	0.000	0.000
	311	0.016	0.000	0.000	0.000	0.008	0.000

Supplementary Table 4 (Cont.)

Locus	Allele	LBI	LBI14	MER	MER14	TAU	TAU14
*Pnova*_27	**315**	0.000	0.000	0.000	0.000	0.016	0.000
	319	0.000	0.016	0.000	0.000	0.000	0.000
	323	0.008	0.000	0.000	0.009	0.000	0.008
	379	0.000	0.000	0.009	0.000	0.000	0.000
*Pnova*_28	**254**	0.025	0.056	0.036	0.025	0.016	0.062
	266	0.008	0.000	0.009	0.000	0.000	0.000
	269	0.033	0.000	0.000	0.000	0.000	0.000
	272	0.000	0.000	0.009	0.000	0.000	0.000
	275	0.000	0.000	0.000	0.017	0.016	0.000
	278	0.000	0.024	0.000	0.000	0.008	0.031
	281	0.041	0.016	0.009	0.017	0.000	0.031
	284	0.025	0.024	0.018	0.025	0.008	0.031
	287	0.008	0.024	0.018	0.025	0.016	0.038
	290	0.008	0.016	0.054	0.025	0.032	0.038
	293	0.033	0.008	0.027	0.033	0.032	0.069
	296	0.049	0.048	0.054	0.083	0.056	0.023
	299	0.131	0.048	0.080	0.075	0.040	0.023
	302	0.098	0.089	0.045	0.117	0.143	0.092
	305	0.057	0.105	0.071	0.075	0.119	0.092
	308	0.041	0.056	0.036	0.083	0.056	0.062
	311	0.082	0.065	0.045	0.017	0.071	0.015
	314	0.049	0.048	0.045	0.042	0.079	0.031
	317	0.049	0.032	0.018	0.017	0.056	0.031
	320	0.033	0.056	0.036	0.042	0.040	0.031
	323	0.016	0.048	0.045	0.025	0.008	0.038
	326	0.008	0.040	0.036	0.025	0.024	0.031
	329	0.008	0.016	0.045	0.025	0.008	0.046
	332	0.025	0.040	0.018	0.033	0.032	0.015
	335	0.008	0.000	0.027	0.008	0.008	0.023
	338	0.033	0.032	0.027	0.025	0.008	0.008
	341	0.033	0.000	0.027	0.008	0.024	0.015
	344	0.008	0.016	0.036	0.017	0.032	0.015
	347	0.033	0.032	0.018	0.025	0.016	0.038
	350	0.025	0.016	0.036	0.042	0.008	0.023
	353	0.000	0.008	0.018	0.008	0.024	0.008
	356	0.008	0.016	0.036	0.025	0.016	0.023
	359	0.008	0.000	0.000	0.017	0.000	0.008
	362	0.016	0.008	0.009	0.000	0.008	0.008
	365	0.000	0.008	0.018	0.000	0.000	0.000
*Pnova*_32	**173**	0.000	0.000	0.008	0.000	0.000	0.008
	175	0.685	0.578	0.583	0.690	0.536	0.538
	177	0.202	0.297	0.308	0.267	0.348	0.311
	179	0.065	0.016	0.033	0.034	0.058	0.045
	181	0.016	0.070	0.017	0.000	0.036	0.061

Supplementary Table 4 (Cont.)

Locus	Allele	LBI	LBI14	MER	MER14	TAU	TAU14
*Pnova*_32	**183**	0.032	0.039	0.050	0.009	0.014	0.038
	185	0.000	0.000	0.000	0.000	0.007	0.000
*Pnova*_33	**159**	0.000	0.000	0.009	0.009	0.000	0.000
	164	0.061	0.056	0.060	0.044	0.065	0.144
	169	0.298	0.306	0.164	0.404	0.225	0.303
	174	0.316	0.395	0.388	0.219	0.283	0.235
	179	0.193	0.137	0.241	0.254	0.275	0.235
	184	0.035	0.073	0.060	0.026	0.051	0.068
	189	0.053	0.032	0.017	0.035	0.058	0.008
	194	0.026	0.000	0.009	0.000	0.007	0.000
	199	0.000	0.000	0.026	0.000	0.022	0.000
	204	0.009	0.000	0.000	0.009	0.014	0.000
	209	0.009	0.000	0.000	0.000	0.000	0.008
	214	0.000	0.000	0.017	0.000	0.000	0.000
	229	0.000	0.000	0.009	0.000	0.000	0.000