

**Environmental preferences, impacts and population dynamics of the  
invasive screwshell *Maoricolpus roseus***

Thesis submitted by

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Submitted in fulfilment of the requirements for the

Degree of Doctor of Philosophy,

Institute for Marine and Antarctic Studies,

University of Tasmania (July, 2013).

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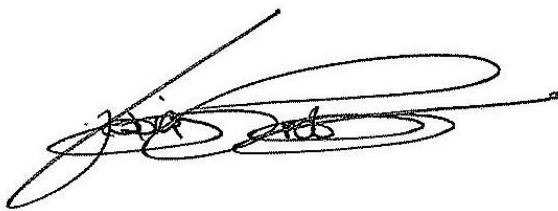
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Tobias Adrian Probst

July 2013

## **Abstract**

Biological invasions in the marine environment have become a major concern globally, as non - indigenous species can dramatically alter community composition and ecosystem functioning. A study on the turritellid *Maoricolpus roseus* (Quoy and Gaimard 1864) was conducted to increase the understanding of the invasive success of this native species and its potential impacts on the environment. *Maoricolpus roseus* is a prosobranch gastropod believed to have been introduced into Tasmania (Australia) in the 1920's, and despite its wide distribution, dense populations, and success in invading several different environments, knowledge of its habitat, reproductive biology and ecological impacts is poor.

This thesis investigated habitat preferences of *M. roseus*, its impact on co - occurring macromolluscs and described its larvae. This information is important for effective management to understand the spread of this species and the extent and magnitude of its potential impacts on coastal ecosystems. Many of the previous surveys did not differentiate between live *M. roseus* or shells from dead animals, therefore many past descriptions on its preferred habitat are questionable.

A survey was carried out in the D'Entrecasteaux Channel (SE Tasmania) to investigate *M. roseus* habitat. It was found that the spatial distribution of live and dead animals varied within the surveyed area and that differentiation between animal types was important to determine the patterns of distribution of *M. roseus*. High live animal density sites were generally characterised by sand. Some relatively high densities were also found on finer mud substrate, indicating its ability to adapt to different environments. The study also found that *M. roseus* were present at all the

depths surveyed (down to 40 m) and that generally shell size class was larger at the shallower depths (< 30m).

From the survey it was noted that large densities of *M. roseus* on the finer mud substrate were located in close proximity to sites with the highest densities of live *M. roseus* and characterised by sand. Further laboratory experiments on habitat choice showed that there was a significant increase in the number of *M. roseus* that moved onto mud with an increase in the density of this gastropod on sand. This suggests that this response may be partially density - dependent.

Investigation of the impact of *M. roseus* on the distribution of other macromolluscs in the D'Entrecasteaux Channel demonstrated that *M. roseus* live and dead animals and substrate type correlated in variable ways with macromollusc richness and abundance. Within its favoured habitat of sand, live *M. roseus* were significantly correlated with the macromollusc species community composition. Areas of higher live *M. roseus* densities had a lower number of suspension feeding macromolluscs, while the opposite occurred for areas with a lower density of live *M. roseus*. These results suggest that live *M. roseus* may be inhibiting the accumulation of other suspension feeding macromolluscs in its vicinity.

Studies on two *M. roseus* populations in the D'Entrecasteaux Channel showed a sexual dimorphism, a 1:1 sex ratio, with females relatively larger than males, and up to 70 % of females carrying larvae over consecutive austral summer seasons. Larvae released from egg capsules were all relatively well developed and planktotrophic.

This new information on planktonic larvae helps explain the expansion of this species around the Australian coastline.

The results of this study are important to understanding the successful introduction and expansion of *M. roseus*, and its impact on the Tasmanian environment. This new knowledge will support improved management of this introduced species.

## **Acknowledgements**

Firstly I would like to thank my supervisor Dr Christine Crawford for advice and support throughout the study since the start of the project. I deeply appreciate all the time spent on guiding me through this study. It was a long project, and for your help and encouragement I am very grateful. I would also like to thank Dr Jeff Ross for supervision and guidance. Professor Craig Johnson, Professor Nic Bax, and Dr Alastair Hirst for supervision help on various stages throughout my study. Thank you to the staff and students from the University of Tasmania. Especially the Marine Research Laboratories at Tarooma, part of the Institute for Marine and Antarctic Studies (formerly Tasmanian Aquaculture and Fisheries Institute). There were many hours spent in the laboratories, offices, in the field, and lengthy discussions on the topic. Many people helped in several parts of the project. Thanks go to Tim Alexander, Cynthia Awruch, Neville Barrett, Steve Battaglione, Alan Beech, Stewart Dickson, Graham Edgar, Sam Foster, Julian Harrington, Bob Hodgson, Dane Jones, Allan Jordan, Jeremy Lyle, Catriona Macleod, Hugh Pederson, Anthony Reid, Ryuji Sakabe, Simon Talbot, Sean Tracey, Simon Willcox, Bill Wilkinson, and Philippe Ziegler. Simon Grove and Liz Turner from the Tasmanian Museum for assistance in taxonomic identification. Thank you also to Mark Davey and Carolyn Trewin for reviews of parts of the manuscript. The project was financially supported by the former Tasmanian Aquaculture and Fisheries Institute. Thank you also to Anthony Hurst from the NSW Fisheries Department for supporting the project.

Finally, I am very grateful to my family. I would have not been able to complete this long journey without the support of my wife Sarah and my children Gabriella, Pablo, and Sacha. I will be eternally grateful for your help and patience. I would like to dedicate this study to you.

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## **1. Chapter One**

### **General Introduction**

#### **1.1 Introduction**

An introduced species can become invasive and as such is defined as a species that is non - native to an ecosystem under consideration and whose introduction causes or is likely to cause economical or environmental harm or harm to human health (NISC 2005). As further defined by the United Nations Environmental Programme (UNEP 2011), invasive species are organisms which successfully establish themselves in, and then overcome, otherwise intact, pre - existing native ecosystems. Invasive species constitute a global - scale problem and their control can be difficult, if not impossible, making prevention particularly important. These species can act as vectors for diseases, alter ecosystems processes, reduce biodiversity, and have negative economic impacts (e.g., Vitousek *et al.* 1994, Simberloff 2001, Reaser 2007).

Biological invasions in the marine environment have become a major concern globally, as non - indigenous species can dramatically alter community composition and ecosystem functioning (e.g., Carlton 1989, Grosholz and Ruiz 1996, Mack *et al.* 2000, Ruiz *et al.* 2000a, Ruiz *et al.* 2000b, Wonham and Carlton 2005). Many of these species are benthic and an increasing number of studies have highlighted the impact that they can have on habitats and native species. For example, in North - America, the non - indigenous species *Carcinus maenas* (European green crab) has had a significant impact on the abundance of invertebrates in Bodega Bay Harbour (Grosholz *et al.* 2000). Similarly, establishment of the Asian clam *Potamocorbula amurensis* in San Francisco Bay resulted in the displacement of whole benthic

communities (Nichols *et al.* 1990). Other examples include the mussel *Mytilus galloprovincialis*, which changed benthic community composition in Saldanha Bay in South Africa (Robinson *et al.* 2007), and the bivalve *Mya arenaria*, introduced from North America into Denmark, which altered food - web interactions and impacted coastal ecosystems (Thomsen *et al.* 2009).

In Australia there are over 250 introduced marine species (CRC 2011) and many have impacted the local environment, such as the macroalgae *Caulerpa taxifolia* (e.g., Taylor *et al.* 2010), the Japanese kelp *Undaria pinnatifida* (e.g., Valentine and Johnson 2003), the Mediterranean fanworm *Sabella spallanzanii* (e.g., Clapin and Evans 1995, Ross *et al.* 2007), the Pacific seastar *Asterias amurensis* (e.g., Ross *et al.* 2006), and the exotic clam *Corbula gibba* (e.g., Talman and Keough 2001).

Another species introduced into Australia is the New Zealand screwshell *Maoricolpus roseus* (Quoy and Gaimard 1834). It is a benthic marine gastropod (Subclass Caenogastropoda, Family Turritellidae) native to New Zealand and is thought to have been accidentally introduced into Australia in the 1920's, via semi - dry ballast in vessels or shipment of oysters (*Tiostrea chilensis* and *Crassostrea glomerata*) to Tasmania (Greenhill 1965, Paul 1979, Hewitt *et al.* 2002, Bax *et al.* 2003). The imported oysters supported the failing Tasmanian native oyster industry and were kept alive in crates in the Derwent estuary during the 1920's to the late 1930's (Dartnall 1969 in Bax *et al.* 2003). This import of oysters to Tasmania ceased many decades ago.

*Maoricolpus roseus* is now well established in Tasmania (Bax *et al.* 2003) and has also been reported from South Australia (Wiltshire *et al.* 2010), Victoria (Bax and Williams 2001), New South Wales (Pollard and Rankin 2003) and Queensland (SERQLD 1999). In some locations *M. roseus* densities can occur in excess of 1000 individuals m<sup>-2</sup> (Bax *et al.* 2003) and it does not have any known extensive predators in Australia (Allmon *et al.* 1994, Scott 1997). Such large densities have the capacity to change benthic habitats in Tasmania (Edgar 2000). This could occur via competition for resources with native species, and by changing the structure of the benthic environment through creating a non - natural substrate.

*Maoricolpus roseus* has the potential to impact on native Tasmanian species such as the turritellid gastropod *Gazameda gunnii* and the scallop *Pecten fumatus* (Bax *et al.* 2003). *Gazameda gunnii* is listed as a threatened species (TTSL 2009) under the Tasmanian Threatened Species Protection Act (TTSPA 2005), and *P. fumatus* is an important recreational and commercial species (Haddon *et al.* 2005). *Maoricolpus roseus* could out - compete *G. gunnii* for habitat and feeding resources. It is a suspension feeder (Scott 1997) and it may impact on *P. fumatus* directly through predation of their larvae and competition for food.

Ecological studies are very limited on turritellid gastropods in general and *M. roseus* is no exception (Allmon 2011). While there is some information available on paleontological history, growth rates, anatomy, mode of fertilisation and larval behaviour, there is no comprehensive study on their habitat and how turritellids interact with other organisms. There is also no comprehensive information on *M. roseus* biology (e.g., developmental biology). Allmon (2011) attributed the lack of



interest in studies on turritellids in the past to their low economic importance and that they are not amongst the most diverse marine gastropod groups. However, this recently changed with the recognition of the potential impact of the introduced *M. roseus* on native environments (Bax *et al.* 2003). Recent investigations on ecological interactions of *M. roseus* in the benthic environment showed that *M. roseus* can promote hermit crab aggregations (Reid 2004), impact soft - sediment faunal assemblages (Reid 2010), and the accumulations of shells from dead *M. roseus* can potentially have an effect on the benthic environment (Nicastro *et al.* 2009).

Information on the biology and ecology of a species is important for invasive species management (e.g., Bax *et al.* 2001a, Buhle *et al.* 2005, Finnoff *et al.* 2005, Leung *et al.* 2005, Saphores and Shogren 2005). Knowledge of environmental preferences of a non - indigenous species can help predict further invasions and provide a framework for management. As noted by Bax *et al.* (2001a), preventing the introduction and establishment of non - indigenous species must be first priority, but where species have already established, management frameworks should be established to control future invasions. The management framework consists of several steps, the first of which is to establish the nature and magnitude of the problem. Studies of environmental preferences of invading species are fundamental to understanding their current distribution, and predicting and avoiding future spread. This information combined with management will assist in developing successful regulatory frameworks (Williams and Grosholz 2008), and after the establishment of a non - native species, effective control is possible (Forrest *et al.* 2009, Jing *et al.* 2012). Some management practises can achieve a full eradication of an invasive species. Examples of successful eradication programs include the green lipped

mussel *Perna canaliculus* in Australia (Bax *et al.* 2001b), the sabellid parasite of abalone *Undaria pinnatifida* in North America (Culver and Kuris 2000), the seaweed *Undaria pinnatifida* in New Zealand (Wotton *et al.* 2004), and the Atlantic rockweed *Ascophyllum nodosum* in North America (Miller *et al.* 2004).

In its native New Zealand, information on *M. roseus* mainly relates to distribution (Morton and Miller 1968, McKnight 1969, Allmon *et al.* 1994), with limited data on life history (Marwick 1971, Pilkington 1974). In Australia, Scott (1997) described some initial information on *M. roseus* feeding, respiration and growth, while Bax and Williams (2001) and Bax *et al.* (2003) summarised available data on population distribution in south - eastern Australia, habitats, shell size, reproduction, and predation. But information on *M. roseus* preferred habitat is unclear. This species has been found on a variety of substrate types, from coarse to muddy sediments (e.g., Greenhill 1965, McKnight 1969, Grange 1979, Allmon *et al.* 1994, Bax and Williams 2001, Bax *et al.* 2003, Beaman *et al.* 2005, Abraham *et al.* 2007). However, some past descriptions of the distribution of *M. roseus*, based on the abundance of shells, may be misrepresented as the position of the operculum well within the shell cavity makes it difficult to determine whether the animal is alive or dead without destroying it. As noted in Summerson *et al.* (2007), identifying whether establishment has occurred is difficult due to complications associated with delineating between live and dead animals.

Since the start of this thesis, some new facts have become available, as summarised in Allmon (2011). For example one article (Probst and Crawford 2008) published out of this thesis (Chapter Five) and another by Gunasekera (2005), have described

*M. roseus* larvae. Planktonic larvae had not been identified before the start of this thesis. Additionally, a recent study demonstrated that *M. roseus* can impact soft - sediment fauna assemblages (Reid 2010).

In summary, most of the available data on *M. roseus* are on its geographical distribution with limited knowledge of its preferred habitat, impact on native species, and developmental biology. All of this information is essential to understanding the success of this invasive species and its potential future spread. Molluscs can be important ecosystem engineers. Aggregations of molluscs introduce complexity and heterogeneity into benthic environments and they are important elements of habitat structure affecting populations, community and ecosystem processes (e.g., McLean 1983, Gutierrez *et al.* 2003, Newell 2004). Many molluscs are successful invaders (Carlton 1999) with impacts on native environments (e.g., Robinson *et al.* 2005, Reise *et al.* 2006, Werner and Rothhaupt 2008, Buhle and Ruesink 2009, Darrigran and Damborenea 2011, Schmidlin *et al.* 2012).

The overall objective of this thesis was to improve our understanding of successful invasions of introduced species in the marine environment and the effects they can have on native communities from a detailed study of the biology and ecology of *M. roseus* in Tasmanian coastal waters. This information is important to predicting and managing invasions of this species.

The aims of this thesis are to provide information on four components:

1. Understanding the habitat of *M. roseus* and which environments are susceptible to future invasions;

2. Further clarity on the importance of differentiating between live and dead *M. roseus*, that otherwise may lead to incorrect descriptions of its distribution;
3. Description of the likely impact of *M. roseus* on similar native species by investigating associations with co - occurring macromolluscs;
4. Description of *M. roseus* population characteristics, such as the proportion of females carrying eggs, description of its larvae, and period of larvae release.

The overall objective was addressed by investigating key areas as outlined below.

Chapter Two focused on describing the habitat of *M. roseus*. As mentioned previously, some past descriptions of the environmental preferences of *M. roseus* may have been misrepresented because they were based on the total abundance of shells (most probably including shells with live animals and empty shells). Therefore, I initially focused on differentiating between live and dead animals. Once I knew how to determine these differences, I investigated potential environmental factors that characterised *M. roseus* habitat.

Following on from results from Chapter Two, the focus of Chapter Three was to investigate *M. roseus* preferred habitat types in laboratory trials. Experiments were used to test the substrate preference of this species, and possible density - dependent response to substrate type.

Chapter Four investigated the impacts *M. roseus* may have on other macromolluscs by examining patterns of association between the distribution of *M. roseus* and other

macromolluscs. The environmental variables substrate type, total organic carbon content, and water depth were also included in the analyses.

A small experiment to investigate the potential impact of *M. roseus* on the commercial scallop *Pecten fumatus* was carried out to support Chapter Four. Experimental trials investigated if *M. roseus* predated on *P. fumatus* larvae.

*Maoricolpus roseus* population characteristics, including female maturity and larval characteristics were described in Chapter Five. From experiments in aquaria and monthly population surveys, detailed information was provided on aspects of reproductive biology and new information on *M. roseus* larvae. The relationship between population characteristics and environmental factors was also investigated.

Finally, in the general discussion in Chapter Six, I summarise the applied significance of the results from this study. I put forward reasons for the invasive success of *M. roseus*, propose potential impacts from the introduction of *M. roseus* into non - native environments, and discuss if environmental factors can be used as predictors for future habitats that may be susceptible to *M. roseus* invasions. The importance of these findings to improved management of this species is also discussed.

The chapters have generally been written as manuscripts for publication. Therefore, there is some repetition between chapters, mainly introducing the species that was studied and general objectives of this work. Also, Chapter Five has already been

published, therefore the format and writing was maintained for this thesis as it has been peer reviewed.

## **2. Chapter Two**

### **Understanding the habitat preferences of *Maoricolpus roseus*: a case study of the D'Entrecasteaux Channel, Tasmania**

#### **2.1 Abstract**

*Maoricolpus roseus* is a prosobranch gastropod (Caenogastropoda) believed to have been introduced into Tasmania, Australia in the 1920's. Despite its wide distribution, dense populations, and success in colonising several different environments, knowledge of its habitat preferences are poorly understood. Current information on the preferred habitat and environmental preferences of *M. roseus* is limited and ambiguous, making it difficult to predict the spread of this species and the extent and magnitude of its potential impacts on coastal ecosystems. This study provided further information on the distribution and preferred environmental conditions of *M. roseus* in the D'Entrecasteaux Channel, southeast Tasmania. The spatial distribution of live and dead *M. roseus* varied within the surveyed area, thus differentiating between these types is important in determining the distribution patterns of the species.

Live *M. roseus* were present at 52 of the 60 sites surveyed. The highest density found was 1807 shells m<sup>-2</sup>. High densities were generally characterised by a sandy habitat. However, some sites characterised by the finer mud substrate also had relative large numbers of *M. roseus*, suggesting the ability of *M. roseus* to adapt to different environments if needed, a typical characteristic of a successful invader. The study also found that *M. roseus* were present at all depths surveyed (down to 40 m) and that generally larger shells were present at the shallower depths (< 30 m).

## **2.2 Introduction**

The dramatic changes in community composition and ecosystem functioning related to biological invasions in the marine environment have become a major concern globally, (e.g., Carlton 1989, Grosholz and Ruiz 1996, Ruiz *et al.* 2000a, Ruiz *et al.* 2000b, Wonham and Carlton 2005). Recent studies of invasive species have highlighted the impact that they can have on benthic habitats and native species. Examples include the European green crab *Carcinus maenas* (Grosholz *et al.* 2000) and the Asian clam *Potamocorbula amurensis* (Nichols *et al.* 1990) in North America, the mussel *Mytilus galloprovincialis* in South Africa (Robinson *et al.* 2007), and the bivalve *Mya arenaria* in Europe (Thomsen *et al.* 2009).

In Tasmania, Australia, there are nearly 400 known introduced faunal species (Terauds 2005), however, investigations on marine species were overlooked until recently (Edgar *et al.* 2005a). The New Zealand screwshell *Maoricolpus roseus* (Quoy and Gaimard 1834) is a benthic marine gastropod (Subclass Caenogastropoda, Family Turritellidae) native to New Zealand, which is believed to have been initially introduced into Tasmania in the 1920's to the late 1930's via semi - dry ballast water or shipment of oysters from New Zealand (Greenhill 1965, Paul 1979, Hewitt *et al.* 2002, Bax *et al.* 2003). *Maoricolpus roseus* does not have any known extensive predators in Australia (Scott 1997, Bax *et al.* 2003, Nicastro *et al.* 2009) and densities in excess of 1000 individuals m<sup>-2</sup> have been reported (Bax *et al.* 2003).

High densities of invading molluscs may alter benthic habitats by the accumulation of large numbers of shells (Edgar 2000), through competition for resources with native species, and from changing the structure of the benthic environment by



creating a non - natural substrate. The organisms involved in these processes (ecosystem engineers) can control the availability of resources to other species by changes in abiotic or biotic factors (Jones *et al.* 1994, 1997). For example, in Mission Bay (North America) the impacts caused by the physical structure created by the non - indigenous bivalve *Musculista senhousia*, were as important as the impacts the animal itself had on other faunal densities (Crooks and Khim 1999).

Further information is required on the habitat preferences of *M. roseus* in order to understand its distribution and, subsequently, the impact it may have on benthic communities. Information on the ecology of a species is important for invasive species management (e.g., Bax *et al.* 2001a, Buhle *et al.* 2005, Finnoff *et al.* 2005, Leung *et al.* 2005, Saphores and Shogren 2005) Assessment of habitat characteristics such as substrate type aid in understanding the distribution of an introduced species. For example, knowledge of the distribution of the introduced mollusc *P. amurensis* and preferred substrate type assisted in understanding why it rapidly increased in abundance in San Francisco Bay (North America) (Carlton *et al.* 1990). Other recent studies on the habitat of the non - indigenous bivalves, *Corbicula fluminea* in São Paulo (Brazil) (Vianna and Avelar 2010), and *Xenostrobus securis* in Ria de Vigo (Spain) (Pascual *et al.* 2010), found that snail density and shell size were correlated with substrate type and organic matter content.

Understanding the biotic and abiotic factors that determine the distribution and abundance of marine organisms is complex (Vernberg 1981, May 1984, Defeo and McLachlan 2005). However, for sediment resident organisms, key factors include the composition of the substrate, particularly grain size composition and organic

matter content (e.g., Gray 1974, Snelgrove and Butman 1994, Snelgrove *et al.* 1997, Alongi 1998, Newell *et al.* 2001).

Another factor to be considered is the spatial scales of the faunal distribution. Benthic organisms in marine soft sediments can have a patchy distribution, which can vary at different spatial scales from metres to kilometres apart (Barry and Dayton 1992, McIntosh 1992). For some faunal assemblages spatial variability can be homogeneous across spatial scales (Dye and Barros 2005, Webb *et al.* 2009), or increase at larger spatial scales (Montagna 1991, Li *et al.* 1997), while many studies demonstrated the importance of incorporating smaller spatial scales in order to accurately determine the faunal distribution (Mannino and Montagna 1997, Edgar and Barrett 2002, Hirst and Kilpatrick 2007, Chapman and Underwood 2008). Identifying the spatial scales of distribution are imperative in assessing faunal abundances and their relationships to environmental variables. Differences in faunal abundances in two locations may seem to relate to a particular environmental attribute when in fact they occur due to natural spatial variability, or vice - versa. Using appropriate scales for benthic data sampling are essential to avoid confounded interpretations (Morrissey *et al.* 1992).

For *M. roseus*, available information on its distribution related to its environmental preferences is limited and ambiguous. Therefore it is difficult to predict the further spread of this species, and the extent and magnitude of impacts it may have on coastal ecosystems. In New Zealand, *M. roseus* have been found on a variety of substrate types, from sandy to muddy environments (e.g., McKnight 1969, Grange 1979, Allmon *et al.* 1994, Abraham *et al.* 2007). Similarly, in Australia *M. roseus* are

reported to occur on a wide variety of substrates and at different depths, and populations were characterised by varying mean shell sizes (e.g., Greenhill 1965, Allmon *et al.* 1994, Bax and Williams 2001, Bax *et al.* 2003, Beaman *et al.* 2005). However, no detailed analyses on the relationship between *M. roseus* and these environmental variables have been carried - out in any of these studies.

Some past descriptions of the environmental preferences of *M. roseus*, based solely on the abundance of shells, may be incorrect, as the position of the operculum well within the shell cavity makes it difficult to determine whether the animal is alive or dead without destroying it. Summerson *et al.* (2007) noted that identifying whether establishment has occurred is difficult due to complications associated with delineating between live and dead animals. Therefore differentiating between live or dead *M. roseus* is likely to be an important factor in understanding the distribution of this species.

The aims of this study were to fill gaps in knowledge of the relationship between population characteristics of *M. roseus*, such as density, shell size, the proportion of live to dead animals, and the environmental attributes of its habitat.

A summary of the available information on the ecology and biology of turritellids was gathered by Allmon (2011). The report showed that there is relatively limited information on natural history. Turritellids in general were described to be a significant marine macrofossil group and currently well distributed in the world. They are marine organisms, do not tolerate brackish or estuarine environments, and are found mostly in water below 20 °C. Most are suspension feeders, believed

mainly to have a planktonic larval stage. Typical features of this group of gastropods are the characteristic high - spired shell consisting of round to angulated whorls, ranging from approximately 10 to 175 mm.

Information on the abiotic environment favoured by turritellids is very general and limited. This group of gastropods seems to be found in a variety of environments. However, from studies on turritellids (Allmon 2011) and *M. roseus* (Knight 1974, Allmon *et al.* 1994, Hayward *et al.* 1997, Bax *et al.* 2003), they are essentially sedentary, spending most of their time stationary in their feeding orientation and buried shallowly in the sediment. The substrate groups gravel, sand, and mud were described as being the major substrate types characterising their habitat. Therefore, this study focused on assessing whether *M. roseus* distribution was correlated with these substrate types. Diversity in nutrient levels and water depth also have been described as being characteristic of the turritellid abiotic environment (Allmon 2011).

The shell sizes of *Maoricolpus roseus* populations have been observed to vary between geographical locations (Bax *et al.* 2003). This variability in population shell sizes is probably related to differences in environmental attributes between locations (Chapter Four), or age of populations in turritellids (Allmon 2011). The suitability of a habitat can be reflected in the different shell sizes of a population (Garcia-March *et al.* 2007, Vianna and Avelar 2010). This study therefore also assessed if there was any emerging patterns between the shell sizes of *M. roseus* populations and abiotic data.

The proportion and distribution of both live and dead *M. roseus* was investigated first to determine whether density and distribution based on total shell counts are representative of live animals. Additionally, the distribution of live animals and shells from dead animals was compared at two spatial scales to assess their spatial variability. Next, to better understand environmental preferences which influence the distribution of *M. roseus* and, therefore to improve the capacity to predict further spread, the distribution, density and shell size of *M. roseus* were assessed in relation to the abiotic variables fraction of gravel, sand, mud, TOC, and water depth.

