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Researcher Contact Details		**FRDC Contact Details**	
Name:	Caleb Gardner		
Address:	Nubeena Crescent Taroona. TAS. 7053	Address:	25 Geils Court Deakin ACT 2600
Phone:	03 6227 7233	Phone:	02 6285 0400
Fax:	03 6227 8035	Fax:	02 6285 0499
Email:	Caleb.Gardner@utas.edu.au	Email:	frdc@frdc.com.au
Web:	www.imas.utas.edu.au	Web:	www.frdc.com.au

In submitting this report, the researcher has agreed to FRDC publishing this material in its edited form.

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Acknowledgments

Executive Summary

This research is an extension of two previous projects on SRL translocation (CRC2006/220 and CRC 2011/744), which showed that translocation of slow growing lobsters to better habitat can be used as a management tool to increase production in the fishery. It's currently being used on a small scale to increase production in the Tasmanian fishery by 50 tonnes per annum though a fully-industry funded program.

The growth rate of Southern Rock Lobsters varies spatially with a general trend of growth slowing along a gradient from western Victoria to southern Tasmania. Previous research for defining locations of capture and release of rock lobster translocation relied on general models of this spatial trend in growth. The research reported here involved more detailed spatial analyses of growth to try to refine those operations. In particular, the aim was to find locations that would provide for high growth of translocated lobsters with less travel distance (cost) than the sites currently being used.

The two components of this project dealt with changes in growth associated with changes in food availability and density, which was investigated by measuring growth of lobsters in translocation sites with a Before-After-Control-Impact (BACI) design. This involved examining growth under different conditions of prey availability and density. The third component identified fine scale spatial locations where lobsters had unusually high growth, based on a historical dataset of tag returns from non-translocated lobsters. That is, we identified the premium paddocks for release of translocated lobsters.

These analyses were data intensive and in some cases there were insufficient tag-recapture records so growth was not assessed for all release sites. Nonetheless, in TAS sufficient data was available to update and improve quantification of the scale of growth increases when lobsters from deep

water were translocated to shallow sites. There was also some evidence of the scale of growth reduction that can occur at high density of SRL. Growth of lobsters at the source site increased after translocation, presumably due to lower density.

This research will enable refinement of translocation operations to lower costs and improve productivity gains. The beneficiaries will primarily be owners of quota.

Keywords

1.   Introduction

1.1. Background

This project extends the outputs from two previous CRC projects on translocation of rock lobsters, a large scale experimental project (Improving yield and profitability of southern rock lobster by spatial management, CRC2006/220) and an extension project (Commercialising translocation of southern rock lobster CRC 2011/744).

The previous projects showed that translocation can be used to address several problems that affect the Tasmanian lobster fishery. Some areas of the fishery are "growth overfished", meaning that larger harvests would be sustainable if lobsters were able to grow a little more before being caught. At the other extreme, large areas in deep water off the remote west coast are avoided by fishers because the animals are pale and fetch a lower price. These areas are however good areas for juvenile lobsters to settle from the plankton and grow as juveniles. Density of lobsters in these areas is extraordinarily high, with an average catch of over 30 per pot. Although lobsters are numerous, they contribute less to the harvest than lobsters that settle in other areas because of slow growth. Translocations simply involves moving lobsters from places where they are abundant to places where they are depleted. Although conceptually simple, there were naturally a lot of issues and concerns that required research. Translocations have now progressed to commercial scale operations. The research conducted here completes analysis of some of the research data collected through the course of the earlier work. In particular, it involves analysis of growth information that has continued to be collected since the previous projects finished. This new data comes from tag return data that continues to trickle in as fishers capture and report tagged translocated lobsters.

1.2. Need

The project conducted three sets of analyses related to growth of translocated rock lobsters. These are not critical for current operations which are locked in for a three-year period. However, they may be important for addressing industry concerns when the operations are next voted on in 2016. Aside from that need they maximise the benefit from investments into research on translocation of rock lobsters over the last decade.

1.3. Objectives

Complete three papers dealing with growth of rock lobsters to enable improved outcomes from

Translocation:

- To assess growth compensation in lobsters moved inshore

- To assess density dependent changes in lobster growth

- To describe fine scale variations in growth of lobsters off western Tasmania

2. Methods

The methods described below were applied to meet the objectives 1) Assess compensatory growth of lobsters translocated from of high density and slow growth to faster growth areas, and 2) assess density-dependent changes in lobster growth. A detailed description is presented in Appendix II.