## **2.3 Materials and methods**

### **2.3.1 Study sites and sampling procedures**

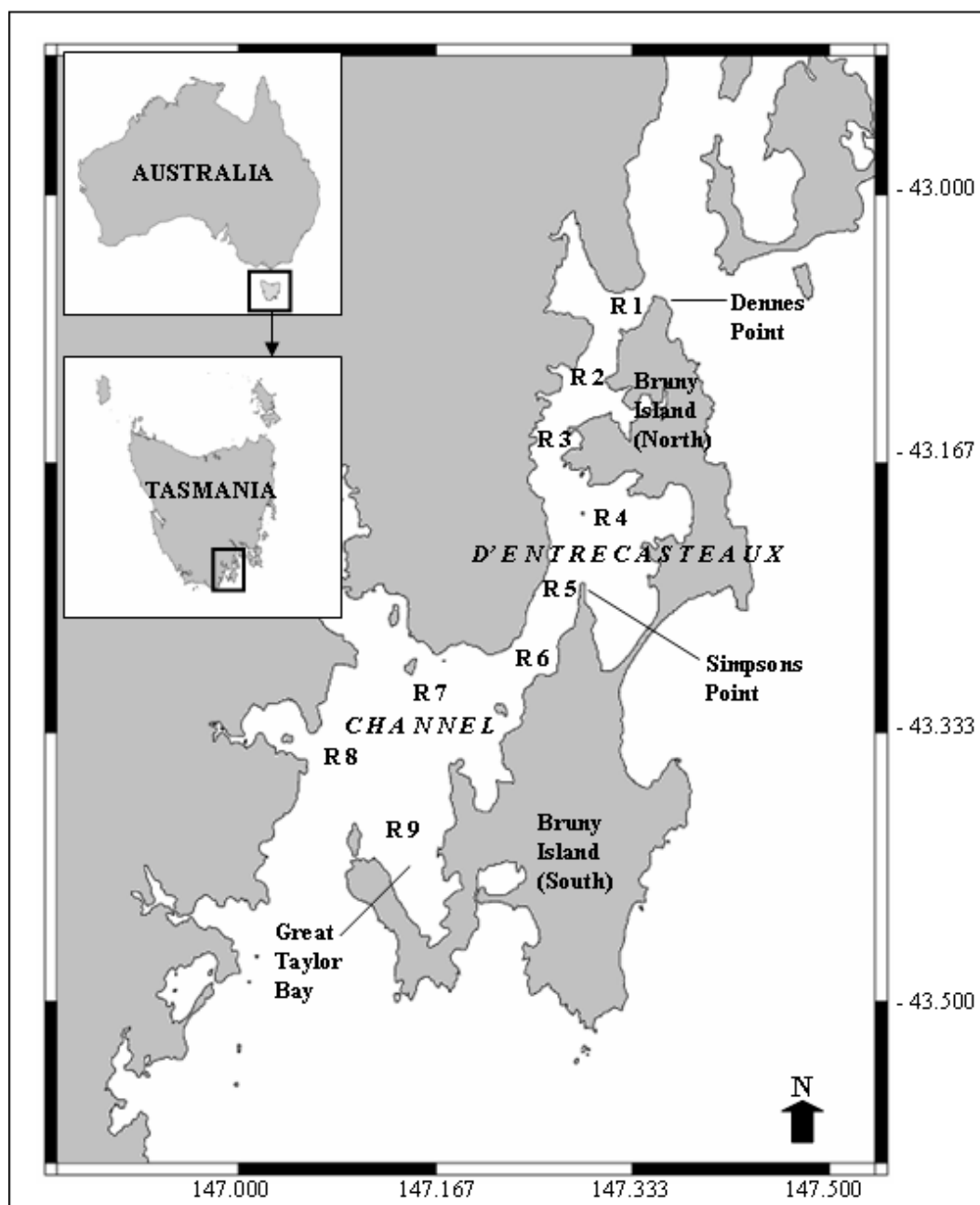
Sampling was conducted between February and May 2004 at 60 sites in the D'Entrecasteaux Channel. *Maoricolpus roseus* was first observed in this area in the 1920's (Greenhill 1965, Paul 1979) and has been present in the region since.

The exact location of the initial invasion is not known but thought to be in the lower Derwent estuary. It is not known if repeated invasions have occurred, and details of the subsequent extension of the range of *M. roseus* into the D'Entrecasteaux Channel are not known. However, the area has high densities of *M. roseus* at various locations and it is assumed that this area is in close proximity to the initial point of entry of this invasive species (Bax *et al.* 2003). The area is known for the presence of other introduced species (e.g., European clam *Corbula gibba* and East Asian clam *Theora lubrica*), however *M. roseus* has one of the highest abundances (Edgar *et al.* 2005b).

The D'Entrecasteaux Channel is located in the south east of Tasmania between the mainland of Tasmania and Bruny Island (Figure 1), and the channel is open to the ocean at the northern and southern end. The main area of the channel is primarily characterised by oceanic influences (e.g., salinity, temperature, oxygen; Wild-Allen *et al.* 2005), and water temperatures generally vary between 9 °C and 17 °C (Probst and Crawford 2008). The exception is the area where the Huon Estuary connects to the D'Entrecasteaux Channel near the southern limit east of the channel. Under high flow conditions of the Huon River, this salt wedge estuary can be characterised by freshwater conditions close to the entry to the channel (Herzfeld *et al.* 2005). The D'Entrecasteaux Channel supports some local aquaculture and recreational boating, and in some areas catchment run-off can have high nutrient levels after heavy rain fall (Wild-Allen *et al.* 2005). When selecting the sampling sites, attention was given to not locate them in close proximity to estuarine outlets and any aquaculture facilities.

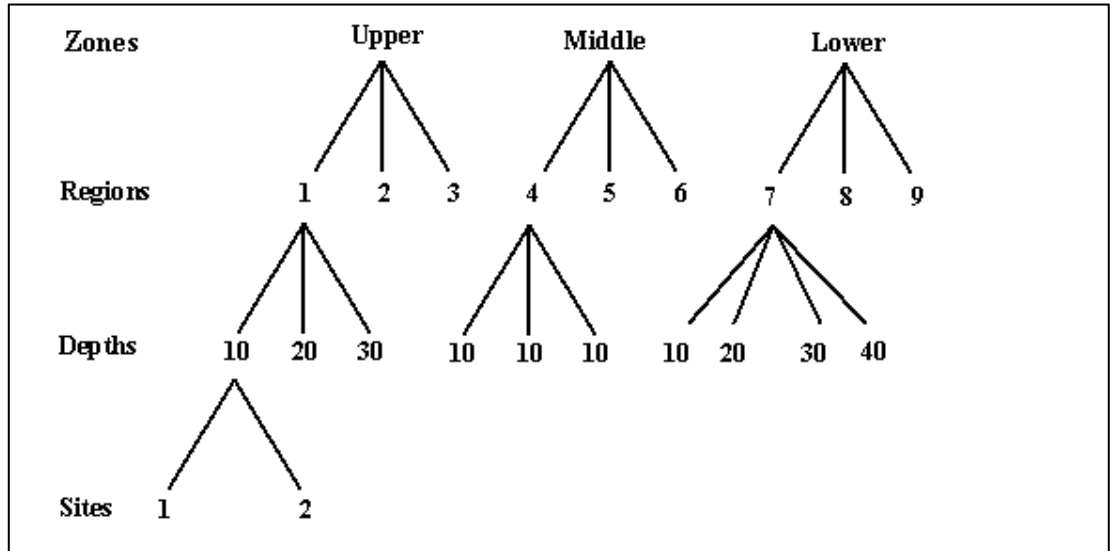
It is assumed that the distribution of *M. roseus* in the area has increased since its introduction in the 1920's, however, the exact extend of the invasive rate and specific distribution is not known. Therefore sampling sites were distributed based on a nested sampling design (Figure 2), this also aimed to cover for potential spatial heterogeneity of the variables (Andrew and Mapstone 1987, Underwood 1997). The D'Entrecasteaux Channel was divided from north to south (Dennes Point to Great Taylor Bay respectively (Figure 1), into nine regions, approximately five square kilometres in area and spaced approximately four kilometres apart. Regions were grouped into three standard zones base on their location within the channel (upper, middle, and lower). Each region contained sites that were approximately one

kilometre apart. Due to differences in the bathymetry in the surveyed area, sites were distributed according to the available depth in each zone as follows: each region in the upper zone was composed of six sites, with two sites in the 10, 20, and 30 m depth categories; each region in the middle zone was composed of six sites with all sites in the 10 m depth category; and each region in the lower zone was composed of eight sites, with two sites each in the 10, 20, 30, and 40 m depth categories. Density and shell size of *M. roseus*, and data on sediment particle size distribution (PSD) and total organic carbon (TOC) were collected at each site.



**Figure 1** D'Entrecasteaux Channel with outlined sampling regions (R) 1 - 3 = upper zone, regions 4 - 6 = middle zone, and regions 7 - 9 = lower zone. (Map coastline based on NGDC (2007))





**Figure 2** *Maoricolpus roseus* sampling design used for the D’Entrecasteaux Channel (Tasmania) survey.

### 2.3.2 Fauna sampling procedures

Information on the density of *M. roseus* was collected from video transects and a dredge towed along the same 100 m transect at each site. The density of *M. roseus* was calculated from video data while the dredge provided information on the proportion of live to dead animals. *Maoricolpus roseus* density was not directly calculated from the dredge samples, as pilot studies demonstrated that the dredge may fill before sampling the entire transect, which would introduce bias in density estimates. In determining the proportion of live animals from dredge samples it was assumed that the fraction of live *M. roseus* in the dredge did not change along the length of that transect.

#### *Video samples*

Video recordings of the 100 m transect was carried out prior to dredging of the transect at each site. The video camera was attached to an aluminium frame

providing a field of view of 0.6 m<sup>2</sup> and benthic images were recorded along the transect. *Maoricolpus roseus* density was subsequently estimated in the laboratory from an average of ten random still images taken from the transect using digital image analyses via IMDA software (Wilcox *et al.* 2002). The proportion of live *M. roseus* calculated from dredge samples was used in conjunction with the video data to estimate density of live *M. roseus* for each site.

Where shell assemblages of *M. roseus* accumulated in layers, only the top layer (approximately 100 mm) was considered as pilot studies conducted with the dredge demonstrated that it collected samples from this top layer only. A pilot study conducted in the D'Entrecasteaux Channel via SCUBA diving demonstrated that if any live *M. roseus* were present (as opposed to empty shells), they tended to occur mainly in this layer (ANOVA:  $F_{1,22} = 634.15$ ,  $P < 0.01$ ). Live *M. roseus* essentially laid horizontally on the seafloor or partially burrowed within this top layer of sediment. The partially burrowed animals normally had the wider part of the shell exposed with extruded operculum. This was similar to observations by Allmon (1994).

#### *Dredge samples*

The dredge used in this study was an open - box tooth - type dredge (approximate volume of 1.2 m<sup>3</sup>) with a bottom and a top to back mesh size of 10 mm and 2 mm, respectively. This mesh size was similar to that used in other studies on benthic fauna (e.g., Schlacher and Wooldridge 1996, Tanaka and Leite 1998, Callaway *et al.* 2002, Ferraro and Cole 2004). A rope - length of twice the water depth at each sampling site was utilised on the dredge and a vessel speed of 2 to 3 knots was

maintained, ensuring maximum sampling performance as described by Eleftheriou and Holme (1984). Where samples retrieved were larger than 5 kg, the sample was wet weighed, and a 2.5 kg random sub - sample was collected for processing. Sub - sampled data were subsequently adjusted to provide a total density. Samples were frozen until processing in the laboratory, which consisted of further washing the sample through a 2 mm sieve and breaking open *M. roseus* shells to determine if they contained a live animal. Additionally the total length of shells was measured (1 mm scale) from 100 random selected animals at each site when available.

### **2.3.3 Abiotic data sampling procedures**

Sediment samples were collected using a Van Veen grab (approximate volume of 0.30 m<sup>3</sup>) at the beginning and end of each transect. From each grab sample two replicate cores, each 70 mm in diameter and 100 mm in depth, were taken and frozen in the laboratory for later analyses of particle size distribution (PSD) and total organic carbon (TOC).

Particle size distribution was determined using a standard method of substrate grain size analysis (Buchanan 1984) by wet sieving samples through a nested series of sieves (0.063, 0.125, 0.25, 0.5, 1, 2, and 4 mm). The processed material included organic and inorganic fractions. A pilot analysis used each individual sieve groups, and the primary size categories used for data analyses were fractions of gravel (> 2 mm), sand (2 - 0.063 mm), and mud (< 0.063 mm). Total Organic Carbon of the sediment was calculated by loss on ignition at 500 °C (Greiser and Faubel 1988), and expressed as a percentage of the total weight of sample (Kingsford and Battershill 1998).

#### **2.3.4 Data analyses**

Initially, the total number of *M. roseus* was plotted against the proportion of live *M. roseus* to assess whether *M. roseus* total numbers were a suitable proxy for live animals. The live and dead *M. roseus* spatial distribution was analysed using a nested ANOVA, with zones and regions as factors. Sites were not entered as a factor in this analysis as only one observation per site was available. Also, the 40 m depth sites were not included in this analysis to allow for a balanced design. The percentage contribution to the total variance for zones and regions in the ANOVA was calculated and compared to assess the relative variability of the data at both levels (Variance Component Analysis (VCA)).

As the above analyses demonstrated that total *M. roseus* (including live and dead animals) were not a suitable proxy for live *M. roseus*, the remaining data analyses only used live animal numbers as the aim of this study was to describe the habitat of *M. roseus* without the interference of dead animals.

The distribution of live *M. roseus* in relation to abiotic variables was assessed. An initial pilot analysis was conducted with each individual grain size series processed. However no significant relationship occurred. Correlations of live *M. roseus* with the environmental variables gravel %, sand %, mud %, TOC %, and water depth (m) were assessed using Spearman tests (exploratory plots demonstrated non - linear associations) (Dytham 2003).

The multivariate relationship between *M. roseus* density and environmental variables was investigated using a Principal Coordinates Analyses (PCO) plot produced via the PERMANOVA procedure (Anderson *et al.* 2008). The analysis combined all abiotic variables on the basis of a similarity matrix to calculate their contribution to the distribution of the data. Live *M. roseus* were then superimposed on the PCO ordination plot to show any trends of live *M. roseus* density to the abiotic variables. This was followed by a BIOENV procedure (Clarke and Gorley 2006) to test the association between live *M. roseus* density and the abiotic environmental variables.

Finally, the length frequency distribution of *M. roseus* shells was plotted and Kolmogorov - Smirnov tests (Quinn and Keough 2002) were carried out to assess the differences in relation to substrate type categories (sand and mud), TOC, and water depth. Gravel was not included in this analysis as there were no animals available in sites belonging to this substrate type category. Data analyses were carried out on raw data (1 mm scale) and length frequency distributions were plotted in 5 mm length categories.

Univariate and multivariate statistical analyses were undertaken using the SPSS software package (SPSS 2008) and PRIMER (Clarke and Gorley 2006) respectively. Before any statistical analyses were carried - out all data variances were tested for normality of distribution and homogeneity of variances (Sokal and Rohlf 2003) via Kolmogorov - Smirnov and Levene tests respectively (Dytham 2003). Data were transformed accordingly if heterogeneous (Underwood 1981). *M. roseus* density data were log transformed and abiotic percentage data were arcsine transformed. For

the multivariate analysis, the abiotic variables were normalised and biotic data were fourth root transformed.

## **2.4 Results**

### **2.4.1 Distribution of live *M. roseus* and shells from dead animals.**

Abiotic and biotic data are provided in Table 1. From the 60 sites surveyed *M. roseus* (including live and dead animals) were present at 57 sites and live *M. roseus* were recorded at 52 sites. Regions one and six in the upper and middle zones of the D'Entrecasteaux Channel had the highest densities of live *M. roseus* (Figure 3). While *M. roseus* shells were broadly distributed across the surveyed area, there was no consistent pattern between the total number of shells and the proportion of live *M. roseus* ( $y = 12.076x + 27.337$ ,  $R^2 = 0.082$ ) (Figure 4). The data variances (VCA results) of *M. roseus* spatial distribution showed there were significant differences in the density distribution of both live and dead *M. roseus* at the level of zones and regions. In general, dead *M. roseus* density had greater variability between zones, whereas live *M. roseus* density varied more at the smaller regional level (Table 2). Also, a large proportion of the total variance of live *M. roseus* was from the residual variance, which indicates there was patchiness at the smaller spatial scale of sites. The non - significant correlation between the total number of shells and the proportion of live *M. roseus* and the differences in distribution between live and dead animals demonstrated that the total *M. roseus* shell density should not be used as a proxy for live *M. roseus* density. Therefore, total *M. roseus* shells and dead *M. roseus* were not included in further data analyses, as the aim of this study was to describe the habitat of live *M. roseus*.

**Table 1** Particle Size Distribution (PSD), Organic Carbon (TOC), Depth, and *M. roseus* density at sampling sites in each region.

Site	Region	PSD			TOC (%)	Depth (m)	<i>Maoricolpus roseus</i> density	
		Gravel %	Sand %	Mud %			Total (m <sup>-2</sup> )	Live (m <sup>-2</sup> )
1	1	1.2	97.2	1.6	4.5	10	8	3
2	1	16.9	68.8	14.4	8.2	11	2100	1807
3	1	12.2	59.6	28.2	11.7	19	223	106
4	1	0.2	11.4	88.3	13.2	30	210	151
5	1	2.1	45.1	52.8	10.4	20	163	104
6	1	1.0	52.2	46.8	9.9	30	581	396
7	2	7.2	64.3	28.5	9.2	31	285	206
8	2	0.7	15.5	83.7	9.9	20	41	2
9	2	2.0	15.5	52.0	9.5	28	51	14
10	2	4.3	81.9	13.8	4.8	10	105	50
11	2	19.6	60.4	20.0	8.5	10	66	40
12	2	0.1	6.4	93.5	11.8	20	45	21
13	3	3.0	68.7	28.3	7.5	30	54	24
14	3	6.4	30.8	62.8	7.6	10	26	1
15	3	1.0	20.9	78.2	9.7	10	12	0
16	3	2.4	63.2	34.3	8.7	19	162	44
17	3	23.9	59.6	16.5	6.5	30	43	0
18	3	1.8	54.2	44.0	7.4	20	35	7
19	4	0.5	84.7	14.8	3.8	10	6	5
20	4	0.4	90.7	8.9	3.4	10	8	5

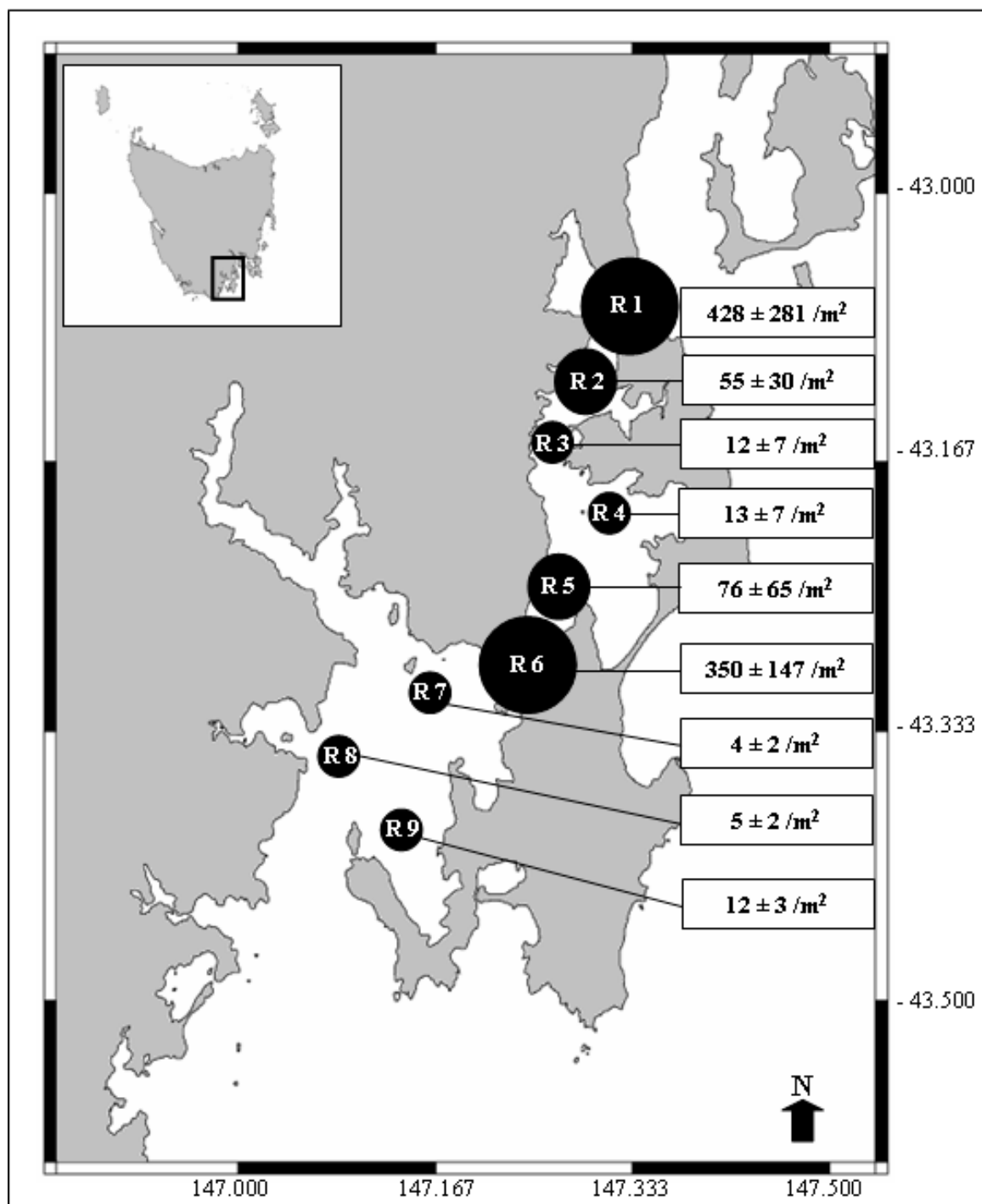
**Table 1 (continued)** Particle Size Distribution (PSD), Organic Carbon (TOC), Depth, and *M. roseus* density at sampling sites in each region.

Site	Region	PSD			TOC (%)	Depth (m)	<i>Maoricolpus roseus</i> density	
		Gravel %	Sand %	Mud %			Total (m <sup>-2</sup> )	Live (m <sup>-2</sup> )
21	4	0.9	81.7	17.4	5.9	11	62	14
22	4	1.9	79.2	18.9	4.6	11	54	46
23	4	4.0	85.2	10.8	2.8	10	12	4
24	4	0.8	94.4	4.8	2.4	9	9	5
25	5	17.6	77.5	4.9	3.4	10	15	0
26	5	3.7	92.1	4.2	4.2	12	84	36
27	5	13.9	83.7	2.3	4.9	10	23	1
28	5	10.6	81.9	7.5	8.7	13	883	404
29	5	36.1	61.8	2.1	3.9	10	45	6
30	5	5.0	93.4	1.6	6.7	10	45	10
31	6	14.2	82.1	3.6	5.7	10	167	52
32	6	8.8	83.9	7.3	10.2	13	1065	231
33	6	2.6	87.9	9.5	5.5	10	932	786
34	6	4.8	82.0	13.3	6.0	13	932	816
35	6	3.4	92.1	4.5	6.4	10	285	204
36	6	0.5	92.4	7.2	4.1	10	10	8
37	7	0.2	89.8	10.0	3.6	12	23	18
38	7	3.5	91.0	5.4	3.7	12	6	3
39	7	0.8	3.2	95.9	13.1	30	3	0
40	7	0.1	77.9	22.0	3.7	20	8	7

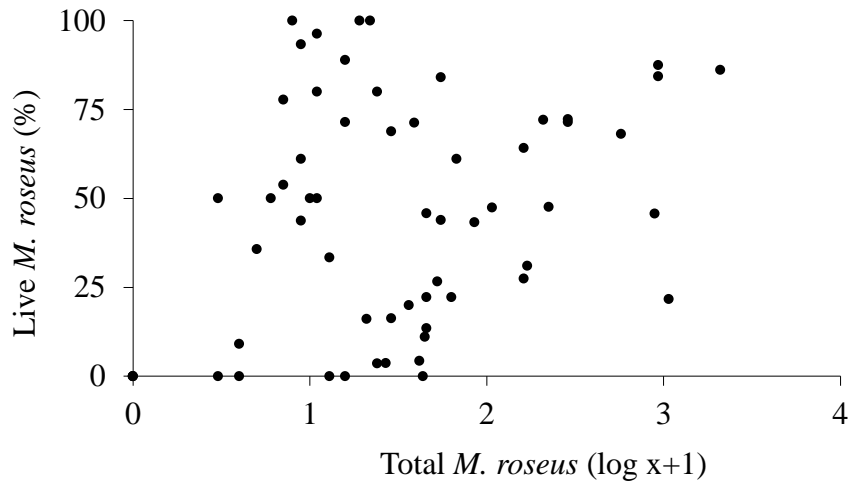


**Table 1 (continued)** Particle Size Distribution (PSD), Organic Carbon (TOC), Depth, and *M. roseus* density at sampling sites in each region.

Site	Region	PSD			TOC (%)	Depth (m)	<i>Maoricolpus roseus</i> density	
		Gravel %	Sand %	Mud %			Total (m <sup>-2</sup> )	Live (m <sup>-2</sup> )
41	7	0.1	14.6	85.2	15.2	40	0	0
42	7	0.3	70.8	28.8	6.7	21	5	3
43	7	2.1	68.6	29.3	6.7	28	44	5
44	7	0.1	13.4	86.5	15.5	40	2	0
45	8	0.2	96.7	3.1	2.8	10	10	5
46	8	7.1	90.4	2.4	3.4	10	7	7
47	8	1.0	64.5	34.5	13.1	39	2	1
48	8	2.6	88.4	9.0	8.5	20	15	13
49	8	0.3	94.7	5.1	3.8	29	20	3
50	8	1.6	94.4	3.9	4.1	20	3	0
51	8	2.9	85.1	12.0	8.7	30	15	11
52	8	0.5	85.8	13.6	5.8	40	4	1
53	9	2.1	34.8	63.1	12.4	30	28	5
54	9	0.1	14.0	86.0	13.4	40	0	0
55	9	0.7	66.7	32.6	6.3	27	38	27
56	9	0.2	90.8	8.9	2.3	20	21	21
57	9	1.2	20.1	78.8	11.8	39	0	0
58	9	0.1	97.0	2.9	2.1	8	18	18
59	9	8.4	89.0	2.6	5.2	10	10	10
60	9	0.2	86.3	13.5	4.1	20	28	19



**Figure 3** Density of live *M. roseus* in the D'Entrecasteaux Channel. Sites grouped by regions 1 to 9. Sizes of bubble plots are relative to *M. roseus* densities.



**Figure 4** Proportion of live *M. roseus* versus the density of total *M. roseus* (density  $\text{m}^{-2}$ ).

**Table 2** Spatial data variance component analysis (VCA) results for dead and live *M. roseus* distribution.

	DF	Expected mean square	Estimated variance component	% of total variance	P
<i>Dead M. roseus</i>					
Zone	2	8.05	0.41	55.84	< 0.001
Region	6	0.66	0.07	9.15	< 0.05
Residual	51	0.26	0.26	35.01	
Total	59		0.74		
<i>Live M. roseus</i>					
Zone	2	3.76	0.10	12.28	< 0.001
Region	6	2.02	0.27	34.01	< 0.001
Residual	51	0.42	0.42	53.71	
Total	59		0.78		

#### **2.4.2 Data relationships**

##### *Distribution of M. roseus and abiotic characteristics*

The deeper upper and lower zones of the D'Entrecasteaux Channel were characterised by higher mud content and higher percentage of TOC, while the middle part of the channel had a higher amount of coarse material and lower TOC (Table 3). Particle size distribution for the collected samples were generally classified as well sorted, based on Blott and Pye (2001).

No significant relationship occurred between live *M. roseus* densities and any individual abiotic variable (Table 4). The multivariate PCO produced a component factor combination PC 1 and PC 2 that accounted for 65.8 % and 20 % of data variability respectively (Figure 5). From the PCO plot it is clear that the proportion of sand was the variable that contributed most to the distribution of live *M. roseus* with greater densities on sand. There was also an increase in TOC with the increase in percentage mud and water depth. The BIOENV analysis demonstrated a significant correlation between the abiotic variables and live *M. roseus* densities (BIOENV:  $\rho = 0.35$ ,  $p < 0.001$ ).

**Table 3** Fractions of gravel, sand, mud, TOC, and water depth (mean  $\pm$  SE) by zones in the D’Entrecasteaux Channel.

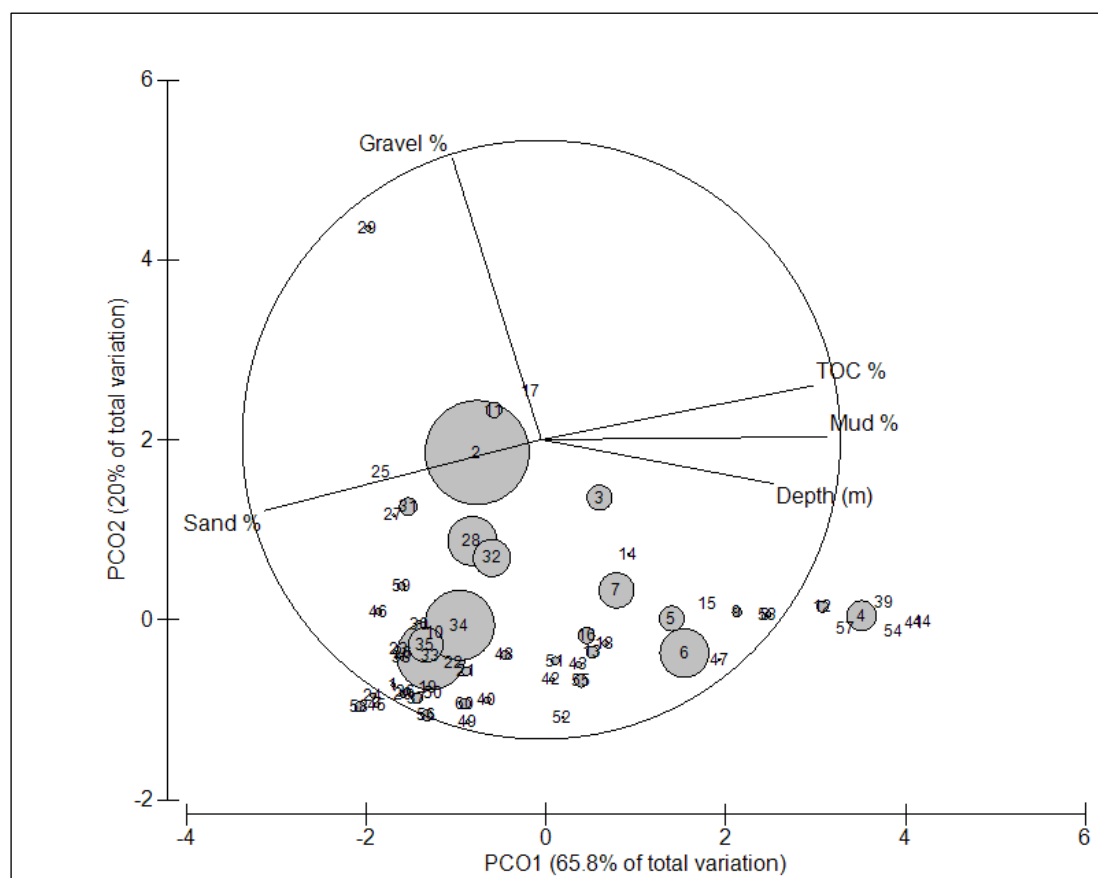
	Gravel %	Sand %	Mud %	TOC %	Depth (m)
Upper Zone	7 $\pm$ 1.7	49 $\pm$ 6.2	44 $\pm$ 6.6	8.8 $\pm$ 0.54	20 $\pm$ 2.0
Middle Zone	8 $\pm$ 2.1	85 $\pm$ 1.8	7 $\pm$ 1.2	5.1 $\pm$ 0.47	10 $\pm$ 0.0
Lower Zone	2 $\pm$ 0.4	68 $\pm$ 6.5	30 $\pm$ 6.6	7.3 $\pm$ 0.9	25 $\pm$ 2.3

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**Table 4** Correlation analyses between live *M. roseus* density and abiotic factors (gravel %, sand %, mud %, TOC %, and water depth). Table outlines Spearman correlation coefficients. None of the relationships were statistically significant.

	Gravel %	Sand %	Mud %	TOC %	Depth (m)
Live <i>M. roseus</i>	0.21	0.10	-0.11	0.06	-0.15

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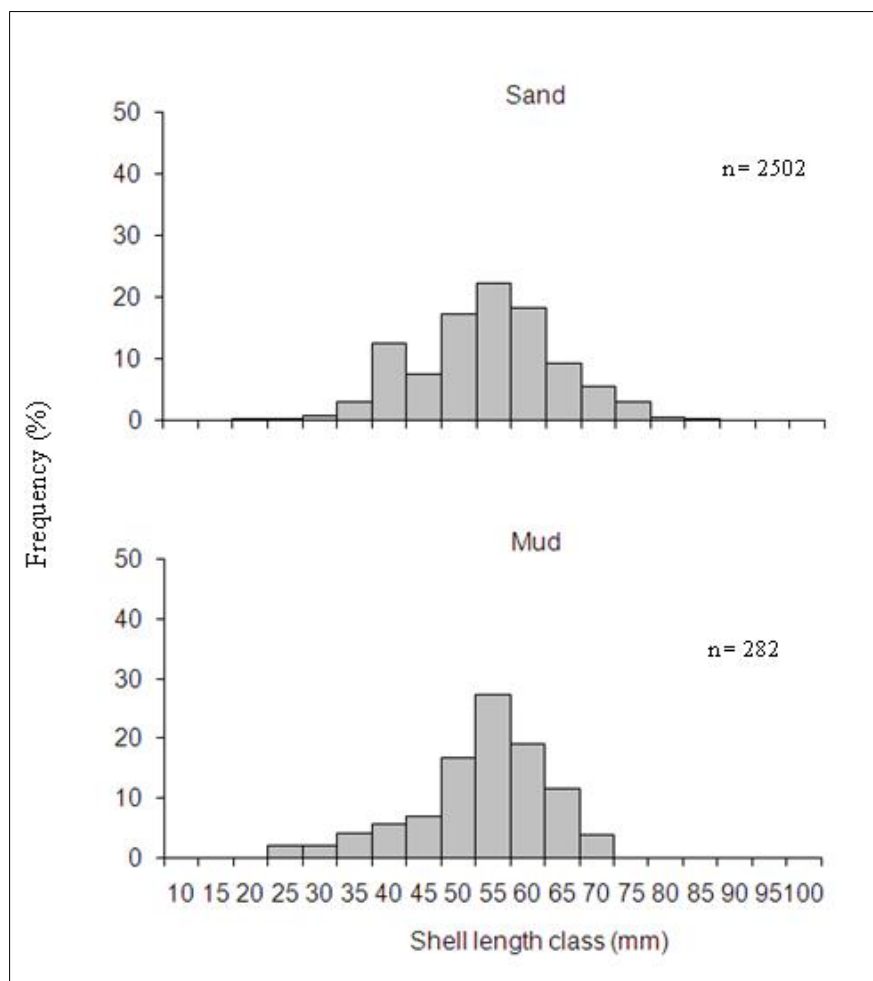
**Figure 5** Multivariate Principal Coordinate Analyses (PCO) with substrate fractions (gravel, sand, and mud), TOC, and water depth (m). Live *M. roseus* for each site is shown as bubble plots relative to their density. Density description for each site is listed in Table 1. Components PC1 and PC2 accounted for 65.8 % and 20 % respectively of the total variation across the abiotic variables.

### *Maoricolpus roseus* shell length

Information on shell size was collected from 52 sites in the D'Entrecasteaux Channel. Total lengths ranged between 20 mm and 85 mm ( $n = 2784$ ). *Maoricolpus roseus* in sand and mud had similar shell length frequency distribution, with a mean of  $51.5 \pm 0.2$  (SE) mm and  $51.3 \pm 0.6$  (SE) mm respectively (Figure 6). However, in the substrate type mud, shells measured were not larger than 70 mm compared to 85 mm in sand.

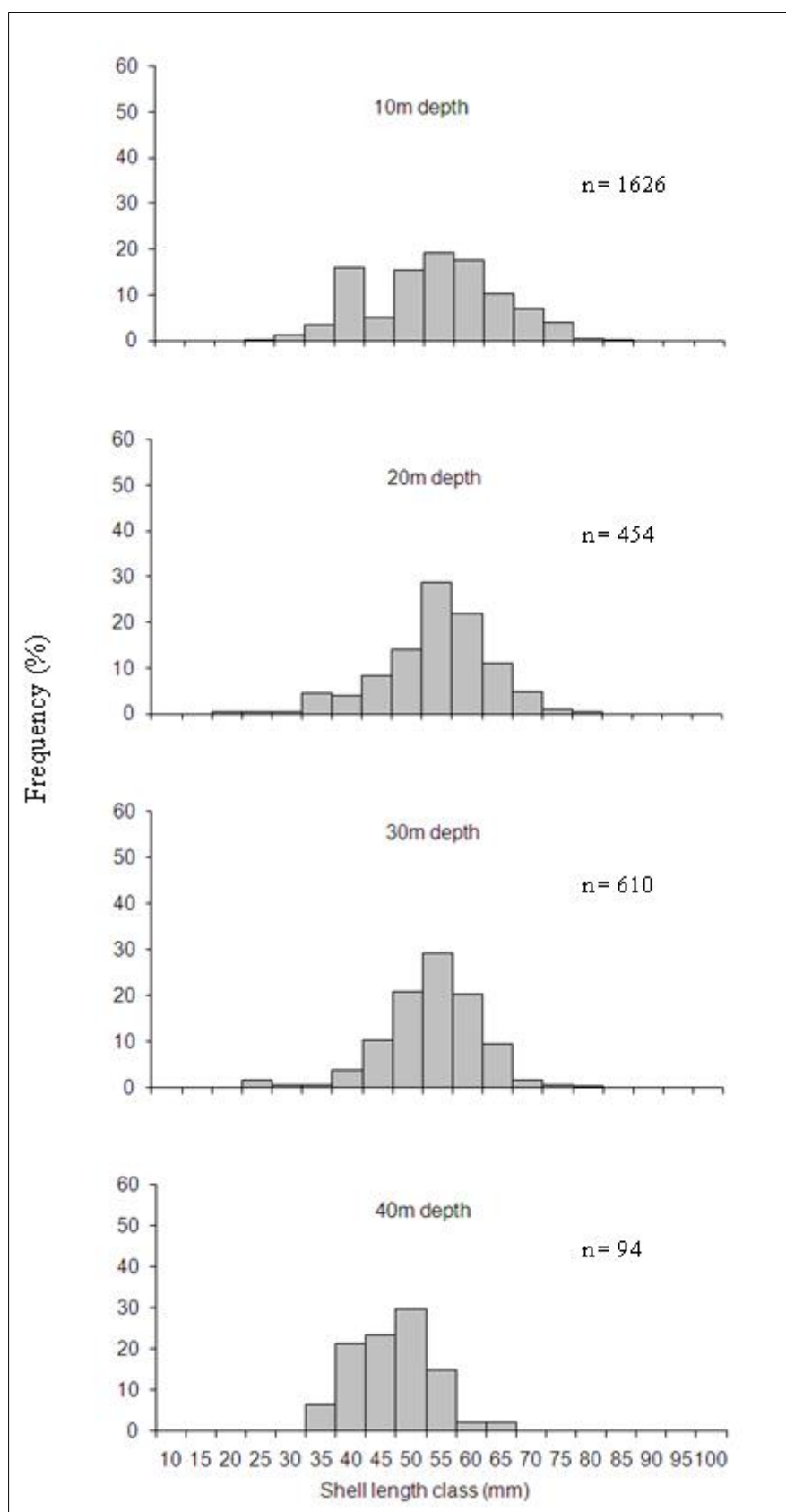
A comparison of shell lengths with depth showed that *M. roseus* collected at 40 metres depth were significantly smaller than those at the shallower sites (Kolmogorov - Smirnov:  $Z = 4.38$ ,  $P < 0.001$ ,  $n = 2784$ , Figure 7). *Maoricolpus roseus* shells ranged between 35 - 65 mm (mean =  $45.1 \pm 0.6$  (SE) mm) and between 20 - 85 mm (mean =  $52.3 \pm 0.2$  (SE) mm), respectively. For the shallow sites at 10 m depth, *M. roseus* were also more evenly spread over the 30 to 60 mm size classes than at greater depths.

Total Organic Carbon was grouped into the low ( $< 10\%$ ) and high ( $\geq 10\%$ ) groups based on previous studies (e.g., Simonini *et al.* 2004, Afli *et al.* 2008, Borja and Dauer 2008). Both low and high groups had animals in the range of 25 to 85 mm (Figure 8) and were not significantly different in their length frequency distributions.

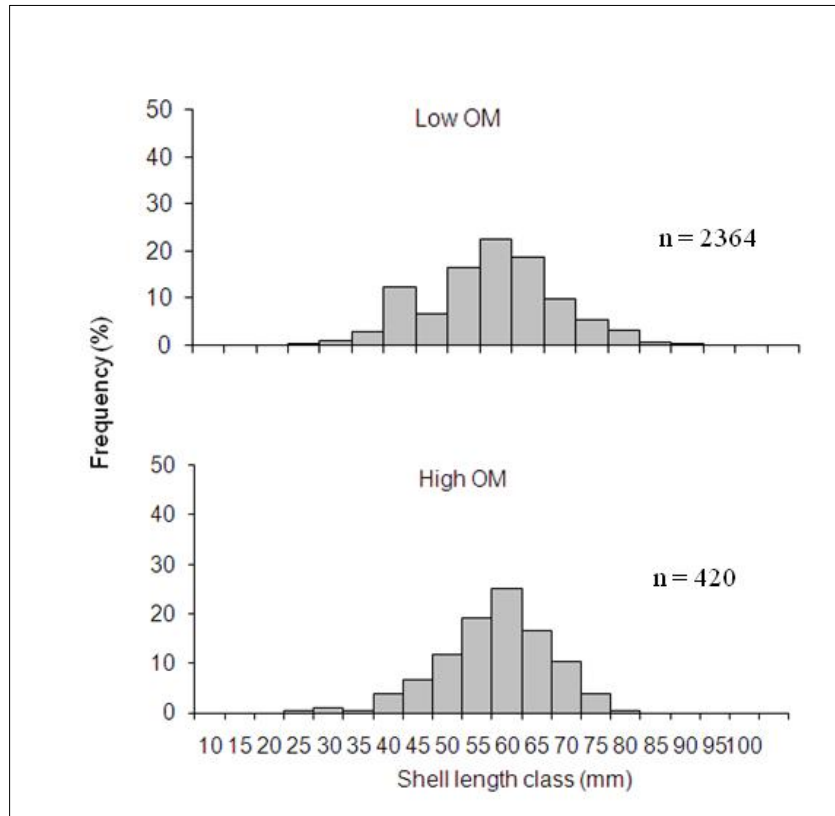


**Figure 6** *Maoricolpus roseus* size frequency distribution in the D'Entrecasteaux Channel for substrate type sand and mud.





**Figure 7** *Maoricolpus roseus* size frequency distribution in the D'Entrecasteaux Channel for depths 10, 20, 30, and 40m.



**Figure 8** *Maoricolpus roseus* size frequency distribution in the D'Entrecasteaux Channel for organic matter groups low (< 10 %) and high ( $\geq$  10 %).

## 2.5 Discussion

Results on abiotic characteristics demonstrated that the deeper parts of the D'Entrecasteaux Channel were generally characterised by sites with finer substratum and higher proportion of organic material. This is likely associated to depositional environments. The deposition of smaller particle sizes with an increase in depth is well documented in coastal geomorphology (e.g., Komar 1976, Thom 1984, Dyer 1986). These environments are generally also characterised by higher organic matter content (e.g., Whitlatch 1981, Snelgrove and Butman 1994, Woodin 1999, Reise 2002).

The survey demonstrated that *M. roseus* were present at most of the sites confirming its wide distribution in the D'Entrecasteaux Channel. The distribution of live *M. roseus* followed a similar pattern to that observed in other studies with the variability generally increasing at smaller spatial scales (e.g., Morrissey *et al.* 1992, Thrush *et al.* 1994, Edgar and Barrett 2002, Chapman and Underwood 2008). At the smaller scale factors such as localised population interaction, local hydrodynamics, and variability of sediments types normally have a relative greater impact on population distribution (Thrush 1991). However, the distribution of dead *M. roseus* differed to live *M. roseus*. Shells from dead *M. roseus* can build up over large areas (Beaman *et al.* 2005, Nicastro *et al.* 2009), due to large scale coastal hydrodynamics such as tidal currents and action of waves. *M. roseus* shell deposition can also occur by large groups of hermit crabs moving shells around (Reid 2004). However, the impact of the hermit crabs is probably relatively smaller.

The study acknowledges that the nested ANOVA analysis was limited by the geographical location of the regions and the zones. Locations were set-up in a spatial continuum manner (Figure 1). Also, not all depth categories were available throughout the whole surveyed area. However, the test was considered suitable to compare the relative distributions of live animals and shells from dead animals.

The variability in the distribution of live and dead *M. roseus*, suggests that counts of total shell are therefore not a good proxy for assessing the distribution of *M. roseus*. Thus some previously identified distribution patterns of live *M. roseus* based on total shell counts are likely to be inaccurate. Future studies investigating the variables

driving the distribution of *M. roseus* at different scales should differentiate between live and dead animals, and concentrate on collecting data on live *M. roseus*.

When investigating the univariate relationship between live *M. roseus* and the abiotic data, no significant association occurred with any individual variable. However, the multivariate PCO outputs showed a relative tendency of higher densities of live *M. roseus* at the sites characterised by sand. The PCO plot was supported by the multivariate BIOENV analysis, which demonstrated that a combination of abiotic variables was significantly correlated to live *M. roseus* densities. The poor univariate correlation between faunal distribution and abiotic factors is not uncommon. Many of the variables driving benthic fauna distributions are indirect (Snelgrove and Butman 1994) and therefore a combination of factors considered by the multivariate analyses can identify relationships (Barros *et al.* 2001). *Maoricolpus roseus* demonstrated a pattern typical for a suspension feeder of higher densities on coarser sandy environments. A strong relationship between benthic suspension feeders and these environmental characteristics is common and is often associated with the relative stronger water flow promoting larger nutrient availability within the water column (Sanders 1958, Hawkins *et al.* 1989, Shimeta and Jumars 1991, Riisgard and Larsen 2001, Gardner 2002). The sites in regions one and six with the highest densities of *M. roseus* were characterised by coarser substrate at shallower water depths. These areas in the D'Entrecasteaux Channel were noted to have relative higher water current levels by Mitchell and Crawford (1995).

However, some sites with finer substrate also had relative high numbers of *M. roseus*, and these sites tended to occur in areas adjacent or close to sites with the

highest *M. roseus* densities. This high number in the finer substrate sites adjacent to sandy sites could be due to a density - dependence effect. Mollusc responses to population density have been largely attributed to competition for feeding resources (e.g., Connell 1961, Underwood 1978, Boaventura *et al.* 2003). This density - dependence relationship is further investigated in Chapter Three.

*Maoricolpus roseus* thus appears to have the versatility to survive in different substrate types if needed. This is likely related to its anatomy. Turritellids have a feeding mechanism that filters suspended particulate matter through a specialised anatomical arrangement of their water current system (Graham 1938, Fretter and Manly 1979). This filtering mechanism is composed of a curtain of tentacles set close along the mantle edge acting as a sieve. They also possess a sorting mechanism in a series of folds on the stomach wall to allow sorting of material into large and small particles. Turritellids have a rapid rate of water flow capability and they also have an increased gill surface and large surface area where gas exchanges occur during the respiration process (Allmon *et al.* 1994). Filtration rates of *M. roseus* were also described to be relatively constant in different environments between the dark, the light, and the low and high water temperatures (Scott 1997). These features suggest that *M. roseus* possesses the capability of surviving in a range of different environments, including the optimal coarser substrate to the finer particle substrate characterised by lower water currents.

Past surveys in New Zealand also demonstrated that *M. roseus* occurs over a range of substrate types, characterised by a combination of coarse substrates such as sand (Grange 1979, Rainer 1981), mud (McKnight 1969), or a variety of substrates from

fine to coarse (Allmon 1988, Allmon *et al.* 1994, Abraham *et al.* 2007). Similar distributions have been observed in Australia (Greenhill 1965, Allmon *et al.* 1994, Bax and Williams 2001, Bax *et al.* 2003, Spruzen and Richardson 2008), although past studies did not statistically compare the abundances among different substrates. These published descriptions of *M. roseus* habitat are also possibly incorrect, as the surveys did not differentiate between live and total animals.

*Maoricolpus roseus* length frequency analyses demonstrated that in general there were a relatively higher number of larger animals at the shallower depths (< 30m) in the D'Entrecasteaux Channel. The shallower environments in the Channel generally have higher oxygen levels (Wild-Allen *et al.* 2005) and higher nutrient concentrations in the water column (Butler *et al.* 2000, Macleod and Helidoniotis 2005, Wild-Allen *et al.* 2005) which can affect population growth of suspension feeders (Bayne and Newell 1983, Bayne and Hawkins 1990, Vianna and Avelar 2010). From laboratory studies *M. roseus* had faster growth rates in environments with higher concentration of planktonic microalgae (Scott 1997). Hence, the combination of these factors probably influenced the proportion of larger *M. roseus* in the shallower parts of the D'Entrecasteaux. No significant differences in the size categories occurred related to substrate type or TOC. While both variables can have an impact on growth of suspension feeding molluscs (Garcia-March *et al.* 2007, Vianna and Avelar 2010), they did not seem to have an effect on *M. roseus* in this survey.

Predation and pressure from interspecific competition are also factors that can impact the population shell size and distribution of some molluscs (e.g., Peterson and Andre

1980, Naddafi *et al.* 2010). However there is limited evidence for this on *M. roseus*, though, in a fish survey conducted on the southeast coast of Australia (Bulman *et al.* 2001), *M. roseus* remains were found in fish gut contents in 17 % of species, although with low frequencies of occurrence (approximately 20 %). As noted by Bax *et al.* (2003), the occurrence of *M. roseus* parts in the gut contents may overestimate the actual predation, as in some cases no shell fragments were found, only opercula that may have been ingested by the fish accidentally while selecting material from the benthos. Bore holes have been found in shells and some predatory gastropods have been observed to prey on *M. roseus*, however this was not considered to have a significant impact on the overall screwshell population characteristics (Scott 1997, Bax *et al.* 2003, Nicastro *et al.* 2009). Predation or interspecific competition are also unlikely to have a major impact on population characteristics (e.g., shell size) due to the high density of screwshells. Studies on the gastropod *Caracollus caracolla* demonstrated that large populations of a species can neutralise the effect of interspecific competition (Bloch and Willig 2009).

Measurements, similar to this study, for *M. roseus* shell size class distributions were previously described for the D'Entrecasteaux Channel (Bax *et al.* 2003), other locations in Australia (Scott 1997, Bax and Williams 2000, Bax *et al.* 2003), and New Zealand (Greenhill 1965, Powell 1979). However, no analyses related to environmental variables were conducted in those studies, although *Maoricolpus roseus* growth pattern was suggested to change depending on environmental conditions or sexual maturity (Bax *et al.* 2003). Also, the time of the collection of the data for this study could have an impact on the shells sizes depending on the time of initial recruitment of the sampled population. Size of a population can be affected

by the timing of its recruitment (Thorson 1966, Teusch and Guralnick 2003). However, based on information on their sexual maturity (Chapter Five) this is unlikely as probably only adult animals were collected. To further support and compare the above, further experimental studies are recommended on *M. roseus* shell size incorporating local environmental variables, sex type, and the age of the animals.

Of interest is that *M. roseus* specimens smaller than 33.5 mm were not found in the locations sampled in this study. This could be due to bias towards the collection of larger animals due to the sampling techniques used. Smaller specimens of *M. roseus* may be buried in the substrate and were potentially not collected or retained in the dredge samples. *Maoricolpus roseus* may have a short post - settlement period with rapid growth from juveniles into adults, or settlement might occur in a different type of substrate, with juveniles migrating during post - recruitment period into adult environments. Settlement of larvae is induced by particular physical and / or chemical cues in the habitat (Pawlik and Hadfield 1990, Satuito *et al.* 1997, Hadfield and Paul 2001) and larvae to metamorphose into juveniles are stimulated by similar specific signals (Hadfield 1984, Hirata and Hadfield 1986, Levantine and Bonar 1986, Pawlik and Hadfield 1990). Some benthic juvenile species recruit in areas different to where initial settlement occurred (Huxham and Richards 2003). Further field studies are required to search for juveniles in faunal core samples of the benthos in known *M. roseus* habitats and adjacent areas.

Other factors such as the local hydrodynamics (Herzfeld *et al.* 2005) of the D'Entrecasteaux could also be impacting on the distribution of the species. While substrate type is generally a good proxy for many of these factors, others such as



local tidal currents, seafloor topography, suspended sediment (turbidity), and general water chemistry could also be having an impact on the *M. roseus* distribution. Water quality in the D'Entrecasteaux varies due to natural and anthropogenic influences, such as water runoff from land and aquaculture facilities (Wild-Allen *et al.* 2005). However, in this study the sampling sites were positioned away from known influences to keep disturbance to a minimum. Biotic factors such as the relationship of *M. roseus* with other benthic communities, in particular to other macromolluscs, may also be affecting the distribution on *M. roseus*. This is investigated in Chapter Four.

In summary, *M. roseus* appears to be able to live in a variety of environments and, consequently is capable of distribution over a range of habitats, a characteristic typical of a successful invader (Miller *et al.* 2007, Miller and Ruiz 2009). This makes predicting and managing the spread of this species difficult. Its large distribution in Australia, across several habitat types, is a reflection of its invasive success, and suggests that other non - invaded areas are highly vulnerable

### **3. Chapter Three**

#### ***Maoricolpus roseus* habitat choice and responses to population density**

##### **3.1 Abstract**

Recent surveys of *M. roseus* population distribution in the D'Entrecasteaux Channel (SE Tasmania, Australia) found that generally this gastropod's habitat was characterised by sand. However, it was noted that some large densities of *M. roseus* were found in areas characterised by the finer muddy (silt and clay) substratum. These muddy sites were located in close proximity to the sites with the highest densities of live *M. roseus*. It was suggested that the animals moved into the finer substrate due to a potential density - dependant effect. While this notion was difficult to test in the field, it could potentially be examined in experimental trials in laboratory.

Firstly, experimental trials demonstrated that when *M. roseus* was put on a substrate with no sediments and was given the option to move into habitat characterised by sand or mud, they favoured the sand substrate. Results also demonstrated that when this gastropod was placed in either sand or mud, most animals stayed in the substrate they were initially placed on (92 % and 66 % for sand and mud correspondingly). However, of the animals that moved away from the initial substrate, a significantly higher number of animals moved away from mud compared to sand. Finally, experiments also demonstrated that there was a consistent increase in *M. roseus* that moved into the less favoured muddy substrate with an increase in numbers of *M. roseus* in the adjacent habitat characterised by sand.

This supports the hypothesis that this species prefers a habitat characterised by coarser substratum environments such as sand. Additionally, it demonstrated the versatility of *M. roseus* as it could move to the initially less favourable muddy sediments if needed, in response to population density pressures in sand.

### **3.2 Introduction**

Invasion of a non - indigenous species can dramatically alter the composition of a community and the functioning of its ecosystem (e.g., Carlton 1989, Grosholz and Ruiz 1996, Ruiz *et al.* 2000a, Ruiz *et al.* 2000b, Wonham and Carlton 2005). Understanding, and potentially predicting these invasions, requires knowledge of the characteristics of the habitat of the successful invader (Williamson and Fitter 1996). The habitat of benthic marine organisms is strongly influenced by substrate type (e.g., Gray 1974, Snelgrove and Butman 1994, Snelgrove *et al.* 1997, Alongi 1998, Newell *et al.* 2001). Also, within similar habitats, the movement of a species within a population can be density - dependent due to competition for resources. Community patterns related to population density are often attributed to competition for feeding resources (e.g., Frank 1965, Bonabeau *et al.* 1999, Barnes and Kuklinski 2004). When population density increases the core habitat may not be large enough to sustain all individuals, and some part of the population may shift to use more marginal habitats for resources. This density - dependent habitat use can play an important role in population regulation (Rodenhouse *et al.* 1997).

The invasive New Zealand screwshell *Maoricolpus roseus* (Quoy and Gaimard 1834) is a benthic marine gastropod (Subclass Caenogastropoda, Family Turritellidae) that reaches very large densities in its habitat (Chapter Two). This gastropod is believed

to have been introduced into Tasmania (Australia) in the 1920's (Greenhill 1965, Paul 1979, Hewitt *et al.* 2002) and is currently well distributed in Australia (SERQLD 1999, Bax and Williams 2001, Pollard and Rankin 2003, Wiltshire *et al.* 2010). Due to its large accumulation of shells, *M. roseus* can potentially impact on the distribution of native species via the alteration of coastal habitats (Edgar 2000). Surveys in New Zealand demonstrated *M. roseus* distribution over a range of habitats characterised by sand and mud (McKnight 1969, Grange 1979, Rainer 1981, Allmon 1988, Allmon *et al.* 1994, Abraham *et al.* 2007), and a similar distribution within those environments was described in Australia (Greenhill 1965, Allmon *et al.* 1994, Bax and Williams 2001, Bax *et al.* 2003, Spruzen and Richardson 2008).

In the past, ecological information on *M. roseus* was mostly about its geographical distribution, with limited and ambiguous data on species specific environmental preferences. However, a recent study (Chapter Two) of *M. roseus* population distribution in the D'Entrecasteaux Channel (SE Tasmania, Australia) found that their favoured habitat was characterised by sand. Some large numbers were also found in areas characterised by mud, and it was noted that these muddy sites were in close proximity to the sites with the highest densities of live *M. roseus*. It was hypothesised that while the preferred habitat of *M. roseus* was characterised by sand, there was a density - dependent effect (crowding) inducing movement of animals onto a less favoured adjacent muddy substratum. To test this hypothesis experiments were conducted whereby *M. roseus* were given a choice between no substratum, and habitats characterised by sand and mud. It was proposed that the highest number of *M. roseus* would be found on sand and that the proportion of animals on mud would increase as the density of *M. roseus* on sand increased.

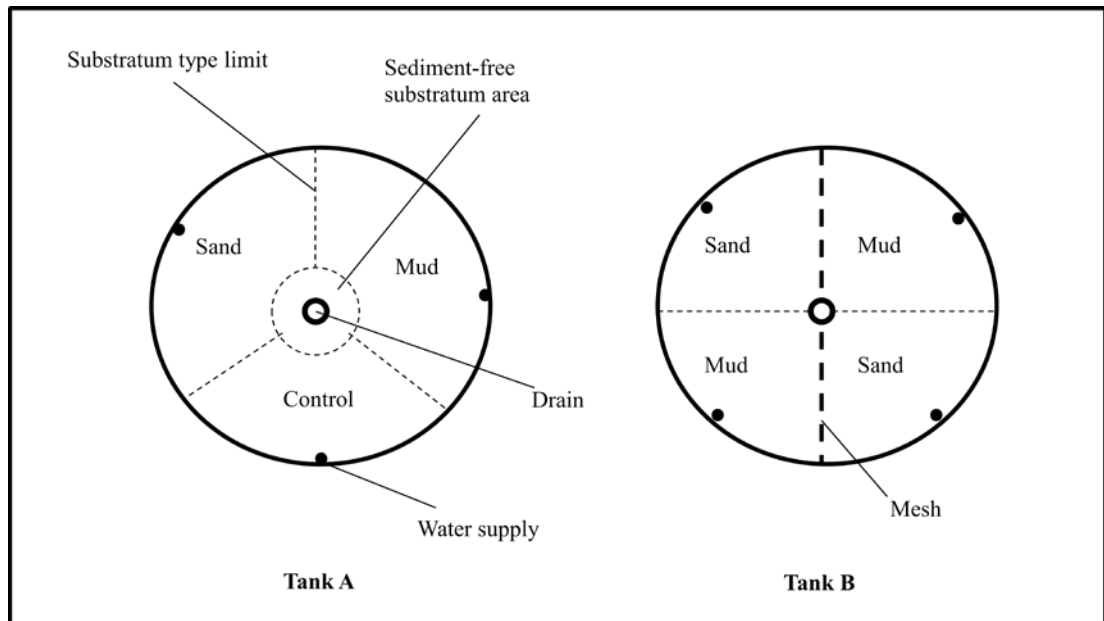
### **3.3 Materials and methods**

The hypotheses on movement to and from different types of habitats by *M. roseus* were tested in three laboratory experiments. Experiment one investigated animal preference between habitats characterised by sand ( $> 0.062$  mm) and mud ( $\leq 0.062$  mm) after animals were initially placed on a substratum free of any sediment. Experiment two investigated substratum selection between animals that were originally placed on sand compared to mud, while a third experiment investigated *M. roseus* selection for the mud substratum in relation to the initial animal density on sand.

For all experiments, animals were collected from two locations (Tinderbox and Simpsons Point area) in the D'Entrecasteaux Channel (43°03'S, 147°18'E) on the southeast coast of Tasmania. Collection sites were chosen based on areas with a large amount of *M. roseus* ( $\geq 500$  / m<sup>2</sup>) and the habitat characterised by sand and mud. *Maoricolpus roseus* were collected via SCUBA diving and had a mean size of  $55 \pm 0.6$  (SE) mm. Sediments for the experiments were collected in the D'Entrecasteaux Channel by a van Veen grab. Aquaria were set - up with flow - through natural seawater at an average flow of 10 litres / min. Experiments were conducted between July and August 2005 with water temperatures ranging between 9 and 11 °C and salinity of 33.5 ‰. Before each experiment, all tanks were thoroughly cleaned to remove any potential mucous trails. New animals were utilised in each trial and they were initially conditioned for at least 48 hours in a tank free of any sediment, with natural water flow - through and aerated system. Water was supplied from the D'Entrecasteaux Channel.

For experiment one (i.e., *M. roseus* substrate choice), three circular 500 litres tanks were set - up Figure 9, Tank A) with a central circular sediment - free substratum area (an artificial polypropylene sheet) of approximately 0.125 m<sup>2</sup>. This area was used for the initial placement of the experimental animals (n = 60). Three equal adjacent areas (of approximately 0.25 m<sup>2</sup>) were connected to the central part of the tank. Each individual adjacent area contained individually 10 cm deep sand, 10 cm deep mud, and a sediment - free substratum area as the experimental control. To minimise for bias towards other factors, the water supply in the tanks was set - up individually above each substratum type area. This experiment was replicated three times.

For experiment two, the three tanks described above were vertically divided into two equal areas (approximately. 0.4 m<sup>2</sup>) separated by a 0.5 cm aperture plastic mesh from the bottom of the tank to 10 cm above the water level in the centre of the tank. Each separated portion in each tank was further divided into two equal adjoining areas of sand and mud, at 10 cm depth, and with individual seawater supply pipes Figure 9, Tank B). Fifty animals were placed in one single sediment type for each divided portion of the tank (i.e. 50 animals in sand and 50 in mud in each portion of the tank that was separated by the central mesh). The experiment was repeated three times.



**Figure 9** Aerial view of experimental tank types A and B for experiment one and two respectively.

Experiment three investigated *M. roseus* substrate usage versus animal density. Preference for mud in relation to the initial animal density in sand was investigated in separate trials using initial population densities of 50, 100, 200, and 300 animals, equivalent to 250, 500, 1000, and 1500 animals m<sup>-2</sup>. These densities were similar to those found in the D'Entrecasteaux Channel (Chapter Two). For each density trial, animals were initially placed centrally into the sand area in each mesh separated portion in every tank. The number of animals in the mud substrate was subsequently recorded and all trials were run twice for each density type, resulting in 12 replicates.

In all experiments, the number of animals on each substratum type was recorded after a period of four days. A pilot study demonstrated that there was no significant difference in the number of animals found in different substratum types after four

days compared to six, eight, and ten days (ANOVA: control  $F_{3,59} = 0.123$ ,  $P = 0.95$ , mud  $F_{3,59} = 0.156$ ,  $P = 0.92$ , and sand  $F_{3,59} = 0.105$ ,  $P = 0.96$ ).

Statistical analyses on final data were conducted using analyses of variances (ANOVA) and multiple comparisons by post - hoc Tukey tests (Quinn and Keough 2002). Data variances were tested (Sokal and Rohlf 2003) using the Levene and Kolmogorov - Smirnov tests (Dytham 2003) and transformed accordingly (Underwood 1981). Data were log - transformed, and tests confirmed that the transformed data met the assumption of normality and homogeneity of variance.

For experiment one, ANOVA was carried out comparing *M. roseus* numbers between all three substrate types, sand, mud, and control. For experiment two, first an ANOVA was carried out to compare *M. roseus* numbers in the substrates after animals had been placed in sand, and an ANOVA to compare *M. roseus* numbers in the substrates after animals had been placed in mud. Next, an ANOVA assessed the differences between the number of *M. roseus* moving from their initial placing in sand or initial placing in mud. Finally, in experiment three, an ANOVA assessed the number of *M. roseus* moving away from their initial placing in relation to different initial population densities.

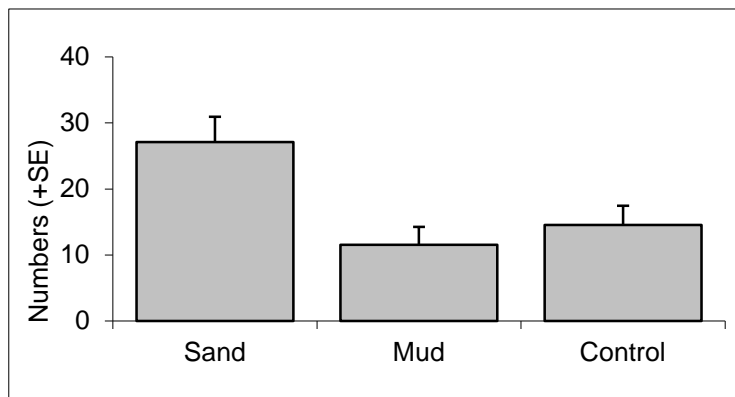
### **3.4 Results**

#### **3.4.1 *Maoricolpus roseus* substratum choice**

For experiment one, after the period of four days, the substratum types sand, mud, and the control sediment - free substratum area had mean animal numbers of  $27.1 \pm 3.82$  (SE),  $11.6 \pm 2.68$  (SE) and  $14.6 \pm 2.87$  (SE) respectively (Figure 10). Numbers

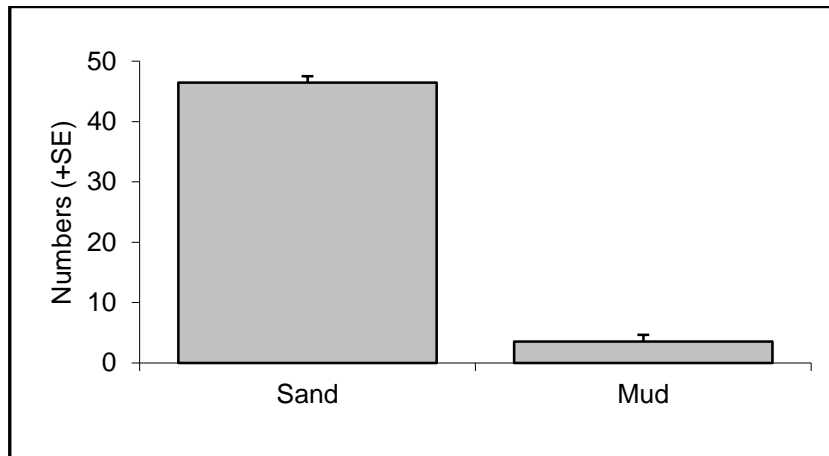


varied significantly among substrate types (ANOVA:  $F_{2, 24} = 6.79$ ,  $P < 0.05$ ). Post-hoc Tukey test indicated that sand had a significantly higher number of *M. roseus* compared to mud ( $P < 0.01$ ) and compared to control ( $P < 0.05$ ), while the mud and the control were not significantly different ( $P = 0.783$ ).

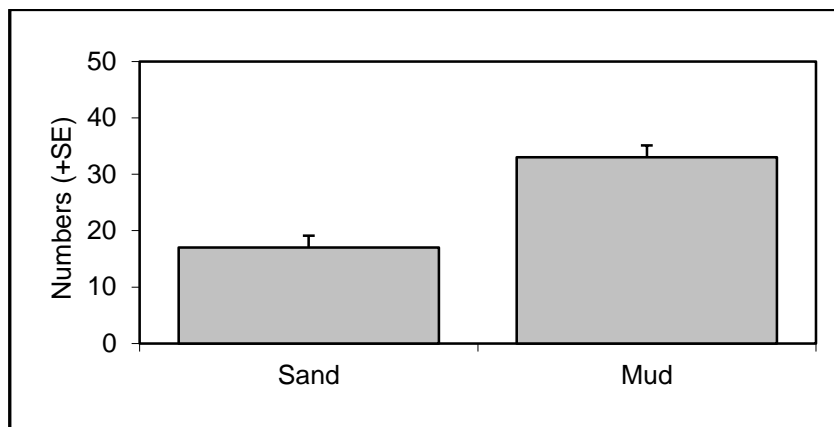


**Figure 10** *Maoricolpus roseus* mean numbers in substrate type sand, mud, and control (sediment-free substratum area) after four days.

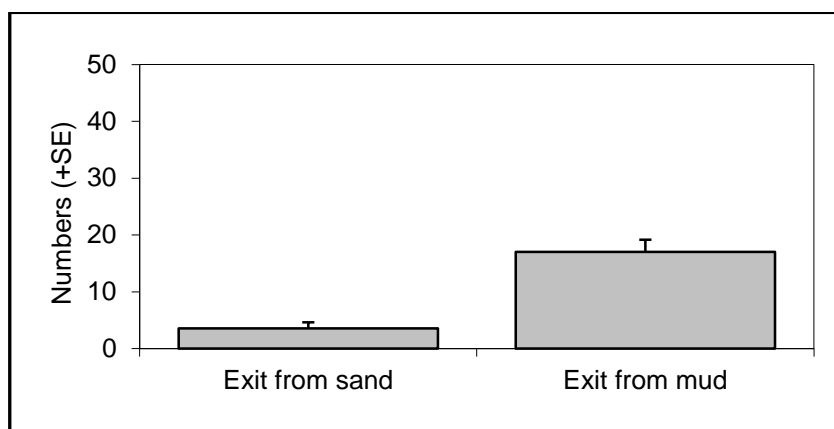
In experiment two the mean number of animals in sand and mud, after the period of four days of initial placement of *M. roseus* on sand, were  $46.4 \pm 1.08$  (SE) and  $3.6 \pm 1.08$  (SE) respectively (Figure 11). The mean number of animals after initial placing on mud was  $17 \pm 2.13$  (SE) in sand, and  $33 \pm 2.13$  (SE) in mud (Figure 12). *Maoricolpus roseus* numbers were significantly different between substratum types when animals were initially placed on either sand or mud (ANOVA:  $F_{1, 7} = 786.26$ ,  $P < 0.001$  and  $F_{1, 7} = 28.10$ ,  $P < 0.001$  correspondingly). However, significantly higher number of animals (ANOVA:  $F_{1, 16} = 32.58$ ,  $P < 0.001$ ) moved away from their initial mud substratum ( $17 \pm 2.13$  (SE), Figure 13) compared to sand ( $3.6 \pm 1.08$  (SE), Figure 13).



**Figure 11** *Maoricolpus roseus* mean numbers in sand ( $>0.062$  mm) and mud ( $\leq 0.062$  mm) following animal placement on sand after four days



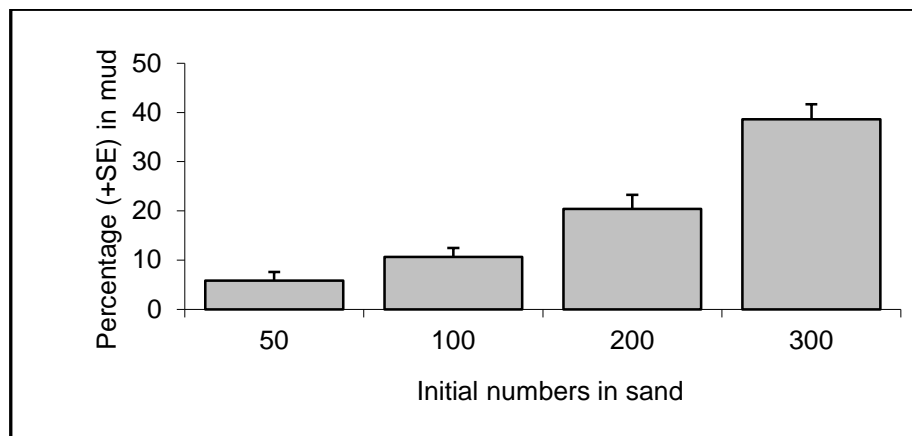
**Figure 12** *M aoricolpus roseus* mean numbers in sand ( $>0.062$  mm) and mud ( $\leq 0.062$  mm) following animal placement on mud after four days.



**Figure 13** *M aoricolpus roseus* mean number of animals that moved away from sand ( $> 0.062$  mm) and mud ( $\leq 0.062$  mm) after four days.

### 3.4.2 *Maoricolpus roseus* substrate usage versus animal density

After four days, the proportion of *M. roseus* found in mud was 5.8 %, 10.7 %, 20.4 %, and 38.6 % in relation to initial numbers of 50, 100, 200, and 300 animals placed in sand, respectively (Figure 14). These final proportions of *M. roseus* in mud were significantly different to the initial number of animals in sand (ANOVA:  $F_{3, 44} = 35.10$ ,  $P < 0.001$ ). Tukey post - hoc tests indicated significant differences in the proportion of *M. roseus* in mud compared with the initial animal numbers in sand, except for the initial numbers of 50 and 100.



**Figure 14** *Maoricolpus roseus* proportions in mud ( $\leq 0.062$  mm) after four days in relation to initial total densities of 50, 100, 200, and 300 animals in sand ( $> 0.062$  mm).

### 3.5 Discussion

When *M. roseus* were initially placed on the sediment - free substrate and had a choice to move between sand and mud, they clearly showed a preference for sand. This result was consistent with findings from the field observations (Chapter Two), which demonstrated that sand had generally a higher density of *M. roseus* than mud from sites surveyed in the D'Entrecasteaux Channel. A large quantity of *M. roseus* found in areas characterised by similar substratum type has also been described in

previous field surveys (Greenhill 1965, Allmon *et al.* 1994, Bax and Williams 2001, Bax *et al.* 2003, Spruzen and Richardson 2008).

From results from experiment two, it was further observed that when *M. roseus* were placed on sand and had the option to move onto mud, the highest number of animals stayed on sand. The preference for this substratum type was consistent with the results from experiment one. Interestingly however, when animals were placed on mud and had the option to move onto sand, the highest proportion of animals stayed on mud (their initial substrate). Possibly many animals placed on their initial sediment type were not aware of the alternative sediment that they could move to due to their relative low motility, or animals were content to remain on any sediment type (sand or mud) as opposed to experiment one, where animals were placed in a sediment - free substrate type.

However, results from experiment two also showed that there was an inclination for *M. roseus* to choose sand over mud, as a higher number of *M. roseus* moved away from mud in contrast to sand. Therefore, while large quantities of *M. roseus* stayed on mud, it was proportionally less than the numbers that stayed on sand. These results support the hypothesis that locations characterised by mud are not the primary habitat choice of *M. roseus*.

In the density related experiments, a significant increase in *M. roseus* moving into mud was observed with an increase of animal density in sand. Mollusc responses to population density have largely been attributed to competition for feeding resources (e.g., Underwood 1978, Boaventura *et al.* 2003). Animals can respond to

intraspecific competition by emigrating out of high density areas and moving into lower density regions (Branch 1975), however with the existence of a natural boundary, such as a change in substratum type, this response might not always occur (Tewfik and Bene 2003). From the experimental results, *M. roseus* did not consider the change of substratum type as an inhibitor. This result supports the observation from the surveys in the D'Entrecasteaux Channel (Chapter Two) of high number of *M. roseus* in mud in areas adjacent to the densely populated regions characterised by sand. For the population dynamics of *M. roseus*, it probably means that intraspecific interactions are influencing the choice between optimal versus marginal habitats.

*Maoricolpus roseus*, as a suspension feeder, would probably limit its movement after locating a favourable environment for feeding. Similar behaviour has been described for other suspension feeding turritellids, burrowing themselves in soft sediments with shell aperture exposed and close to the substrate surface (Fretter and Manly 1979, Allmon 1988, Allmon *et al.* 1992, Kennedy 1995). In the experiments it was observed that most *M. roseus* were at rest on the substrate after 4 days. Most specimens were lying horizontally on the substrate, and about 25 % were vertically buried up to the last 1 - 2 shell whorls in the sediment, with protruding operculum. Similar modes of burial were observed in field surveys on this species (Chapter Two) and in New Zealand (Allmon *et al.* 1994).

This study has provided further information on *M. roseus* habitat dynamics and supports its preference for coarser substratum environments such as sand, and its versatility in living in less favoured muddy sediments in response to population density pressures. However, there are many density dependent factors regulating the

distribution of a population (Fretwell 1972, Boer and Reddingius 1996), such as community interactions, reproduction strategies, population mortality and animal growth rates across different geographical ranges. Further information on these factors is needed for improved understanding of *M. roseus* distribution and to ultimately assess its ecological impact.

## **4. Chapter Four**

### **Effect of *Maoricolpus roseus* on other macromolluscs assemblages in the D'Entrecasteaux Channel, Tasmania**

#### **4.1 Abstract**

Despite the vast distribution of the introduced gastropod *Maoricolpus roseus* in Tasmania, information on its interaction with other benthic species is limited. Molluscs with their large abundances of shells can be important ecosystem engineers and *M. roseus* could potentially modify the physical environment and impact the distribution of other macromolluscs. This study focused on the potential interaction and impact of *M. roseus* on native macromolluscs via a broad scale survey in SE Tasmania, comparing the distribution and density of *M. roseus* (both live and dead animals) with the distribution and abundance of macromolluscs.

A total of 60 macromollusc species were collected in the survey and bivalves were numerically dominant compared to gastropods. *Corbula gibba*, *Nemocardium thetidis*, *Hiatella australis*, and the gastropod *Nassarius nigellus* were the most common species. A combination of *M. roseus* (live and dead) densities and the abiotic characteristics substrate type, total organic carbon content, and water depth were related to macromollusc species richness and abundance, and suspension feeding species richness and abundance. Macromollusc species community composition was significantly correlated to the live and dead *M. roseus* densities and abiotic factors combined. The results suggested complex interactions between the variables. To reduce the variability in the results, the analyses was re - run confined to *M. roseus*' preferred habitat of sand. On sand, live *M. roseus* densities were significantly correlated to the macromollusc community composition. In particular,

areas of higher live *M. roseus* densities were characterised by a higher number of deposit feeding macromolluscs, while in lower densities of live *M. roseus* the community was characterised mainly by suspension feeders. The results are preliminary, however it suggests that high densities of *M. roseus* might be having an impact by inhibiting the accumulation of other suspension feeding macromolluscs.

## **4.2 Introduction**

Understanding the processes which determine the structure of benthic assemblages involves assessments of abiotic and biotic factors (Woodin 1999). Key abiotic factors include the composition of the substrate (e.g., Gray 1974, Snelgrove and Butman 1994, Snelgrove *et al.* 1997, Alongi 1998, Newell *et al.* 2001), while biotic regulating forces between species vary from interspecific competition for resources to predation (e.g., Peterson 1977, Underwood and Denley 1984, Wilson 1990). Interspecific competition is not always direct between two species. Interactions may be indirect by limiting a resource with secondary effects across trophic levels (Bremner *et al.* 2003). Other aspects to be considered are physical and biological processes driven by faunal assemblages that impact on abiotic characteristics via alterations of the benthic environment. This can occur with re - structuring of the substrate via bioturbation such as the action of feeding (Waldbusser *et al.* 2004, Mermillod-Blondin *et al.* 2005), disturbance by foraging predators (Wiltse 1980, Wilson 1990, Seitz 1998), and altering water hydrodynamics by physical assemblages (e.g., deposition of shells) (Hall 1994, Reise 2002, Biles *et al.* 2003, Gutierrez *et al.* 2003). The organisms involved in these processes (ecosystem engineers) can control the availability of resources to other species by changes in abiotic or biotic materials (Jones *et al.* 1994, 1997). For example, accumulations of



shells can promote species richness if they create resources that are not otherwise available and species are present that use these resources (Gutierrez *et al.* 2003).

A biological invasion of a non - indigenous species can dramatically alter the community composition and the functioning of an ecosystem (Carlton 1989, Grosholz and Ruiz 1996, Ruiz *et al.* 2000a). Examples of benthic non - indigenous ecosystem engineers, are the tubeworm *Ficopomatus enigmaticus* (Heiman and Micheli 2010), the Pacific oyster *Crassostrea gigas* (Padilla 2010), the bivalves *Ruditapes philippinarum* (Queiros *et al.* 2011) and *Limnoperna fortunei* (Darrigran and Damborenea 2011), altering the physical environment, and changing the abundance and composition of benthic communities in their non - native environment.

In Tasmania, Australia, introduced marine species are known to impact on native faunal assemblages. For example, it has been demonstrated that the non - indigenous European green crab *Carcinus maenas* predated on the juvenile clam *Katelysia scalarina* which affects the clam fishery (Walton *et al.* 2002), and predation by the seastar *Asterias amurensis* decreases the survivorship of juveniles of the commercial bivalve *Fulvia tenuicostata* (Ross *et al.* 2002). Another example is the sea urchin *Centrostephanus rodgersii*. Due to changes in oceanographic conditions, this urchin is extending its geographical range from mainland Australia to Tasmania (Johnson *et al.* 2011). This non - native species to Tasmania is now grazing and inhibiting the recovery of macroalgae, leading to an impact on the commercially fished abalone *Haliotis rubra* that feeds on algae (Strain and Johnson 2009).

The invasive New Zealand screwshell *Maoricolpus roseus* (Quoy and Gaimard 1834) has a wide distribution in Tasmania, but information on its impact on the non - native environment is unknown. *Maoricolpus roseus* is a benthic marine gastropod (Subclass Caenogastropoda, Family Turritellidae) believed to have been introduced into Tasmania in the 1920's (Greenhill 1965, Paul 1979, Hewitt *et al.* 2002). In some locations *M. roseus* can reach densities exceeding 1000 shells m<sup>-2</sup> (Bax *et al.* 2003). Molluscs can be important ecosystem engineers (Gutierrez *et al.* 2003) and when introduced can alter species community and ecosystem functioning (e.g., Robinson *et al.* 2005, Reise *et al.* 2006, Werner and Rothhaupt 2008, Buhle and Ruesink 2009, Schmidlin *et al.* 2012). Current information on *M. roseus* from its native habitat in New Zealand is limited and mainly based on the species geographical distribution (Morton and Miller 1968, McKnight 1969, Rainer 1981, Allmon 1988, Allmon *et al.* 1994). Investigations on ecological interactions of *M. roseus* with other species are limited. Reid (2004) found that *M. roseus* can promote hermit crab aggregations via accumulation of large quantities of shells from dead *M. roseus*, while Nicastro *et al.* (2009) investigated the potential ecological impact of the accumulation of dead *M. roseus* shells. The latter study did not find significant evidence that accumulation of shells from dead animals had a direct impact on benthic assemblages. Recently, another study by Reid (Reid 2010) demonstrated that *M. roseus* can have variable effects on the benthic community. Areas of high densities of *M. roseus* exhibited elevated species richness and abundances of macroinvertebrates when compared to areas with low densities or no *M. roseus*.

*Maoricolpus roseus* may adversely impact faunal assemblages in Tasmania via the alteration of coastal habitats due to large accumulations of its shells (Edgar 2000). It

could also affect the distribution and abundance of species with similar morphology, such as other macromolluscs, via competition for habitat. Such changes can have further consequences on the distribution of other taxa and alter the functioning of aquatic ecosystems.

Examples of native mollusc species that could potentially be impacted by *M. roseus* include the turritellid *Gazameda gunnii* and the scallop *Pecten fumatus* (Pectinidae) (Bax *et al.* 2003). *Gazameda gunnii* is currently listed as a threatened species (TTSL 2009) under the Tasmanian Threatened Species Protection Act (TTSPA 2005), while *P. fumatus* is an important recreational and commercial fisheries species (Haddon *et al.* 2005). *Maoricolpus roseus* is a larger animal and reaches larger population densities compared to *G. gunnii* (Carrick 1980b, Allmon 1988, Bax *et al.* 2003) and could possibly out - compete *G. gunnii* for habitat and feeding resources. *Maoricolpus roseus* is also a suspension feeder (Scott 1997) and may therefore impact on *P. fumatus* directly through feeding on their larvae. Predation on bivalve larvae by benthic suspension feeders was previously described by Andre *et al.* (1993) and Trost *et al.* (2008).

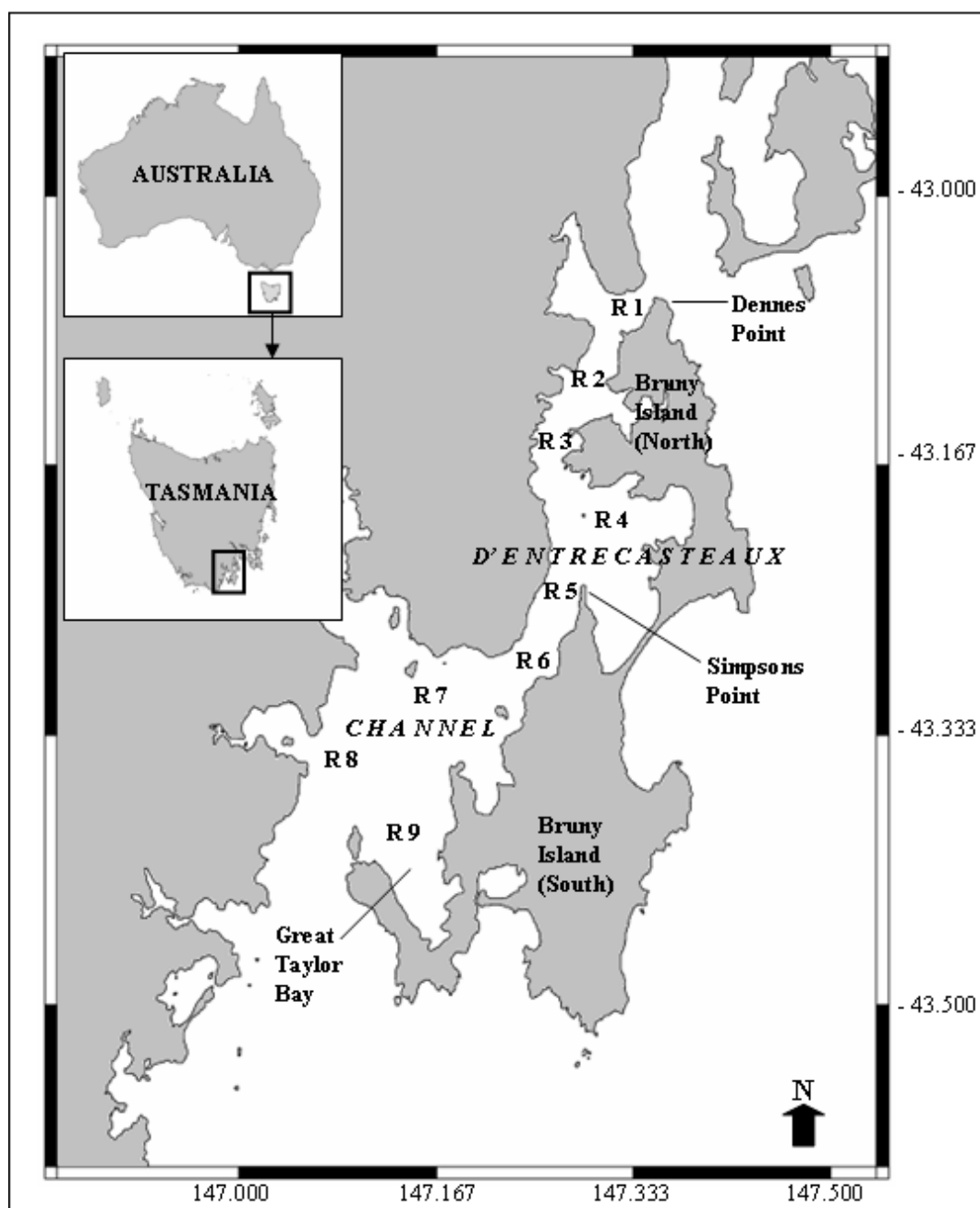
This study aimed to investigate the association of *M. roseus* with co - occurring benthic macromollusc assemblages. Most previous studies on *M. roseus* have not differentiated between live and dead animals and information based solely on the total abundance of shells may be misrepresented (Summerson *et al.* 2007). As the operculum of *M. roseus* is located well within the shell cavity, it is difficult to determine whether the animal is alive or dead without destroying it. This study focused on differentiating between shells with live animals and empty shells (dead

animals). Accumulation of shells from dead *M. roseus* may have ecological interactions with the local benthic environment (Reid 2004, Nicastro *et al.* 2009) that will differ from the impact of live animals. Abiotic environmental variables were also considered. Because *M. roseus* is a suspension feeder, it is predicted that this gastropod could have an impact on macromolluscs with similar feeding mode, due to competition for resources. Therefore, relationships in density and distribution between *M. roseus* and other macromollusc suspension feeding species were investigated.

### **4.3 Materials and methods**

#### **4.3.1 Study sites and sampling procedures**

Macromollusc samples were collected during the same survey that investigated *M. roseus* distribution described in Chapter Two (see Chapter Two for a detailed description of the survey design). At each of the 60 sites, from the nine regions in the D'Entrecasteaux Channel (Figure 15), macromolluscs were collected from the same dredge sample that collected samples for Chapter Two. Samples were processed and sorted in the same manner as *M. roseus*. Macromolluscs were identified to species level and taxonomic acceptance name was based on Appeltans *et al.* (2012). Data on substrate abiotic characteristics were provided from analyses done on sediments samples from the survey conducted in Chapter Two.



**Figure 15** D'Entrecasteaux Channel with outlined sampling regions. Regions 1-3 = upper zone, regions 4-6 = middle zone, and regions 7-9 = lower zone. (Map coastline based on NGDC (2007))

#### **4.3.2 Data analyses**

Macromollusc species richness and abundance, and suspension feeding richness and abundance in the D'Entrecasteaux Channel were investigated. This was followed by an investigation of the association between the densities of live and dead *M. roseus* and other macromolluscs, as well as with other abiotic factors, including fraction of gravel, sand, mud (silt and clay), TOC, and water depth (m). Macromollusc abundance was the total number of individuals of all species except *M. roseus*, while richness was the number of the different species collected from each 100 m transect at each site.

An initial analysis of variance (ANOVA) investigated the differences in the distribution of the macromolluscs in the D'Entrecasteaux Channel. This was followed by a Spearman rank correlation analysis to investigate for relationships among *M. roseus* density and abiotic data with macromollusc species richness and abundance, and suspension feeding species richness and abundance. Before statistical analyses, data were tested for normality of distribution and homogeneity of variances (Sokal and Rohlf 2003) via Kolmogorov - Smirnov and Levene tests respectively (Dytham 2003). Data were transformed accordingly if heterogeneous (Underwood 1981). *M. roseus* density data were log transformed and abiotic substrate data were arcsine transformed. The statistical analyses were undertaken using the SPSS software package (SPSS 2008).

The relationship between *M. roseus* (live and dead) density and macromollusc community composition was analysed using multivariate techniques in PRIMER (Clarke and Gorley 2006). Substrate characteristics (gravel %, sand %, mud %, TOC

%) and water depth were also included in the analyses. To identify the differences in the structure of macromollusc communities, a Bray - Curtis similarity calculation on standardised fourth root transformed abundances was carried out producing a non - metric MDS ordination (Clarke and Warwick 2001). Data were standardised to homogenise for the dredge sampling efficiency in variable soft benthic substrate types (e.g., Currie and Parry 1999, Cohen *et al.* 2000). An analysis of similarity (ANOSIM) was used to test for differences in macromollusc community structure among zones in the D'Entrecasteaux Channel, and the BIOENV procedure (Clarke and Gorley, 2006) was used to test the association between macromollusc community composition, the abiotic environmental attributes, and live and dead *M. roseus* densities. Before the analysis, *M. roseus* data were log transformed, substrate fractions and TOC data were arcsine - transformed and all variables were normalised to homogenise for the different scale of measurements used (Clarke and Gorley 2006).

Finally, data analyses were carried - out for a subset of the sites within *M. roseus* favoured habitat characterised by sand (0.25 - 0.125 mm Wentworth scale, Buchanan 1984). This was based on results from surveys and experiments carried - out in Chapter Two and Three respectively. This investigation was performed to try to minimize the effect of the substrate variability on the benthic faunal assemblages to aid in investigating how *M. roseus* could interact with the macromollusc community composition. Multivariate analysis with Bray - Curtis similarity matrices were used to investigate the relationship of the macromollusc community composition to live *M. roseus* densities via the BIOENV procedure. SIMPER analyses investigated the macromollusc species and their functional groups (suspension or deposit feeders) that

most contributed to the community differences. Before data analyses, normality of distribution and homogeneity of variances were initially tested and transformed as per previous section. To minimise complex and low power comparisons, species that were located only at one site were considered as rare and excluded from the analyses.

#### **4.4 Results**

A total of 60 macromollusc species were collected from the transects in the D'Entrecasteaux Channel, with 44 species (Table 5) being considered in the analysis after removal of rare species. Bivalves species were numerically dominant (28) compared to gastropods (19). Bivalves *Corbula gibba*, *Nemocardium thetidis* and *Hiatella australis*, and the gastropod *Nassarius nigellus* and *Anachis atkinsoni* were the most abundant and common species across the 60 sites. The bivalves *Nucula oblique*, *Venericardia bimaculata* and *Pecten fumatus* were relatively less abundant, but were also present across most sites.

Biotic and abiotic characteristics are summarised in Table 6 and Figure 16. Overall there was a significant difference in the macromollusc species richness and abundance, and suspension feeding species abundance among the regions in the D'Entrecasteaux Channel ( $F_{8, 51} = 2.64$ ,  $P < 0.05$ ;  $F_{8, 51} = 3.11$ ,  $P < 0.01$ , and  $F_{8, 51} = 2.60$ ,  $P < 0.05$  respectively). Correlation analyses are summarised in Table 7. Individual correlations between the variables showed that dead *M. roseus* were significantly correlated to macromollusc abundances and suspension feeding species abundances. The abiotic variable gravel % had significant positive correlation to macromollusc abundance and suspension feeding species abundance, while mud %



and water depth had a significant negative correlation to macromollusc richness and suspension feeding species richness.

**Table 5** Macromollusc species with taxonomic class Gastropoda (G) or Bivalvia (B); mode of feeding suspension (S) and deposit feeding (D); density (as percentage of the total number of individuals); and occurrence (as percentage of the total number of sites).

Species	Common name	Class	Family	Feeding mode	Density %	Occurrence %
<i>Gazameda gunnii</i>	Gunn's Screw Shell	G	Turritellidae	S	0.47	18.33
<i>Bittium granarium</i> ( <i>Cacozeliana granarium</i> )	Granulated creeper	G	Cerithiidae	D	1.44	13.33
<i>Corbula gibba</i> *	Common basket shell	B	Corbulidae	S	20.02	56.67
<i>Nassarius nigellus</i>	-	G	Nassariidae	D	19.1	76.67
<i>Tawera gallinula</i>	Feathered venus	B	Veneridae	S	1.42	18.33
<i>Cuna delta</i>	-	B	Condylocardiidae	S	0.25	8.33
<i>Nucula obliqua</i> ( <i>Ennucula grayi</i> )	-	B	Nuculidae	S	2.00	28.33
<i>Thraciopsis sp</i>	-	B	Thraciidae	S	0.98	20.00
<i>Fulvia tenuicostata</i>	Thin-ribbed cockle	B	Cardiidae	S	0.65	11.67
<i>Anachis atkinsoni</i>	-	G	Columbellidae	S	13.62	30.00
<i>Nemocardium thetidis</i>	Thetis cockle	B	Cardiidae	S	4.12	46.67
<i>Hiatella australis</i>	Southern crypt dweller	B	Hiatellidae	S	11.09	53.33
<i>Placamen placidum</i>	Placid venus	B	Veneridae	S	0.58	10.00
<i>Hemitoma subemarginata</i> ( <i>Hemitoma emarginata</i> , <i>Montfortia emarginata</i> )	-	G	Fissurellidae	D	1.26	11.67
<i>Cardita excavate</i> ( <i>Cardita aviculina</i> )	-	B	Carditidae	S	1.10	6.67
<i>Venericardia bimaculata</i> ( <i>Verericardia sp</i> )	False cockle	B	Carditidae	S	2.57	28.33
<i>Neotrigonia margaritacea</i>	Trigonia	B	Trigoniidae	S	0.97	11.67
<i>Callista diemenensis</i>	Tasmanian notocallista	B	Veneridae	S	0.35	6.67
<i>Cuna hamata</i> ( <i>Hamacuna hamata</i> )	-	B	Condylocardiidae	S	0.08	1.67
<i>Chlamys asperrimus</i> ( <i>Chlamis sp</i> )	Doughboy Scallop	B	Pectinidae	S	1.95	11.67
<i>Pseudamycla dermestoidea</i>	-	G	Columbellidae	D	1.02	16.67
<i>Musculus impactus</i>	-	B	Mytilidae	S	2.12	16.67

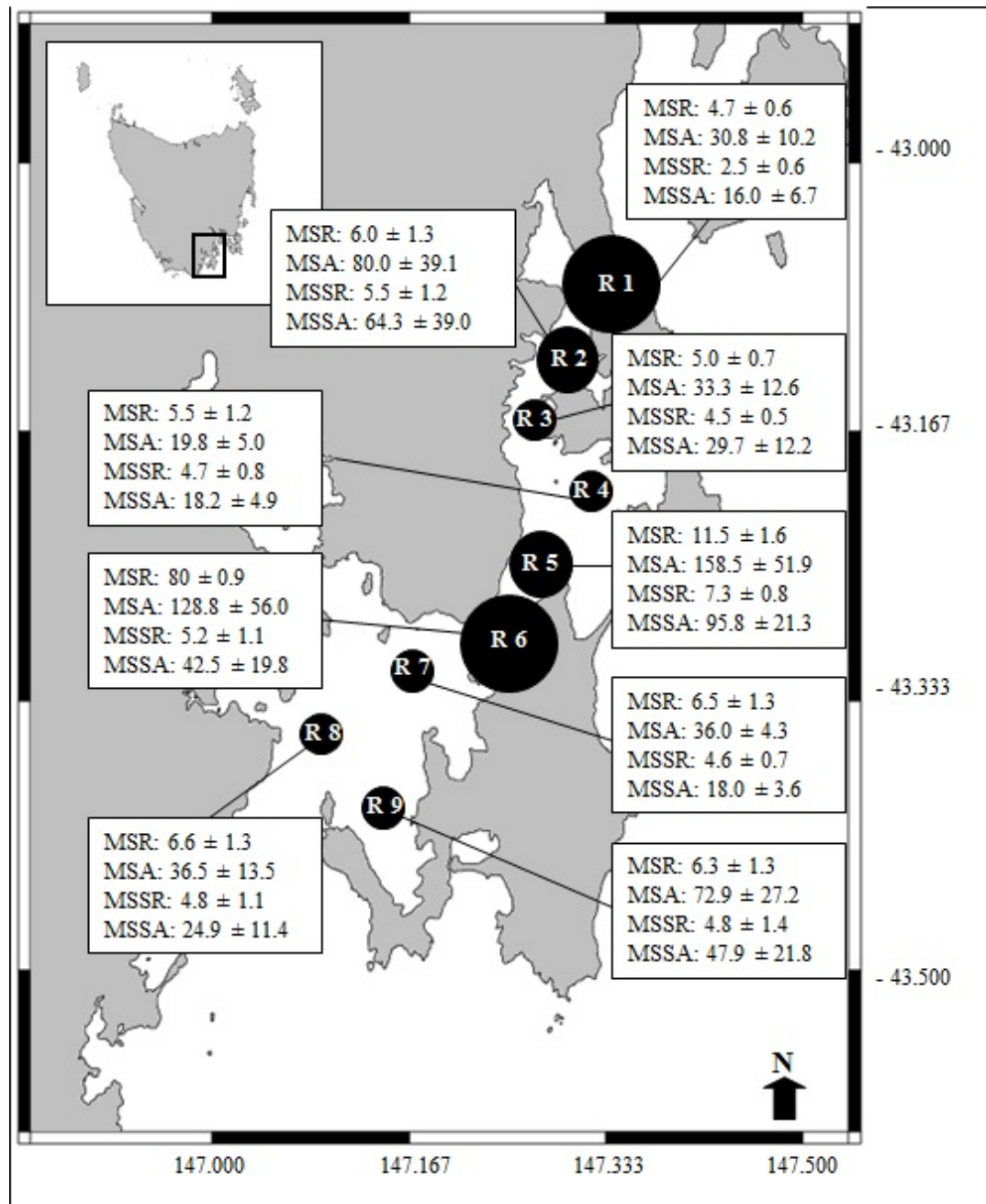
\* Non native species (from TLIIS 2010)

**Table 5 (continued)** Macromollusc species with taxonomic class Gastropoda (G) or Bivalvia (B); mode of feeding suspension (S) and deposit feeding (D); density (as percentage of the total number of individuals); and occurrence (as percentage of the total number of sites).

Species	Common name	Class	Family	Feeding mode	Density %	Occurrence %
<i>Timoclea cardioides</i> ( <i>Timoclea</i> sp.)	Cockle-like Venus	B	Veneridae	S	1.42	11.67
<i>Equichlamys bifrons</i>	Queen Scallop	B	Pectinidae	S	2.07	16.67
<i>Amygdalum beddomei</i> ( <i>Amygdalum striatum</i> )	-	B	Mytilidae	S	0.23	10.00
<i>Fusinus novaehollandiae</i>	New Holland spindle shell	G	Fascioliariidae	D	0.46	11.67
<i>Calyptreaa calyptraeformis</i> ( <i>Calyptreaa</i> sp)	Shelf Limpet	G	Calyptreaeidae	D	0.37	8.33
<i>Clanculus aloysii</i>	-	G	Trochidae	D	0.72	6.67
<i>Austromitra analogica</i>	Mitre shell	G	Costellariidae	D	0.58	5.00
<i>Guraleus</i> sp	-	G	Mangeliidae	D	0.24	5.00
<i>Amoria undulata</i>	-	G	Volutidae	D	0.08	1.67
<i>Pleuroploca Australasia</i> ( <i>Australaria australasia</i> )	Tulip shell	G	Fascioliariidae	D	0.08	1.67
<i>Sassia subdistorta</i>	Distorted rock whelk	G	Ranellidae	D	0.08	1.67
<i>Limatula strangei</i> ( <i>Limatula bullata</i> )	Strange's file shell	B	Limidae	S	0.21	6.67
<i>Dosinia grata</i>	-	B	Veneridae	S	0.33	3.33
<i>Solamen recens</i>	-	B	Mytilidae	S	0.10	3.33
<i>Leionucula</i> sp	-	B	Nuculidae	S	0.46	15.00
<i>Phasianotrochus irisodontes</i>	Rainbow kelp shell	G	Trochidae	D	0.08	3.33
<i>Myrtea botanica</i> ( <i>Myrtea</i> sp)	-	B	Lucinidae	S	0.08	5.00
<i>Electroma Georgiana</i> ( <i>Electroma</i> sp)	Butterfly shell	B	Pteriidae	S	0.25	5.00
<i>Myadora complexa</i>	Rounded myadora	B	Myochamidae	S	0.15	5.00
<i>Vexitomina coxi</i>	-	G	Horaiclavidae		0.08	3.33
<i>Ostrea angasi</i>	Common mud oyster	B	Ostreidae	S	0.48	6.67
<i>Pecten fumatus</i>	Commercial Scallop	B	Pectinidae	S	2.40	25.00

**Table 6** Biotic and abiotic characteristics (mean  $\pm$  SE) by regions over the 100 m transects.

Regions	1	2	3	4	5	6	7	8	9
Macromollusc species richness	4.7 $\pm$ 0.6	6.0 $\pm$ 1.3	5.0 $\pm$ 0.7	5.5 $\pm$ 1.2	11.5 $\pm$ 1.6	80 $\pm$ 0.9	6.5 $\pm$ 1.3	6.6 $\pm$ 1.3	6.3 $\pm$ 1.3
Macromollusc species abundance	30.8 $\pm$ 10.2	80.0 $\pm$ 39.1	33.3 $\pm$ 12.6	19.8 $\pm$ 5.0	158.5 $\pm$ 51.9	128.8 $\pm$ 56.0	36.0 $\pm$ 4.3	36.5 $\pm$ 13.5	72.9 $\pm$ 27.2
Macromollusc suspension feeding species richness	2.5 $\pm$ 0.6	5.5 $\pm$ 1.2	4.5 $\pm$ 0.5	4.7 $\pm$ 0.8	7.3 $\pm$ 0.8	5.2 $\pm$ 1.1	4.6 $\pm$ 0.7	4.8 $\pm$ 1.1	4.8 $\pm$ 1.4
Macromollusc suspension feeding species abundance	16.0 $\pm$ 6.7	64.3 $\pm$ 39.0	29.7 $\pm$ 12.2	18.2 $\pm$ 4.9	95.8 $\pm$ 21.3	42.5 $\pm$ 19.8	18.0 $\pm$ 3.6	24.9 $\pm$ 11.4	47.9 $\pm$ 21.8
Live <i>M. roseus</i>	427.8 $\pm$ 281.0	55.5 $\pm$ 30.9	12.7 $\pm$ 7.3	13.2 $\pm$ 6.7	76.2 $\pm$ 65.8	349.5 $\pm$ 147.0	4.5 $\pm$ 2.1	5.1 $\pm$ 1.7	12.5 $\pm$ 3.6
Dead <i>M. roseus</i>	119.4 $\pm$ 42.8	43.5 $\pm$ 8.5	42.6 $\pm$ 15.5	12.3 $\pm$ 7.2	106.2 $\pm$ 74.8	215.9 $\pm$ 125.3	6.6 $\pm$ 4.6	4.3 $\pm$ 1.9	5.4 $\pm$ 3.0
Gravel %	5.6 $\pm$ 2.9	5.6 $\pm$ 3.0	6.4 $\pm$ 3.6	1.4 $\pm$ 0.6	14.5 $\pm$ 4.8	5.7 $\pm$ 2.0	0.9 $\pm$ 0.4	2.0 $\pm$ 0.8	1.6 $\pm$ 1.0
Sand %	55.7 $\pm$ 11.5	40.7 $\pm$ 13.0	49.6 $\pm$ 7.9	86.0 $\pm$ 2.3	81.7 $\pm$ 4.7	86.7 $\pm$ 1.9	53.7 $\pm$ 13.0	87.5 $\pm$ 3.6	62.3 $\pm$ 12.1
Mud %	38.7 $\pm$ 12.7	48.6 $\pm$ 13.8	44.0 $\pm$ 9.3	12.6 $\pm$ 2.2	3.8 $\pm$ 0.9	7.6 $\pm$ 1.4	45.4 $\pm$ 13.2	10.5 $\pm$ 3.7	36.1 $\pm$ 12.3
TOC %	9.7 $\pm$ 1.2	8.9 $\pm$ 0.9	7.9 $\pm$ 0.5	3.8 $\pm$ 0.5	5.3 $\pm$ 0.8	6.3 $\pm$ 0.8	8.5 $\pm$ 1.9	6.3 $\pm$ 1.3	7.2 $\pm$ 1.6
Depth (m)	20.0 $\pm$ 3.7	20.0 $\pm$ 3.7	20.0 $\pm$ 3.7	10 $\pm$ 0.0	10 $\pm$ 0.0	10 $\pm$ 0.0	25.0 $\pm$ 4.2	25.0 $\pm$ 4.2	25.0 $\pm$ 4.2



**Figure 16** Macromollusc species richness (MSR), macromollusc species abundance (MSA), macromollusc suspension feeding species richness (MSSR), and macromollusc suspension feeding species abundance (MSSA) by regions over the 100 m transects (mean ± SE). *M. roseus* distribution is shown as bubble plots associated to their relative density. Density description is listed in Table 6.

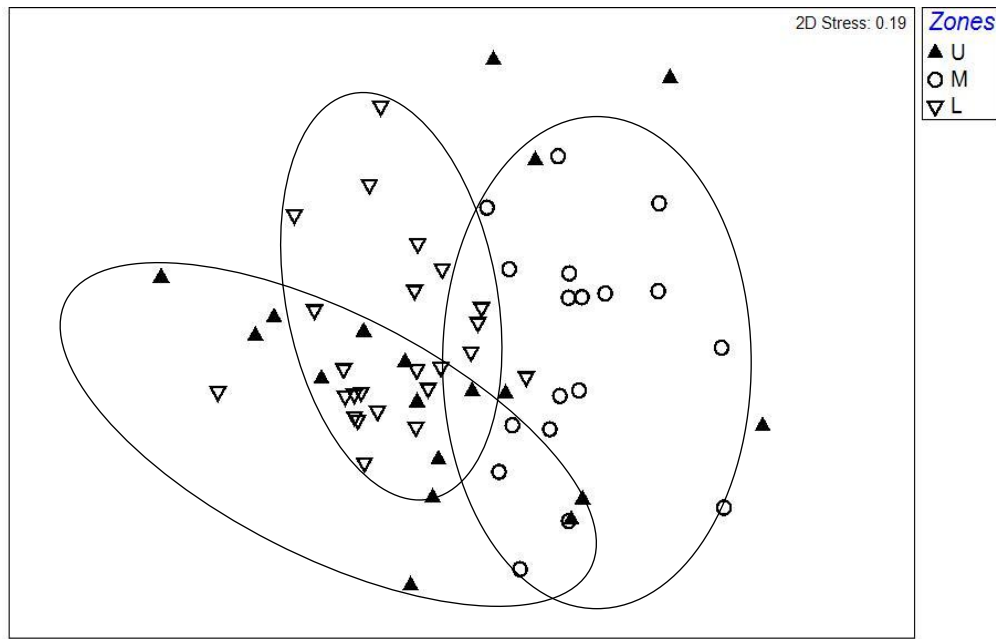
**Table 7** Spearman correlation coefficients between biotic and abiotic variables.

	Macromollusc richness	Macromollusc abundance	Suspension feeding species richness	Suspension feeding species abundance
Live <i>M. roseus</i>	0.10	0.16	- 0.01	0.04
Dead <i>M. roseus</i>	0.21	0.32 *	- 0.13	0.22 *
Gravel %	0.28	0.36 *	0.20	0.37 *
Sand %	0.23	- 0.10	0.16	- 0.10
Mud %	- 0.34 **	- 0.10	- 0.30 *	- 0.14
TOC %	- 0.16	0.10	- 0.15	0.03
Depth (m)	- 0.30 *	- 0.10	- 0.30 *	- 0.13

\*  $p < 0.05$

\*\*  $p < 0.01$

There was a significant variation in the macromollusc community composition within the zones in the D'Entrecasteaux Channel (ANOSIM:  $R = 0.3$ ,  $p < 0.001$ ) (Figure 17). The combined variables *M. roseus* density (live and dead), substrate fractions (gravel, sand, and mud), TOC, and water depth, were significantly correlated to the macromollusc community composition ( $\rho = 0.3$ ,  $P < 0.01$ ). However there was no clear indication between *M. roseus* densities and the abiotic variables as to which variable contributed the most to this association.



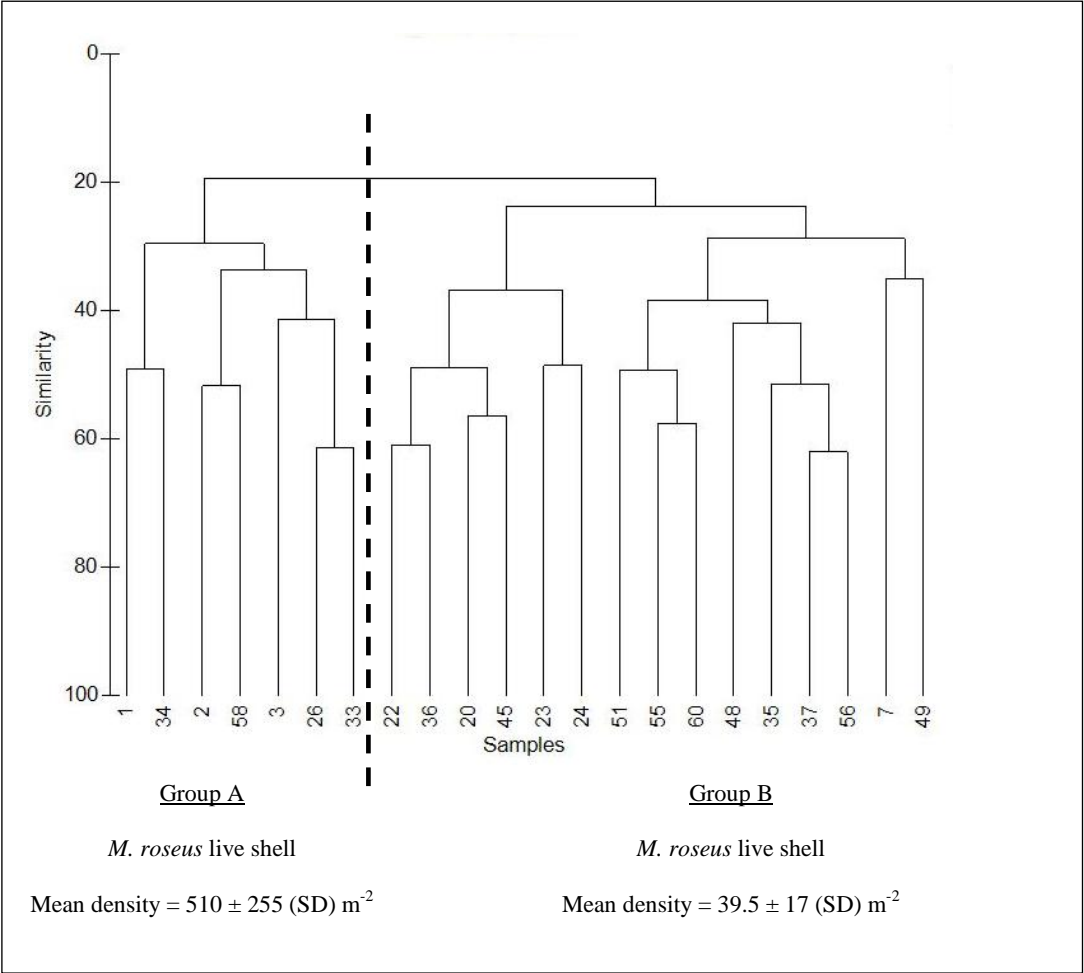
**Figure 17** n-MDS plot based on a similarity matrix for macromollusc species assemblages in the D'Entrecasteaux Channel, with corresponding zones upper (U), medium (M), and low (L). The relative clustering zones are highlighted.

#### 4.4.1 Macromollusc community relationships within the sand substrate class

The BIOENV procedure demonstrated that *M. roseus* live densities were significantly correlated with the species communities ( $\rho = 0.3$ ,  $P < 0.01$ ). A cluster output, produced from Bray - Curtis similarities between sites on the macromollusc community composition, outlined two groups A and B with a similarity level of less than 20 % (Figure 18). Group A and B had a mean *M. roseus* live density of  $510 \pm 255$  (SD)  $\text{m}^{-2}$  and  $39.5 \pm 17$  (SD)  $\text{m}^{-2}$  respectively. SIMPER analysis indicated a species assemblage similarity within groups of 35.33 for A and 31.31 for B. The species *Anachis atkinsoni*, *Pseudamycla dermestoidea* and *Bittium granaria* were dominant in contributing to the similarity within group A, and species *Nassarius nigellus*, *Corbula gibba* and *Hiatella australis* within Group B, with a cumulative contribution of approximately 73% and approximately 70 % correspondingly (Table 8). *Anachis atkinsoni* had the highest ratio of similarity average to the standard

deviation ( $SM / SD = 1.96$ ) in group A, whilst *Nassarius nigellus* had the highest ratio ( $SM / SD = 1.43$ ) in group B. From the species contributing up to 90 % within group similarity, all species were deposit feeders in group A, while in group B all but one species were suspension feeders. Finally, the dominant species contributed 47 % for the dissimilarity between groups (Table 9).





**Figure 18** Dendrogram, based on a cluster analysis produced from Bray-Curtis similarities between sites on macromollusc assemblage data in sand (0.125 - 0.25 mm).

**Table 8** Similarity percentages (SIMPER) analysis results from macromollusc assemblages in sand (0.125 – 0.25 mm), for Cluster group A (live *M. roseus* mean density of  $510 \pm 255$  (SD) / m<sup>2</sup>) and B (live *M. roseus* mean density of  $39.5 \pm 17$  (SD) / m<sup>2</sup>)

Cluster group	Species	Feeding mode	Mean abundance	Mean similarity	Similarity / SD ratio	Contrib. %	Cum. contrib. %
A	<i>Anachis atkinsoni</i>	D	2.14	16.89	1.96	47.82	47.82
	<i>Pseudamycla dermestoidea</i>	D	1.08	4.86	0.84	13.76	61.58
	<i>Bittium granaria</i>	D	1.15	4.12	0.54	11.66	73.24
	<i>Nassarius nigellus</i>	D	1.21	3.70	0.59	10.48	83.72
B	<i>Nassarius nigellus</i>	D	1.81	10.45	1.43	33.38	33.38
	<i>Corbula Gibba</i>	F	1.48	6.17	0.80	19.70	53.08
	<i>Hiatella australis</i>	F	1.18	5.33	0.73	17.04	70.12
	<i>Nemocardium thetidis</i>	F	0.76	1.80	0.49	5.75	75.87
	<i>Nucula oblique</i>	F	0.58	1.27	0.39	4.06	79.93
	<i>Pecten fumatus</i>	F	0.62	1.22	0.31	3.89	83.83
	<i>Venericardia bimaculata</i>	F	0.55	1.06	0.32	3.38	87.21

**Table 9** Similarity percentages (SIMPER) analysis results from macromollusc data in sand (0.125–0.25 mm) for cluster groups A (live *M. roseus* mean density of  $510 \pm 255$  (SD) / m<sup>2</sup>) and B (live *M. roseus* mean density of  $39.5 \pm 17$  (SD) / m<sup>2</sup>). Numbers in bold indicate species that most contributed to similarities within cluster groups (from Table 8).

Species	Mean abundance /site		Between groups mean dissimilarity	Dissimilarity / SD ratio	Contribution %	Cumulative contribution. %
	Cluster group A	Cluster group B				
<i>Anachis atkinsoni</i>	<b>2.14</b>	0.65	8.01	1.39	9.94	9.94
<i>Corbula gibba</i>	0.15	<b>1.48</b>	6.09	1.18	7.56	17.50
<i>Nassarius nigellus</i>	<b>1.21</b>	<b>1.81</b>	5.67	1.09	7.03	24.53
<i>Hiatella australis</i>	0.47	<b>1.18</b>	5.13	1.03	6.36	30.89
<i>Bittium granaria</i>	<b>1.15</b>	0.08	4.97	0.96	6.17	37.06
<i>Pseudamycla dermestoidea</i>	<b>1.08</b>	0.33	4.37	1.20	5.42	42.48
<i>Equichlamys bifrons</i>	0.91	0.00	3.59	1.03	4.45	46.93
<i>Hemitoma submarginata</i>	0.80	0.09	3.30	0.75	4.10	51.03
<i>Nemocardium thetidis</i>	0.00	<b>0.76</b>	2.96	0.84	3.67	54.70
<i>Pecten fumatus</i>	0.15	<b>0.62</b>	2.93	0.67	3.64	58.34
<i>Gazameda gunnii</i>	0.29	0.48	2.83	0.73	3.51	61.85
<i>Musculus impactus</i>	0.23	0.52	2.82	0.59	3.49	65.34
<i>Venericardia bimaculata</i>	0.15	<b>0.55</b>	2.53	0.68	3.15	68.49
<i>Nucula oblique</i>	0.00	0.58	2.50	0.67	3.10	71.59
<i>Tawera gallinula</i>	0.29	0.27	2.11	0.58	2.62	74.22
<i>Clanculus aloysii</i>	0.45	0.12	1.87	0.62	2.33	76.54
<i>Fusinus novaehollandiae</i>	0.24	0.30	1.80	0.62	2.23	78.77
<i>Neotrignia margaritacea</i>	0.27	0.10	1.61	0.47	1.99	80.77
<i>Calyptraea calyptraeformis</i>	0.39	0.10	1.50	0.64	1.87	82.63
<i>Guraleus sp</i>	0.39	0.09	1.48	0.64	1.83	84.47
<i>Chlamys asperrimus</i>	0.37	0.00	1.47	0.40	1.83	86.30
<i>Austromitra analogica</i>	0.39	0.00	1.41	0.57	1.76	88.05
<i>Timoclea cardioides</i>	0.26	0.20	1.32	0.56	1.64	89.69

#### **4.5 Discussion**

The macromollusc species found in the survey were generally typical of the Tasmanian benthic environment (May 1958, Edgar 2000). The most abundant species collected in this study were *Corbulla gibba*, *Nemocardium thetidis*, *Hiatella australis*, and *Nassarius nigellus*, which were also prominent in a study carried - out in the D'Entrecasteaux Channel by Edgar *et al.* (2005b).

Some patterns emerged from an investigation of *M. roseus* densities and the abiotic characteristics associated with the distribution of macromolluscs across the whole D'Entrecasteaux Channel. The central parts of the D'Entrecasteaux Channel supported larger macromollusc richness and abundances. Macromollusc suspension feeding species were also more abundant in the middle parts of the channel. These areas were generally also characterised by higher live *M. roseus* densities when compared to the rest of the surveyed area. Water currents (Mitchell and Crawford 1995) and nutrient levels (Butler *et al.* 2000, Macleod and Helidoniotis 2005, Wild-Allen *et al.* 2005) are relatively higher in the middle regions of the D'Entrecasteaux Channel, and the central parts of the channel are primarily characterised by coarser substrate (sand or greater). Coarser substrate is generally a response to an increase in water flow, which promotes higher nutrient availability (Hawkins *et al.* 1989, Shimeta and Jumars 1991, Riisgard and Larsen 2001, Gardner 2002). This may explain the increase in macromolluscs assemblages in the central regions of the D'Entrecasteaux Channel. Similarly elsewhere, such as in the English Channel (Sanvicente-Anorve *et al.* 2002), Ria de Aldan (Spain) (Lourido *et al.* 2006) and in Port Phillip Bay (Australia) (Poore and Rainer 1974), the distribution of molluscs were primarily related to substrate type and food supply characteristics.

There were some interesting trends in the abundance of macromolluscs with shells of dead *M. roseus*. From the species that most contributed to the high macromollusc abundances across the surveyed sites, the suspension feeding bivalve *Hiatella australis* was present in high numbers in areas with high densities of dead *M. roseus* ( $R = 0.26$  ,  $P < 0.05$ ). This positive relationship probably explains the strong association between dead *M. roseus* and macromollusc abundances, and suspension species abundances in the analyses. Gutierrez (2003) described that shell production can increase species numbers at the landscape level if shells create resources that are not otherwise available. For example, formed shell mats of the introduced bivalve *Musculista senhousia* in Mission Bay (North America) facilitated an increase in macrofauna abundances and species richness (Crooks 1998). In South Africa, the non native *Mytilus galloprovincialis* beds altered the densities of co - occurring benthic fauna (Branch *et al.* 2008). Shells from dead *M. roseus* may be habitat that promotes the recruitment of *Hiatella australis*. A field experiment in Australia, using artificial substrate demonstrated that substrate type can promote the recruitment of *H. australis* (Rule and Smith 2005).

Interestingly, this pattern did not occur to the same extent with live *M. roseus*. Maybe active feeding by *M. roseus* depleted the abundance of *H. australis* larvae. Predation of bivalve larvae by benthic suspension feeders is not atypical (Andre *et al.* 1993, Troost *et al.* 2008). Laboratory investigations where live *M. roseus* and larvae from a bivalve (*P. fumatus*) were both placed in aquaria showed that *M. roseus* reduced the number of larvae (see Appendix). Although the densities of *P. fumatus* larvae and other factors such as water currents may have differed between the natural

environment and experiments in aquaria, the results support the notion that *M. roseus* can potentially feed on *P. fumatus* larvae. Furthermore, remains of the bivalve were found in the gut of *M. roseus*.

Nicastro *et al.* (2009) did not find enough evidence to show that shells from dead *M. roseus* modified benthic community structure, however they acknowledged that their results should not be generalised and further studies were needed in different locations. Their study was carried out in a dynamic coastal lagoon in NSW (Australia). The lagoon entrance had constant changes in geomorphology and physical and chemical attributes. Therefore the shells may not have persisted for long enough in the benthos to produce community change (Hastings *et al.* 2007). Once established, turritellid gastropod shells such as *M. roseus* are able to persist for a long period of time (Marwick 1971, Allmon 1988). Large fossil assemblages of turritellids demonstrate their resilience throughout time (Allmon and Knight 1993, Allmon 2011). Habitat provision generated by faunal assemblages has previously been described (Thompson *et al.* 1996, Crooks and Khim 1999) and has been shown to facilitate increases in the abundance and diversity of some native species (Hewitt *et al.* 2005, Wonham *et al.* 2005). In a recent study, shells from dead *M. roseus* were found to impact on the community structure of some Crustacea, such as promoting aggregations of native hermit crabs (Reid 2004, Reid 2010).

The community composition of macromolluscs varied significantly across the D'Entrecasteaux Channel and the correlation analysis (BIOENV) demonstrated that *M. roseus* densities combined with the abiotic variables explained some of this variation. However, due to the complex interactions it was difficult to separate out

the effects of each of these factors. Patterns of associations between live *M. roseus* and the macromollusc community composition became more apparent in the data analyses carried - out within *M. roseus* favoured habitat characterised by sand.

Within the sand substrate, live *M. roseus* were significantly correlated to the macromollusc species composition. Two faunal groups were observed (Figure 18) with all of the dominant species in one group (A) being deposit feeders, while for the other group (B) all dominant species but one (*Nassarius nigellus*) were suspension feeding species (Table 8). Critical to note, is that group A had *M. roseus* live mean density of a 510 / m<sup>2</sup>, while group B density was 39.5 / m<sup>2</sup>. This suggests an interaction between *M. roseus* and other macromolluscs species with a similar feeding mode. However, this pattern was not apparent when using the whole data set including all substrate types. The results are similar to findings by Reid (2010), where experiments in similar environments demonstrated that benthic communities with high live *M. roseus* densities generally had a lower number of suspension feeding species compared to areas with lower live *M. roseus* densities.

There was also a lower density of the Tasmanian native turritellid *Gazameda gunnii* and the scallop *Pecten fumatus* in group A (Table 9). This supports the view that *M. roseus* may be having an impact on these species (Bax *et al.* 2003). In a recent study by Reid (2010) *Pecten fumatus* showed restricted growth in the presence of live *M. roseus*. Benthic competition for food and space among suspension feeding molluscs in soft bottom environments has been previously described (Peterson and Andre 1980, Talman and Keough 2001) where interactions between species were shown to result in decreased populations due to emigration, rather than direct mortality. This

is supported by the results from this study, where the dominant species from one group were still present in the other group, though at lower abundances.

Although direct competition for food might occur between *M. roseus* and other suspension feeding macromolluscs species, there are other processes that also need to be considered, for example, the ingestion of larvae (Andre *et al.* 1993) and *M. roseus* interference with the substrate surface via the accumulation of shells, potentially impacting the settlement of macromolluscs (Gutierrez *et al.* 2003). The variation in deposit feeding macromollusc densities that occurred in both density groups suggests that processes other than competition amongst the suspension feeders were also occurring. While suspension and deposit feeding molluscs generally have different feeding behavior and nourish on different types of food (Levinton 1972, Kamermans *et al.* 1992, Navarro *et al.* 2008), a direct impact can occur if both groups rely on the same food sources (Kamermans 1994). Also, areas highly populated with *M. roseus* have been observed in Manukau Harbour, Lyttelton Harbour, and Otago Harbour in New Zealand, where this species shared habitats with other dominant molluscs that had both similar and different feeding modes (McKnight 1969, Knight 1974, Rainer 1981, Hayward *et al.* 1997, Abraham *et al.* 2007). Manipulative experiments are needed in order to determine which processes are dominant.

This study suggests that *M. roseus* in combination with other environmental variables affected the co - occurring macromollusc fauna in the D'Entrecasteaux Channel, and individually within *M. roseus*' preferred habitat characterised by sand. It is suggested that *M. roseus* may be having an effect on macromollusc faunal assemblages via changes in the benthic habitat due to their physical presence,



through altering the substrate type, or biological activity via competition through suspension feeding. These effects may be negative (e.g., larval depletion, competition for food) or positive (e.g., providing substrate for larval recruitment). Manipulative experiments are required to identify the potential mechanisms underpinning the relationships between *M. roseus* and other macromolluscs observed in this study.

## **5. Chapter Five**

### **Population characteristics and planktonic larval stage of the New Zealand Screwshell *Maoricolpus roseus***

Published in,

Probst TA, Crawford CA. 2008. Population characteristics and planktonic larval stage of the New Zealand screwshell *Maoricolpus roseus*. Journal of Molluscan Studies, 74(2): 191-197.

**POPULATION CHARACTERISTICS AND  
PLANKTONIC LARVAL STAGE OF THE NEW  
ZEALAND SCREWSHELL *Maoricolpus roseus***

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Running head:

*M. roseus* POPULATION AND LARVAL CHARACTERISTICS

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## ABSTRACT

*Maoricolpus roseus* is a caenogastropoda (prosobranch) gastropod believed to have been introduced into Tasmania (Australia) in the 1920's. Despite its wide distribution, dense populations, and being considered successful in colonising and altering several habitats, detailed aspects of its reproduction and life-cycle are not known. *Maoricolpus roseus* collected from the D'Entrecasteaux Channel (SE Tasmania) over two years showed sexual dimorphism with females relatively larger than males. A 1:1 sex ratio was observed and females were found carrying encapsulated larvae throughout consecutive austral summer seasons (September or October till February), with up to 70 % of females carrying larvae. Larvae released from egg capsules were planktonic, all relatively well developed, and feeding on microalgae, thus proposing that the species has planktotrophic, rather than lecithotrophic development, suggesting high dispersal potential. This information is important to the development of management strategies for this invasive species.

## INTRODUCTION

The New Zealand screwshell *Maoricolpus roseus* is a benthic marine gastropod (Subclass Caenogastropoda, Family Turritellidae) believed to have been introduced into Tasmania, Australia in the 1920's (Greenhill 1965, Paul 1979). This species is found over a wide area on fine to coarse substrates at depths of 0 - 200 m (Bax *et al.* 2003, Beaman *et al.* 2005), with live densities exceeding 1500 /m<sup>2</sup> in the D'Entrecasteaux Channel in south-eastern Tasmania (T. Probst, unpublished data). It is thought to pose a threat to local species, including the native turritellid *Gazameda gunnii*, because large accumulations of living and dead *M. roseus* shells have substantially altered the habitat in many coastal areas around Tasmania (Edgar 2000), potentially making the environment unsuitable for survival of native species.

Despite its wide distribution and dense populations, detailed aspects of *M. roseus* biology and ecological impacts on the Tasmanian marine environment have not been studied (Bax *et al.* 2003). Information from New Zealand mainly relates to distribution (Morton and Miller 1968, McKnight 1969, Allmon *et al.* 1994), with limited data on life history (Marwick 1971, Pilkington 1974). In Australia, Scott (1997) described some initial information on *M. roseus* feeding, respiration and growth, while Bax and Williams (2001) and Bax *et al.* (2003) summarised preliminary information on population distribution in south-eastern Australia, habitat preferences, shell size, reproduction, and predation.

Initial observations on the biology and life cycle (Marwick 1971, Pilkington 1974, Bax *et al.* 2003), and evolutionary patterns (Lieberman *et al.* 1993) of this species

indicated separate sexes, with eggs deposited in egg capsules in the female mantle cavity. The number of developing embryos per capsule decreased as the embryo size increased, and only a few of the embryos became motile trochophore and veliger larvae within the egg capsule (Pilkington 1974, Bax *et al.* 2003). Pilkington (1974) concluded that the larval stage was completed within the egg capsules of females, i.e. direct development. Recent studies, however, proposed a possible planktonic stage and larval hatching period during the austral summer season (Bax *et al.* 2003, Gunasekera *et al.* 2005), although live planktonic larvae were not observed.

The distribution of *M. roseus* around Australia has recently expanded with reported findings in South Australia (SERSA 2003), Victoria (Bax and Williams 2001), New South Wales (Pollard and Rankin 2003) and Queensland (SERQLD 1999). Rapid population expansion over a relatively wide geographical area in a relative short period of time has been described as characteristic of gastropods with a planktonic larval stage (Scheltema 1986, Levin and Bridges 1995). Other turritellids have planktonic veligers (e.g., Marwick 1954, Allmon *et al.* 1992, Kennedy and Keegan 1992, Romero and Valdebenito 2002), further suggesting the possibility of *M. roseus* having indirect larval development.

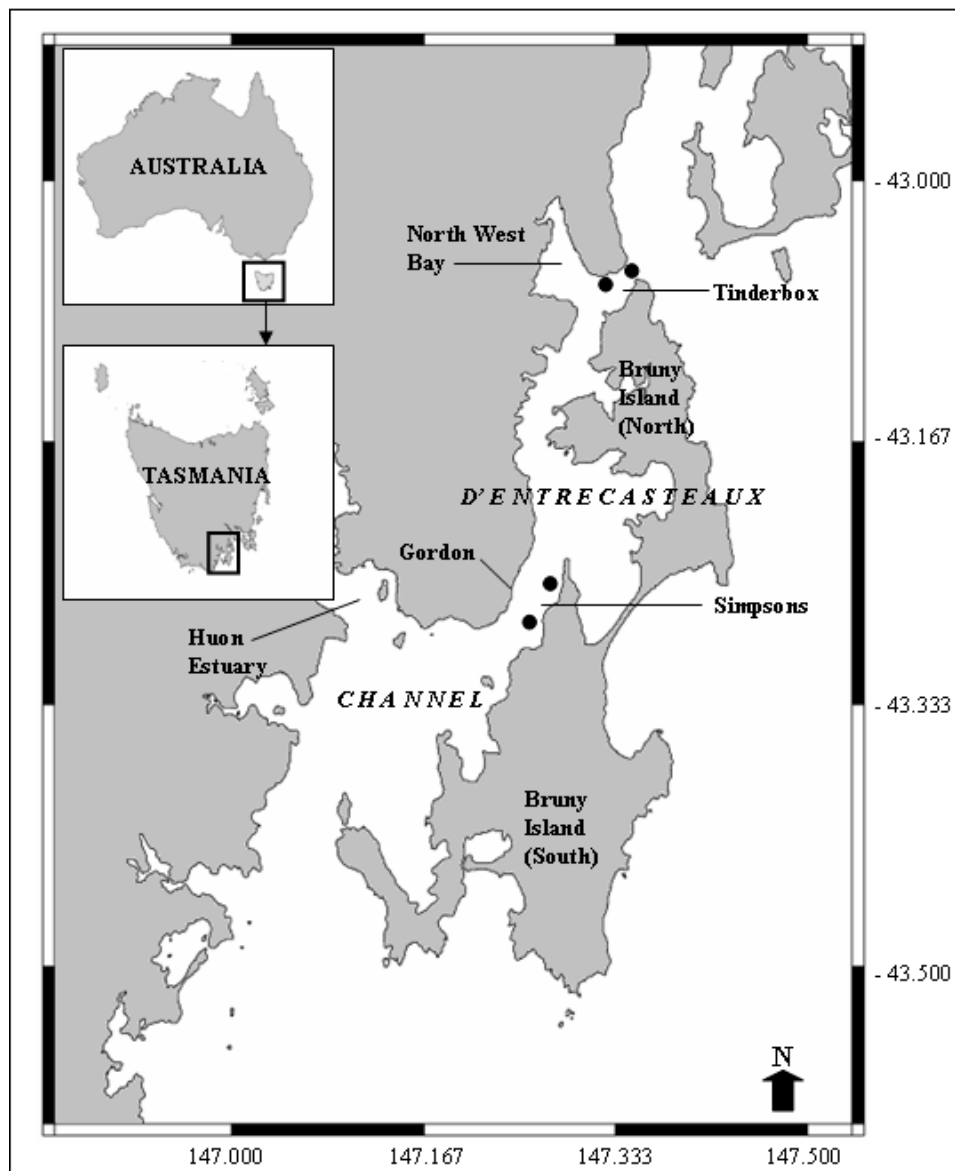
Rearing of *M. roseus* in order to describe its larval development has not been successful in the past (Pilkington 1974, Bax *et al.* 2003). Further information on the life history is essential to understand its current and potential future distribution, and to develop a risk assessment strategy and management of the geographical expansion of the species. Our study aimed to describe aspects of *M. roseus* reproduction and larval characteristics. In particular, the population dynamics of reproductive *M.*

*roseus*, the temporal pattern of egg encapsulation and to clarify whether *M. roseus* has direct or indirect embryonic development.

## MATERIALS AND METHODS

### *Maoricolpus roseus* population dynamics

*Maoricolpus. roseus* were collected from two locations, Tinderbox and Simpsons, in the D'Entrecasteaux Channel (Figure 19). Locations were approximately 30 km apart and had high densities of live *M. roseus* shells ( $\approx 500 \text{ m}^{-2}$ ). Two replicate sites were sampled at each location, with similar type of substratum (fine sand with predominant particle size 0.125 - 0.25 mm), water depth (10 - 15 m) and distance from shoreline (25 m).



**Figure 19** D'Entrecasteaux Channel showing sampling sites (●) at locations Tinderbox and Simpsons. (Map coastline based on NGDC 2007))



At each replicate site within each location, 300 shells were randomly collected each month from September 2003 to October 2005 from an area of 50 m<sup>2</sup> by SCUBA diving. Collected samples were processed in the laboratory within 24 to 48 hours by cracking open the shell until the required number of live animals had been found. From September to November 2003 information on shell length, sex type, and gonad characteristics was recorded from 200 live animals collected at each site. From September 2003 to October 2005, the appearance of egg capsules and the developmental stage of larvae inside the egg capsules in 100 females from each site were examined in the laboratory. The size of females and egg capsules, colouration, and number of eggs / larvae within capsules were recorded. A temperature logger was deployed at Tinderbox (Figure 19) one metre above the sea bed.

Differences in length-frequency distributions of *M. roseus* total population, males, females and females with egg capsules were examined using the Kolmogorov - Smirnov test. Analyses of the male / female ratio were carried out by a G - test (Sokal and Rohlf 2003), while correlation analyses (Spearman correlation coefficient) were performed to test the relationship between temporal patterns of *M. roseus* holding egg capsules and the annual fluctuations of water temperature.

#### *Description of M. roseus larvae*

*Maoricolpus roseus* females holding egg capsules were collected via SCUBA diving from Tinderbox and Simpsons (Figure 19) to investigate larval development.

In an initial trial, animals were placed in six 5 litre tanks (primary tanks) with flow-through unfiltered seawater at ambient conditions (temperature 14 - 18 °C, salinity

30 - 33 PSU, and natural photoperiod). Each primary tank had a water outlet flowing into a five litre drain tank. Any larvae released from egg capsules were retained in the drain tank by placing a retention mesh (100  $\mu\text{m}$ ) on the water outlet. A mesh size of 100  $\mu\text{m}$  was used as pilot studies observed *M. roseus* larvae inside capsules before hatching were approximately 150  $\mu\text{m}$  in size. A small silicone aeration pipe (2 mm in diameter) was attached to the water outlet next to the retention mesh to avoid obstruction of the drain and loss of larvae.

Larvae hatched from egg capsules were collected from drain tanks and transferred to replicated 250 ml plastic containers containing either unfiltered, 200  $\mu\text{m}$  or 5  $\mu\text{m}$  filtered, or ozone treated seawater (water held at  $> 600$  Oxidative Reductive Potential for 10 min before being passed through a UV sterilization unit and charcoal filter tanks). Each tank had a density  $\approx 2$  larvae  $\text{ml}^{-1}$  and was supplied with an equal mixture of microalgae *Isochrysis galbana*, *Pavlova lutheri*, *Nannochloropsis oculata*, and *Chaetoceros muelleri* at a total average density of  $\approx 18 \times 10^4$  cells  $\text{ml}^{-1}$ . Microalgae were added to experimental containers every 2 to 3 days *ad libitum* to maintain this density, which lightly coloured the water and is approximately that used in oyster culture (Helm and Bourne 2004). Larvae were observed on a daily basis to monitor their development and they were measured every 7 days.

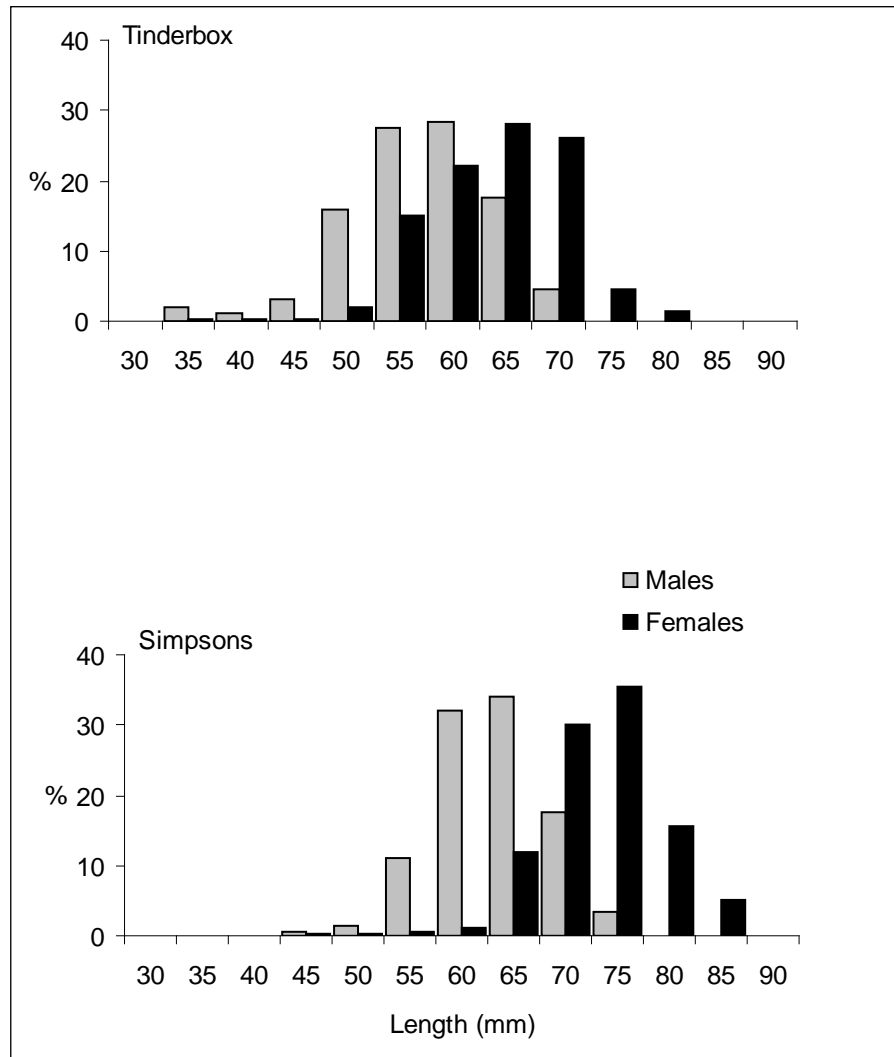
In a second trial, substrates were added to rearing tanks to potentially induce *M. roseus* larval settlement. Larvae were placed at a density of  $\approx 1$  larvae  $\text{ml}^{-1}$  in four 35 L tanks filled with ozone filtered seawater and under ambient conditions. Each tank was aerated and supplied with microalgae as for the initial trial. Every three days approximately two-thirds of the water in each tank was replaced with seawater at a

salinity of 30 - 33 PSU. Two dishes filled with a mixture of shell and sand particles (sizes 0.25 - 1.0 mm and 0.125 - 0.25 mm respectively), and two acrylic plates coated with biofilm (composed mainly of green algae and benthic diatoms) were placed at the bottom of three tanks prior to the addition of larvae. The fourth tank (control) did not contain any added substrate. The sediment was collected from areas within the D'Entrecasteaux Channel where adult *M. roseus* were present. Benthic biofilm plates were conditioned in a flow-through unfiltered seawater tank ( $\approx 120 \text{ m}^3$ ) to allow accumulation of a primary fouling film. Throughout the larvae rearing trials subsamples from the sediment dishes and biofilm plates were examined every three days for the presence of *M. roseus*. Ten larvae were collected from the water column each week to monitor their development and measure their length.

## RESULTS

### *Maoricolpus roseus* population characteristics

*Maoricolpus roseus* collected from September to November 2003 from both locations in the D'Entrecasteaux Channel ranged in length between 33.5 mm and 85 mm ( $n = 2400$ ), with means of  $58.48 \pm 0.21$  mm for Tinderbox, and  $66.1 \pm 0.21$  mm for Simpsons. Total population length-frequency distributions differed significantly between locations (Kolmogorov - Smirnov:  $Z = 9.43$ ,  $P < 0.001$ , Figure 20). Both males and females had lower mean and maximum lengths at Tinderbox than at Simpsons.



**Figure 20** *M. aoricolpus roseus* male and female shell length frequency at Tinderbox and Simpsons. Number of shells measured at Tinderbox males n = 579, females n = 621; Simpsons males n = 612, females n = 588.

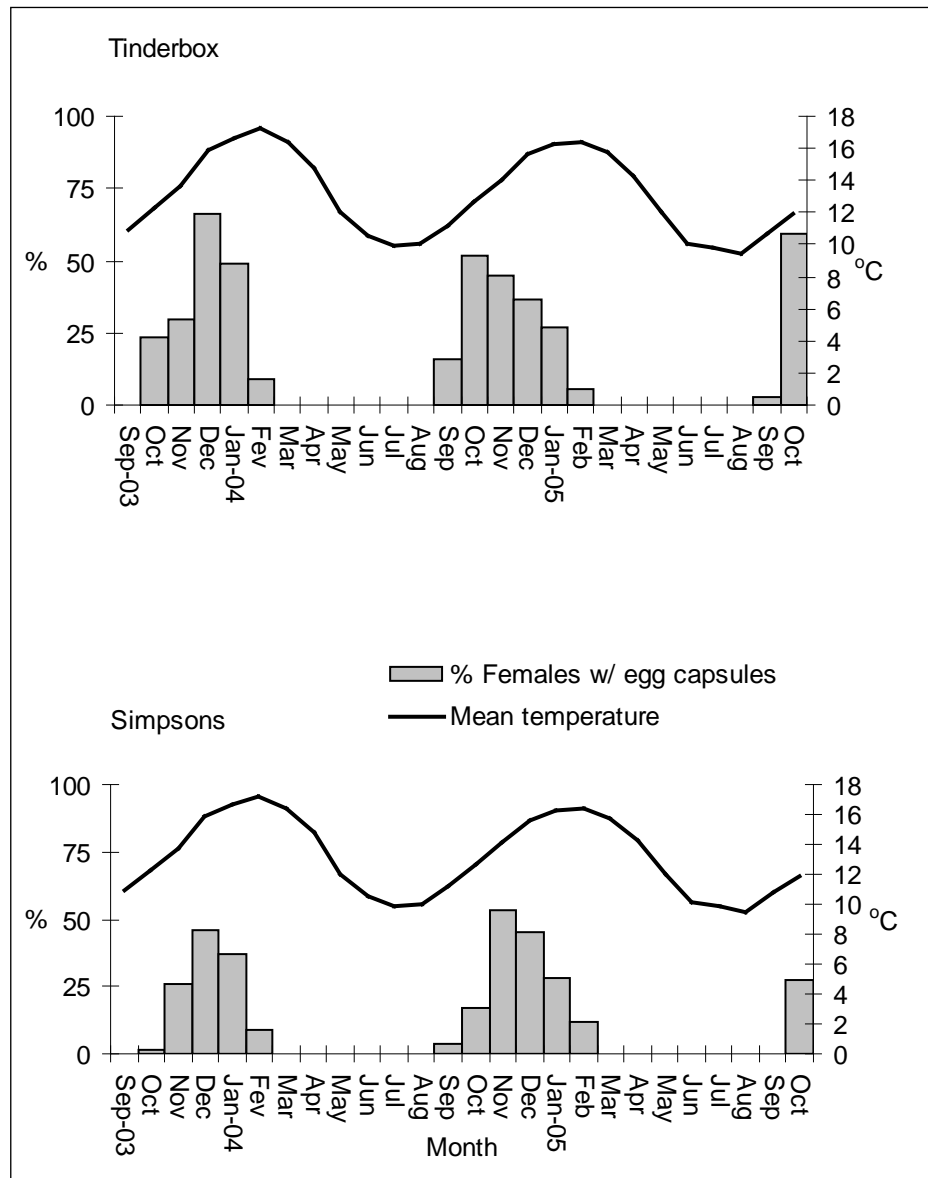
Proportions of females did not depart significantly from the expected 1:1 ratios within each location (G-test:  $G = 1.47$ ,  $P = 0.23$  for Tinderbox, and  $G = 0.48$ ,  $P = 0.49$  for Simpsons), and the mean length of males ( $55.24 \pm 0.27$  mm Tinderbox,  $61.11 \pm 0.21$  mm Simpsons) was less than females ( $61.73 \pm 0.26$  mm Tinderbox,  $71.09 \pm 0.22$  mm Simpsons). There was a significant difference in length-frequency

distributions for sex type within Tinderbox and Simpsons (Kolmogorov - Smirnov:  $Z = 6.582$ ,  $P < 0.001$ , and  $Z = 11.78$ ,  $P < 0.001$  respectively, Figure 20).

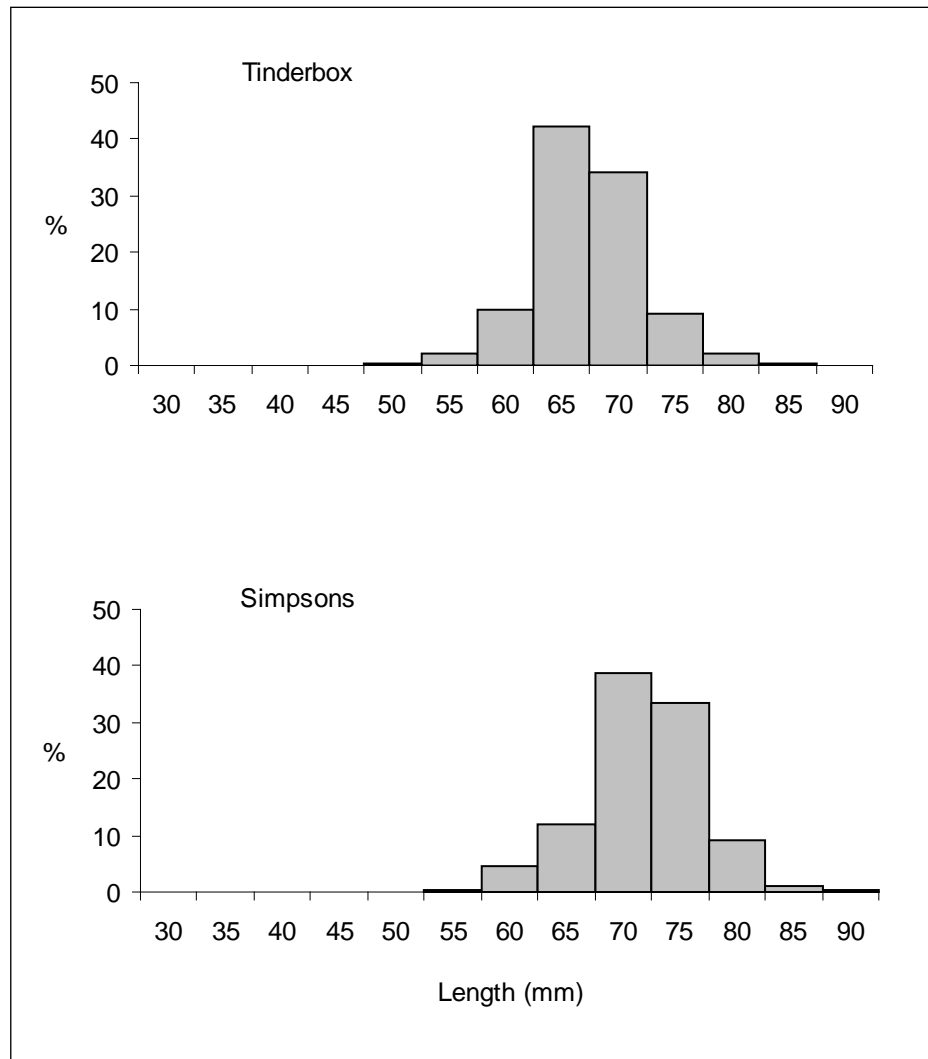
Inspection of gonads showed that males had active biflagellate sperm throughout the whole sampling period (September 2003 to October 2005) with gonads characterised by a red to light-brown colouration in contrast to orange for females. All animals observed ( $n = 2400$ ) had clearly either male or female structures.

Females with egg capsules were found at each sampling period between October 2003 and February 2004, September 2004 and February 2005, and September and October 2005 (when sampling ceased). The water temperature data from the logger deployed at Tinderbox was used for both locations, based on Herzfeld *et al.* (2005) who found that temperatures did not vary significantly between these two locations. There was a 1 to 3 month lag between the peak proportion of females holding egg capsules and the highest water temperature (Figure 21). Taking into account the time-lag, there was a positive association between increasing water temperature and the proportion of females holding egg capsules during the monitored period at both sampled locations (Tinderbox:  $R = 0.84$ ,  $P < 0.01$ ; Simpsons:  $R = 0.80$ ,  $P < 0.01$ ).

Females with egg capsules had a larger mean size at Simpsons ( $69.75 \pm 0.21$  mm,  $n = 601$ ) than Tinderbox ( $65.43 \pm 0.19$  mm,  $n = 667$ ) and there was a significant difference in length-frequency distributions between locations (Kolmogorov - Smirnov:  $Z = 7.41$ ,  $P < 0.01$ , Figure 22).



**Figure 21** Percentage of *M. roseus* females with egg capsules present in each month at locations Tinderbox and Simpsons.



**Figure 22** *Maoricolpus roseus* females with egg capsules shell length frequency at Tinderbox and Simpsons. Number of shells measured at Tinderbox n = 667, and at Simpsons n = 601.

### *Maoricolpus roseus* larvae

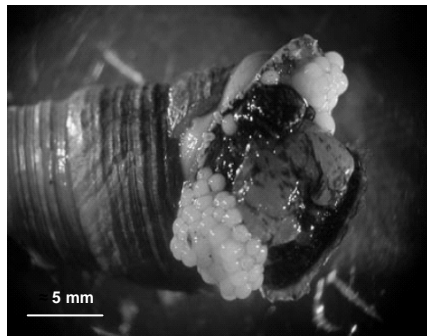
At both locations it was observed that female *M. roseus* (n = 1268) held masses of circular egg capsules within the mantle cavity close to the operculum (Figure 23) which were characterised by white changing to transparent colouration from the start to the end of larval release. Egg masses contained  $126.4 \pm 3.44$  capsules (n = 20 egg masses examined). Early season capsules were 0.9 - 1.1 mm in size and later transparent capsules (size 1.4 - 1.7 mm) enclosed 30 to 50 motile larvae (mean number of veligers =  $42.70 \pm 1.02$ , n = 50 egg capsules) at the veliger stage (Figure



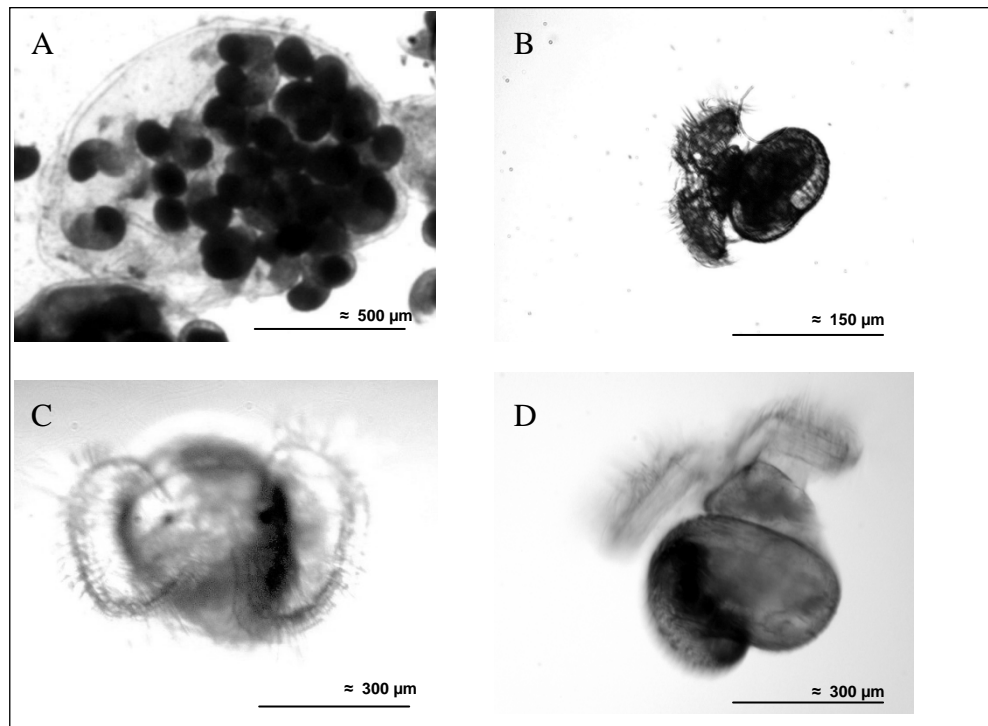
24 A). Veligers developed a one whorl transparent soft shell with a protruding bilobed clear velum (Figure 24 B).

Veligers released from egg capsules had a mean size of  $141.50 \pm 1.86 \mu\text{m}$  ( $n = 100$ ) and  $143.00 \pm 3.00 \mu\text{m}$  ( $n = 40$ ) for trials one and two, respectively. In all rearing tanks in both trials the hatched veligers immediately began feeding on the supplied microalgae, which was clearly visible in their guts. Veligers were motile and moved randomly in a spiral manner through the water column. After one week they had a mean size of  $287.50 \pm 2.18 \mu\text{m}$  (trial one) and  $266.25 \pm 3.75 \mu\text{m}$  (trial two). After two weeks the mean length of veligers was  $507.50 \pm 1.93 \mu\text{m}$  (trial one) and  $510.00 \pm 4.08 \mu\text{m}$  (trial two), with a developed propodium, tentacles and a shell characterised by approximately  $2\frac{1}{2}$  whorls and light-pink colouration ( $n = 100$ , trial one;  $n = 40$ , trial two) (Figure 24 C and D).

There were no significant differences in veliger sizes between the different water types used in the initial rearing trial for the 7 day ( $F_{3,96} = 0.89$ ,  $P = 0.45$ ) and 14 day ( $F_{3,96} = 2.30$ ,  $P = 0.1$ ) periods. There were also no significant differences in veliger sizes between the tanks in trial two for the 7 day ( $F_{3,36} = 0.39$ ,  $P = 0.76$ ) and 14 day ( $F_{3,36} = 0.73$ ,  $P = 0.54$ ) periods. Efforts to rear the larvae beyond the 14 day period failed in both trials. No live juveniles were found in any tanks or on experimental substrate plates, in contrast a large quantity of ciliates and fungal contamination was observed.



**Figure 23** *Maoricolpus roseus* female holding early egg capsules [note that outer shell whorl is broken away (image courtesy Bax *et al.* 2003)].



**Figure 24** Development of *M. roseus*. A. Late egg capsule releasing veligers. B. Early veliger larvae (side view) during release from egg capsule. C, D. Late veliger larvae (frontal C and side view D), 14 days after release from egg capsule.

## DISCUSSION

### Population characteristics of *M. roseus*

The sex-ratio did not depart significantly from 1:1 at either location, and males and females each had gonads with distinctive morphology colouration; the species is gonochoristic. These findings support previous observations of sexual dimorphism in other Turritellidae (Allmon 1988, Kennedy 1995) and separate sexes for *M. roseus* (Allmon 1988, Bax *et al.* 2003). Hermaphroditism is atypical in prosobranchs (Fretter 1984), nevertheless it has been previously described in some gastropods (e.g., Richter and Luque 2004, Calvo and Templado 2005) and the native turritellid *Gazameda gunnii* (Carrick 1980a).

There was a significant difference in shell length *M. roseus* between locations, with the population from Tinderbox having a smaller average shell size than at Simpsons. Both locations had similar geographical characteristics of depth, substrate type, distance from shore, and temperature (Herzfeld *et al.* 2005). *Maoricolpus roseus* is a suspension feeder and growth rates have been described to be positively related to levels of planktonic microalgae (Scott 1997). While both areas have high nutrient concentrations (Butler *et al.* 2000, Macleod and Helidoniotis 2005), Simpsons has relatively higher water current levels than Tinderbox (Mitchell 1995). The association between water currents and food availability has previously been described as affecting population growth of suspension feeders (e.g., Bayne and Hawkins 1990, Shimeta and Jumars 1991, Genovese and Witman 1999). Hence the larger size of *M. roseus* at Simpsons may be related to the higher water flow rate and therefore relatively more rapid replenishment of phytoplankton.

Population density could also have an impact on animal size. Increased competition for space and food at higher population densities have been found to be negatively correlated with the size of suspension feeders (e.g., Alunno-Bruscia *et al.* 2001, Lohse 2002, Lopez and Gonzalez 2003). Mean densities of *M. roseus* in localised areas at the Tinderbox and Simpsons sampling sites were similar at approximately 500 m<sup>-2</sup>. However, over a 5 km<sup>2</sup> area at each location, Tinderbox had a higher overall *M. roseus* density because the population was more uniformly distributed and less patchy than at Simpsons (T. Probst, unpublished data) which could lead to greater competition for food.

Our results for *M. roseus* population shell length are similar to those previously reported by (Bax *et al.* 2003) in the D'Entrecasteaux Channel, where specimens from Tinderbox were relatively smaller in size compared to those at Gordon. Gordon is located opposite Simpsons in the D'Entrecasteaux Channel (Figure 19), demonstrating a similar size pattern for the population in the region.

Females at Tinderbox and Simpsons were found holding egg capsules for almost half the year (September to February). This annual pattern was observed to be closely associated with the annual seasonal water temperature change and confirms preliminary results from Bax *et al.* (2003) and Pilkington (1974).

#### *Maoricolpus roseus* larvae

We observed that *M. roseus* egg capsules were held by females until larvae were released into the water column. This is in contrast to the turritellids *T. variegata*

(Bandel 1976) and *T. gonostoma* (Allmon *et al.* 1992), which were observed to attach encapsulated larval masses to sediments or hard substrata. In our larval rearing trials in both seasons (2003 - 04 and 2004 - 05) *M. roseus* had mature egg capsules with 30 to 50 motile planktotrophic veligers at a similar stage of development, which were released simultaneously into the water column. This differs to the Tasmanian native turritellid *Gazameda gunnii*, where females have been described to release benthic crawling juveniles with an initial developed whorled shell (Carrick 1980a). While we did not observe any direct fertilization of *M. roseus*, male turritellids have been described to spawn sperm into the water column, which are passively taken in by the females through their mantle cavity via their feeding and respiratory system (Morton and Miller 1968, Fretter and Manly 1979). However, active sperm transfer through gregariousness and pseudo-copulation is also a possibility (Kennedy 1995).

*Maoricolpus roseus* planktonic veligers began shell coiling and doubled in size after 2 weeks. These results differ to findings by Pilkington (1974) that of approximately 60 encapsulated embryos, only 7 - 8 were found to develop into veligers. Pilkington (1974) further proposed that the remaining undeveloped embryos could potentially function as nutrient nurse cells for the encapsulated developing veligers, which would later hatch as developed benthic juveniles. The morphology of veligers from our observations was similar to that described by Pilkington (1974) and Bax *et al.* (2003), however no previous studies have found larvae surviving outside the egg capsules. Furthermore, our consistent observations of high numbers of veligers (up to 50) released from egg capsules with highly synchronised development suggest indirect larval development. That this species has a pelagic free swimming larval stage is also supported by the recent detection of the *M. roseus* gene by genetic

probes in plankton hauls from the D'Entrecasteaux Channel (Gunasekera *et al.* 2005).

Attempts to rear larvae past two weeks were unsuccessful despite using differing quality seawater and providing substratum for settlement. As with previous rearing attempts by Pilkington (1974) and Bax *et al.* (2003), a large quantity of ciliates and fungal contamination were observed in the tanks both with and without substratum. Deaths of larvae have previously been described to be related to infection by bacteria and ciliates (Soliman, 1991)(Soliman 1991); however, contamination may have also occurred after larval mortality, having no direct impact on veliger survival. Larval settlement and metamorphosis are generally highly responsive to associated substrate, nutrient, and water borne cues such as salinity, temperature and chemical compounds (e.g., Chia and Rice 1978, Burke 1983, Rodríguez *et al.* 1993, Kingsford *et al.* 2002) and can impact on the temporal duration of the planktonic stage by delaying settlement until ideal conditions are found (Hadfield and Strathmann 1996). It is possible that a lack of settlement cues and unregulated environmental conditions may have contributed to the mortality of *M. roseus*, although it is not known whether the larvae reached the stage where they were competent to metamorphose. Further research is needed to identify the environmental conditions required to support settlement and metamorphosis.

Prosobranch gastropods with a planktonic larval stage have shown to have on average a greater geographical range than species with direct development (Scheltema 1986, Scheltema 1989). The combination of a high percentage of females carrying larvae, with a relatively well developed planktonic life stage and

planktotrophic feeding mode, suggests *M. roseus* has high dispersal potential. This supports the relative rapid extension of distribution of *M. roseus* on the Australian coast since its believed introduction in Tasmania in the 1920's.

## **ACKNOWLEDGEMENTS**

We acknowledge the support of the Tasmanian Aquaculture and Fisheries Institute at the University of Tasmania for providing equipment and research facilities. S. Battaglione, A. Beech, and B. Wilkinson for providing assistance with the aquaria facilities. Special thanks to T. Alexander, S. Dickson, S. Foster, and R. Sakabe for fieldwork assistance. We are also grateful to N. Bax and C. Johnson for discussions on the topic. Thanks to J. Lyle and two anonymous reviewers for comments on the manuscript.



## **6. Chapter Six**

### **Discussion and conclusions**

The principal aim of this thesis was to provide information to improve the understanding of successful marine invasions and the effects this can have on native communities from a study of the introduced gastropod *M. roseus* from New Zealand to Tasmania. This was approached by a study of *M. roseus* habitat, its population characteristics, potential impact on other macromolluscs, and a description of its larvae.

The results demonstrated that distinguishing between live and dead animals has led to a much clearer understanding of the habitat of *M. roseus*. This differentiation will help in identifying whether establishment has occurred or not (Summerson *et al.* 2007). Initially the distribution of this species has been described to cover a wide variety of substrate types (e.g., Greenhill 1965, McKnight 1969, Grange 1979, Allmon *et al.* 1994, Bax and Williams 2001, Bax *et al.* 2003, Beaman *et al.* 2005, Abraham *et al.* 2007). However, a survey of live *M. roseus* demonstrated that this species' main habitat is characterised by a sandy substrate, although there is some habitat variability in its distribution. Some sites in the D'Entrecasteaux Channel with a mud substrate also had high densities of *M. roseus*, indicating that this species is capable of surviving in finer substrate environments. This became clearer from laboratory experiments, where *M. roseus* was given a choice of habitats characterised by substrate type and preferred sand, but moved into the finer mud substrate as the population density increased in the sandy environment. Mollusc responses to

population density have previously been described and attributed to competition for feeding resources (e.g., Connell 1961, Underwood 1978, Boaventura *et al.* 2003). The specialised distinctive digestive and respiratory system of *M. roseus* (Graham 1938, Fretter and Manly 1979, Allmon *et al.* 1994), supports its capacity to survive in several types of environments. Also, *M. roseus* has no known major predators (Scott 1997, Bax *et al.* 2003, Nicastro *et al.* 2009), making many habitats prone to invasion by this species. Similarly, the invasive success of the gastropod *Ovatella myosotis* on the coast of North America has been related to its physiological capabilities that can take advantage of different environments and resources not available to native species (Berman and Carlton 1991).

Understanding *M. roseus* habitat by identifying the factors driving its distribution proved to be complex. Factors that determine the distribution and abundance of marine organisms are multifaceted (Vernberg 1981, May 1984, Defeo and McLachlan 2005) and identifying the main variables driving benthic assemblages are not without its challenges (Underwood and Fairweather 1989, Morrissey *et al.* 1992). However, substrate type was found to be a good indicator of *M. roseus* habitat type. The D'Entrecasteaux Channel is variable in its substrate type (Barrett *et al.* 2001) and is likely to be a good representative of other coastal environments to understand their vulnerability to the invasion of *M. roseus*. The species was also reported to be found at sites deeper than those in the D'Entrecasteaux Channel (Bax *et al.* 2003, Beaman *et al.* 2005). However these samples were taken from video surveys, and the proportion of live and dead *M. roseus* is not certain. This warrants further studies in these environments.

Very high densities of *M. roseus* occur in Australia (especially in Tasmania) and the effect of this on other similar species was investigated. The impact on the native environment from the “littering” of vast quantities of shells (Edgar 2000) is likely to be high. For example, such large densities of an invasive gastropod was described to be a major concern for the native environment in a recent study on *Tarebia granifera* (Appleton *et al.* 2009, Miranda *et al.* 2011). Molluscs can be important ecosystem engineers (Gutierrez *et al.* 2003) and when introduced can alter species community and ecosystem functioning (e.g., Robinson *et al.* 2005, Reise *et al.* 2006, Werner and Rothhaupt 2008, Buhle and Ruesink 2009, Schmidlin *et al.* 2012). This study demonstrated that live and dead *M. roseus* had an association with the distribution of macromolluscs; however, interpretation of the results was complex. When the association of *M. roseus* with macromolluscs was investigated at the sites with *M. roseus* preferred habitat of sand a clearer picture of *M. roseus* impact on the co - occurring species was available. Live *M. roseus* were significantly correlated to the macromollusc species community composition. Also, areas of higher live *M. roseus* densities were characterised by a higher number of deposit feeding macromolluscs, while areas with a lower density of live *M. roseus* had a community of mainly suspension feeders. The impact based on live and dead animals is probably multifaceted (McLean 1983); however, it was established that live and dead *M. roseus* can have a different impact on co - occurring species.

Live *M. roseus* may have a greater detrimental impact on native environments via competition for habitat and feeding with similar species. Examples of such impacts have been described for the invasive gastropods *Mitrella psilla* (Antit *et al.* 2010) and *Strombus persicus* (Galil and Zenetos 2002) in Europe, *Rapana venosa* in South

America (Lercari and Bergamino 2010), *Littorina saxatilis* (Yamada and Mansour 1987) and *Littorina littorea* (Brenchley and Carlton 1983) in North America. Shells of dead animals can promote species richness and abundances by generating substratum or shelter (McLean 1983, Carlton 1999). Although invasive species can increase species abundances and richness in a community (e.g., Drouin *et al.* 2011, Irigoyen *et al.* 2011, Lages *et al.* 2011), the changes in the structure of the community can still have unfavourable effects at higher trophic levels (Ruiz *et al.* 1997, Grosholz 2002, Occhipinti-Ambrogi and Savini 2003). The combined effects of high densities of *M. roseus* and shells that prevail in the environment for a long period (Allmon and Knight 1993, Allmon 2011) are likely to be impacting higher order species in the Tasmanian environment; however, this has not been investigated in detail.

Descriptions of the reproductive biology of an invasive species are important for their invasive management (Bax *et al.* 2001a) and therefore was an important component of this thesis. For *M. roseus*, up to 70 % of females were found carrying encapsulated larvae throughout consecutive austral summer seasons. Larvae released from egg capsules were planktonic, all relatively well developed, and feeding on microalgae (planktotrophic). Prior to this thesis, the description of *M. roseus* larvae was not known and it was proposed that the larval stage could be completed within the egg capsules of females (direct larval development) (Pilkington 1974) or a possible planktonic stage (Bax *et al.* 2003). The latter showed to be the case. From aquaria rearing experiments in this thesis, the planktotrophic larval stage of *M. roseus* was described. This was also supported by detection of *M. roseus* by genetic probes in plankton hauls from the D'Entrecasteaux Channel (Gunasekera *et al.*

2005). Gastropods with a planktonic larval stage have shown to have on average a greater geographical range than species with direct development (Scheltema 1986, Scheltema 1989). The combination of a high percentage of females carrying larvae, with a relatively well developed planktonic life stage and planktotrophic feeding mode, suggests *M. roseus* has high dispersal potential. These findings help to explain the rapid dispersal of this species across the Australian coastline since its introduction in the 1920's. Similarly, favourable traits in life - history, compared to the local species, were suggested to be a main factor for the establishment and spread of the invasive gastropod *Ocenebrellus inornatus* in France (Martel *et al.* 2004). Understanding the population dynamics of the invasive gastropod *Pomacea insularum* in North America, was also considered to be important for predicting their interaction with the environment and for developing a control strategy (Burlakova *et al.* 2010).

The results of this thesis have improved the understanding on the factors driving the success of this invasive marine species and its potential impact on native environments. Similar to other invasive species, *M. roseus* demonstrated its ability to survive in different environments, achieving high densities, over a large geographical range. *Maoricolpus roseus* thus has many of the elements of a successful invader (Scheltema 1986, Scheltema 1989, Ruiz *et al.* 2000a, Miller *et al.* 2007, Miller and Ruiz 2009).

The information provided in this thesis will assist predicting which environments are at risk of invasion by *M. roseus*. Information on habitat and larvae will aid in invasive management (Bax *et al.* 2001a, Buhle *et al.* 2005, Finnoff *et al.* 2005, Leung

*et al.* 2005, Saphores and Shogren 2005), including the identification of larvae in ballast water. Transport in ballast - water of commercial shipping vessels is one of the largest modes of marine introductions (Carlton and Geller 1993, Ruiz *et al.* 2000b). However, the recognition of *M. roseus* as a potentially significant marine invader is only recent and studies are scarce compared to other invaders in Australia such as *Undaria pinnatifida*, *Sabella spallanzanii*, *Asterias amurensis*, and *Corbula gibba*.

The management of invasive species has recently been described in biosecurity management as the national, regional, and international efforts to prevent, reduce, and manage the introduction of pests, diseases, or unwanted organisms via entry and border surveillance, short - term response and long - term control of established pests (Dahlstrom *et al.* 2010). Australia and New Zealand have developed a comprehensive approach to marine biosecurity. While there are some differences in their approaches due to differing legislative arrangements, and challenges in coordinating the respective frameworks of the different managing bodies (Peterson 2006, Dahlstrom *et al.* 2010), both have engaged in the development of national and international regulatory frameworks for the prevention and management of invasive species introductions (Hewitt and Campbell 2007). There are also new methods to detect *M. roseus* larvae in the water column (i.e., genetic probes, Gunasekera *et al.* 2005), however, there is no known management program specifically targeting the control of the invasion of *M. roseus* (McEnnulty *et al.* 2001, Nicholas Bax 2012, CSIRO Australia, pers. comm.).

The findings of this thesis expand the information available on the ecology and biology of *M. roseus*, which is needed for the development of successful ecosystem - based management underpinning biosecurity. This type of information helped model the range expansion of the invasive seastar *Asterias amurensis* in Australia (Dunstan and Bax 2007) and the assessment of the effectiveness of its management (Dunstan and Bax 2008). It was also essential to understanding the state of the environment and data needed for effective management of introduced gastropods in Israel (Roll *et al.* 2009), and provided information for management decisions for the invasive oyster *Crassostrea virginica* in North America (Fulford *et al.* 2011).

However, further research on *M. roseus* is needed as there were some limitations in the study. Helping to investigate the impact of invasive species in more detail requires a multiple method approach, in order to obtain information on its nature, pattern and magnitude (Ross *et al.* 2003, Giménez *et al.* 2006). Quantitative estimates of impacts can be investigated with field surveys and experiments with small spatial and temporal scales repeated at several sites and times to provide estimates at larger scales. It is also important to consider the spatial scales and the life habitats of other organisms to characterise the consequences at the ecosystem - level (Crooks 2002). Manipulative experiments to assess the interaction between the species sharing the habitat with *M. roseus* need to be investigated in more detail to assess the causative agent for their distribution. Further studies on additional factors to predict and manage the invasion of *M. roseus* need to be explored, such as the temporal patterns of population growth in relation to the different habitats of this species, the dominant mechanisms of population regulation, and the full description of its life cycle.

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## **Appendix**

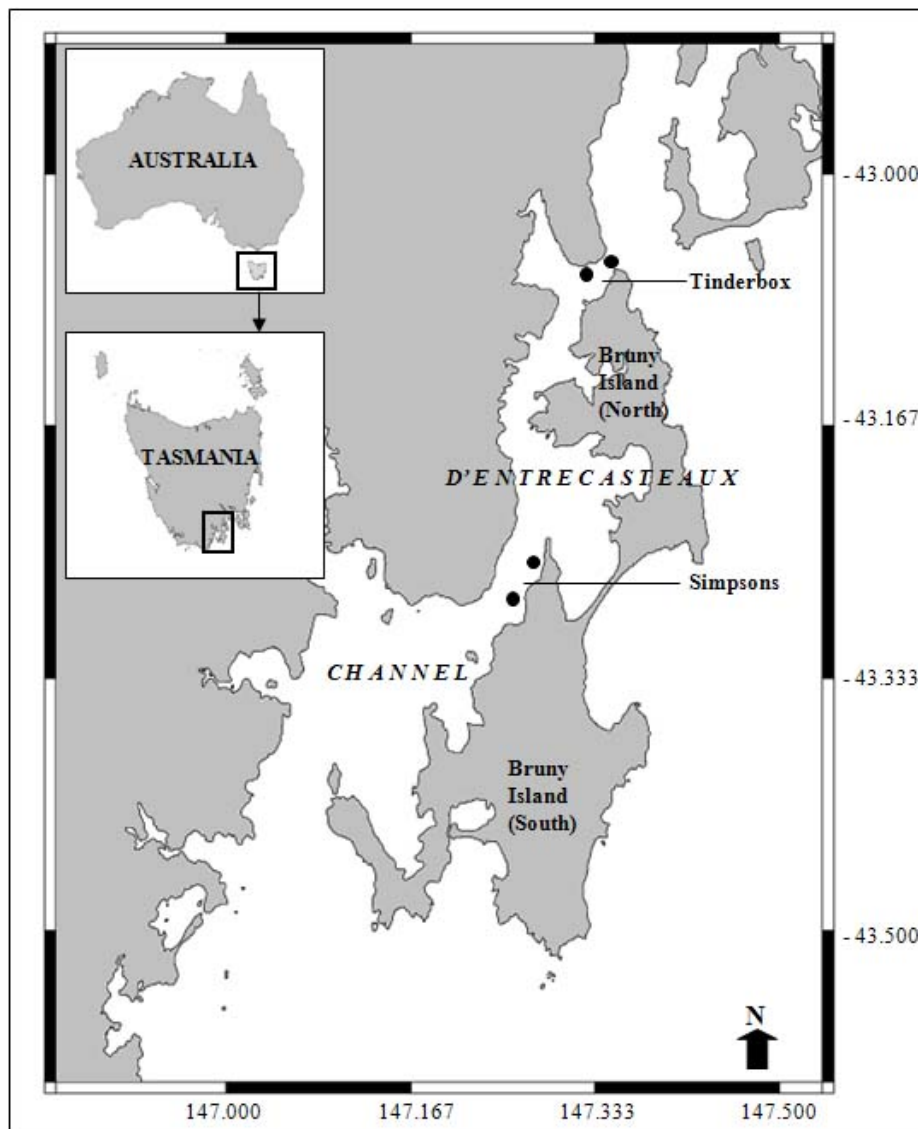
### ***Maoricolpus roseus* impact on *Pecten fumatus* eggs and larvae**

#### **Materials and methods**

The potential impacts of *M. roseus* on scallop *Pecten fumatus* eggs and larvae numbers were evaluated in two aquarium experiments. A total of 12 nine litre round plastic tanks were used for both experiments and were filled with five litres of ozone filtered seawater (water held at  $> 600$  Oxidative Reductive Potential for 10 min before being passed through a UV sterilization unit and charcoal filter tanks), at approximately 33.5 ‰ salinity and approximately 12.5 °C temperature (as per their natural habitat). Each tank was setup with an ambient air supply delivered by a tube inserted vertically from the top to the base of the water column. Six treatment and six control tanks contained 40 *M. roseus* specimens each (average  $60 \pm 0.5$  mm in size). *M. roseus* were collected via SCUBA diving in the D'Entrecasteaux Channel from two sites at two locations typically characterised by the co-occurrence of the gastropod and the bivalve *Pecten fumatus* (Tinderbox and Simpsons Point, Figure A). Spawned *P. fumatus* eggs and larvae to be used for the experiments were supplied by Shellfish Culture Pty Ltd (Tasmania).

An initial density of 40 eggs / ml ( $50 \pm 1$  µm in size) and 30 larvae / ml ( $90 \pm 4$  µm in size) were used for experiment one and two respectively. Densities were measured using a Sedgwick Rafter counting cell (0.1 x 0.1 mm grids) placed under a compound microscope to determine the number of units per millilitre. In experiment two, larval proportion at the start of the experiment for trochophores and pediveligers were of  $48.17 \pm 0.93$  % for the latter. The final density in each tank was measured after 48

hours, by rinsing animals (in treatments) and draining the tanks through a 50  $\mu\text{m}$  mesh and concentrating the contents in 300 ml of ozone filtered seawater. Four replicate 1ml pipette samples were collected after stirring and contents counted using the Rafter cell. Additionally five *M. roseus* were randomly chosen from each treatment tank for examination of gut contents with a compound microscope..



**Figure A.** D'Entrecasteaux Channel showing sampling sites (●) at locations Tinderbox and Simpsons. (Map coastline based on NGDC 2007)



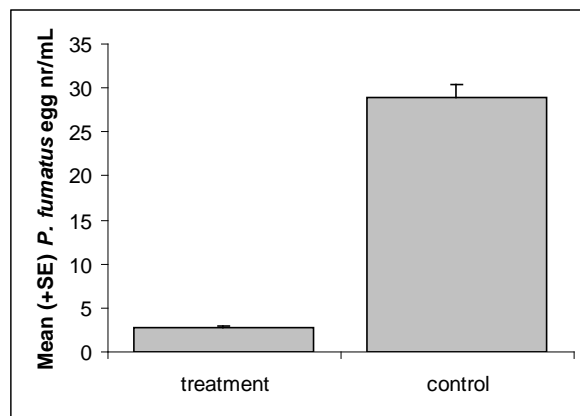
## Results

Significant differences (ANOVA, Table A) occurred between treatments and controls in *P. fumatus* eggs ( $F_{1,10} = 1194.14$ ,  $P < 0.001$ ) and larval densities ( $F_{1,10} = 327.62$ ,  $P < 0.001$ ). After the period of 48 hours, in treatments and controls respectively, in experiment one, scallop egg densities were  $2.75 \pm 0.11$  /ml and  $28.92 \pm 1.55$  /ml (Figure C), and in experiment two, larval densities were  $5.16 \pm 1.31$  /ml and  $17.59 \pm 0.6$  /ml (Figure D). It was also noted that in experiment two most of the veligers ( $96.13 \pm 1.88$  %) left in the treatment tanks had an average size of  $120 \pm 2$   $\mu\text{m}$ . In contrast only  $71.64 \pm 1.68$  % of larvae left in the control tanks were of that size.

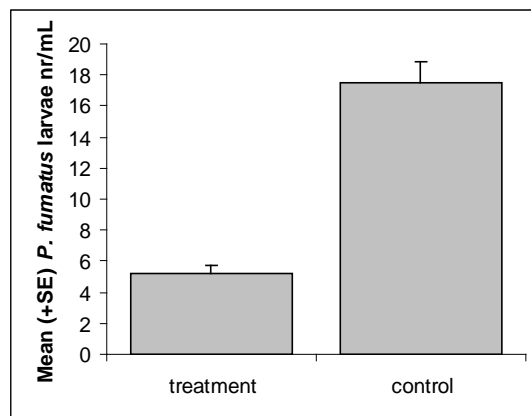
However, gut content analysis of four random *M. roseus* from each treatment tank (total = 48 animals) did not show any evident feature of scallop eggs (expected  $\approx 50$   $\mu\text{m}$  in size) and trochophores (expected  $\approx 75$   $\mu\text{m}$  in size) In contrast a total of four scallop veligers ( $121 \pm 0.1$  (SE)  $\mu\text{m}$  in size) were found in four individual animals.

**Table A** Summaries of ANOVA tests for differences in *P. fumatus* egg and larvae mean numbers (after 48 hours) in treatment (presence of *M. roseus*) and respective control tanks. Table outlines respective MD (mean differences between groups) and P significance values (\*\*\*)  $P < 0.001$ ).

	Source of variation	DF	MS	F	P
<i>P. fumatus</i> eggs	Treatment vs. control	1	2.430	1194.14	***
<i>P. fumatus</i> larvae		1	2.930	327.62	***



**Figure C** *P. fumatus* egg densities ( $\text{ml}^{-1}$ ) after 48 hours in treatment (presence of *M. roseus*) and respective control tanks. Initial number of eggs in all tanks was  $40 \text{ ml}^{-1}$ .



**Figure D** *fumatus* larvae densities ( $\text{ml}^{-1}$ ) after 48 hours in treatment (presence of *M. roseus*) and respective control tanks. Initial number of larvae in all tanks was  $30 \text{ ml}^{-1}$ .