Study sites

A Before-After-Control-Impact (BACI) experiment was carried out in south-east Tasmania (TAS), Victoria (VIC) South Australia (SA), which involved translocating a total of 30,349 lobsters in the curse of three-year (2005-2007). In TAS, one removal site (Maatsuyker Island) was used for the capture, tagging and translocation of lobsters to eight release sites (Whale Head, Riedle Bay and Taroona Reserve, Emerald Bay, Ansons Bay, Gull Island, Georges Rocks), along three degrees of latitude. In Victoria, the removal and release site were a point offshore and inshore at Port Fairy respectively. In South Australia translocations were from deep to shallow water sites within six few kilometres of each other at Ringwood Reef and Robe. Maatsuyker Island is a southern, deep-water (60m-100m), rocky reef, where lobsters grow slowly, are pale in colour (Chandrapavan *et al.* 2009a), and females rarely reach the minimum legal size of 105mm CL (Gardner *et al.* 2006). This phenotype of lobster is indicative of lobsters from offshore deep-water sites in TAS, VIC and SA. While there are sites specific differences

the inshore sites represent shallow rocky reefs where lobsters grow faster and are red in colour (Chandrapavan *et al.* 2009a).

Growth Estimation

To determine the average annual growth rates several stochastic versions of the von Bertalanffy-Fabens growth model were used (Troynikov *et al.* 1998). Inputs to the analyses were carapace lengths at release and recapture and time at liberty. The outputs of the data parameterization were annual means and distributions of the length increments for various lengths at release (80mm, 90mm, 105mm - females and 110mm - males). The deterministic von Bertalanffy-Fabens growth parameters L_∞ and K were estimated for each sex at each site. Since the stochastic growth models are in the form of probability density functions the likelihood - ratio test was used for comparison of growth between different sites.

The methods described below were applied to meet the objective 3) to describe fine-scale variations in growth off western Tasmania.

Data

This study included southern rock lobster data from South Australia (SA) and TAS (TAS), which was compiled from databases maintained by South Australia Research and Development Institute (SARDI), SA government; and by the Institute for Marine and Antarctic Studies (IMAS) respectively.

Growth estimates

The Faben's parametrization of the von Bertalanffy growth function (VBGF) was used to determine growth coefficients. This approach avoids the difficulties of unknowing the age at-first-capture in crustacean because this is based on the moulting increment and intermoult period from tag-recapture (Chang *et al.* 2012). Databases contained numerous records of specimens with multiple recaptures that biases growth estimation. To address this issue, just the first recapture was used to fit the growth models.

Growth estimates were obtained for females at a large spatial scale (90x90 km blocks). In each case, estimations were carried out for a unique size group (64 -198 mm), because sample size became insufficient while we split the data into more specific size categories. Hence, growth coefficients were estimated for seven sites in TAS. We kept the same CL size group to calculate growth coefficients with data from SA, based on a 20x20 km blocks and data was sufficient to obtain estimation in nine sites.

Size at onset of maturity

The proportion of mature females at different sizes was modelled with a logistic function at the same large scale than growth was estimated in TAS and SA. Additionally, new values of size at maturity were calculated at a small scale (1.5-3.0 km). They were used to predict values of spatial variation in growth, termed "potential growth".

Potential growth

Size at onset of maturity data was to estimate potential growth at sites where there were insufficient tag recaptures. The ratio L_{mat}/L_∞ was used as an approach to growth, as this represents the proportion of the potential growth span covered before maturation, henceforth termed "potential growth". This ratio has better properties than separate values of L_{mat} and L_∞ when studying relations between growth and sexual maturity (Beverton 1992; Froese and Binohlan 2000; He and Stewart 2001). A linear model between this ratio and L_{mat} was fitted to predict the potential growth from estimates of L_{mat} at a small spatial scale (1.5-3.0 km). Also, the relationship between K growth coefficient vs. the ratio L_m/L_∞ and K vs. the asymptotic size (L_∞) was described, as they aid the interpretation of the potential growth and its relation with the SOM (He and Stewart 2001).

Effect of latitude, longitude and depth on potential growth

The relationship between potential growth and depth, latitude and longitude did not show a clear linear pattern. Therefore, an Additive Model was fitted with a smoothing function for each explanatory variable. Interactions between depth and spatial location as a factor improved the

model. The Akaike information criterion (AIC), Generalised cross-validation score (GCV), explained deviance and parsimony were used as a guideline to choose a model; thus, the selected model was:

$$L_{mat}/L_\infty = \alpha + f_1(Depth) \times Location + f_2(East) + f_3(North)$$

Where α is the intercept; Location is the categorical geographical area with the levels, W, SW, SE, E and NE; East and North are the projected longitude and latitude respectively, and f represents a smoothing function.

3. Results

A detailed description of the result is separately presented for each objective in Appendix II, with a summary provided below.

Objective 1. To assess compensatory growth of lobsters translocated from sites with high density and slow growth to faster growth areas

The growth rate of translocated *Jasus edwardsii* showed flexibility in growth rates in response to a changed environment. Those lobsters moved from deep water sites inshore to shallow water sites significantly increased and reached a growth rate that was similar to the growth rate of resident inshore lobsters at sites in TAS, VIC and SA.

The mean growth of lobsters moved to sites along a latitudinal gradient (translocation in TAS) exceeded the growth of the source (removal) site. Also, mean growth at the release sites increased by up to 400%. Growth increased the further north the animals were moved. In TAS, the increase in growth rate was higher in females and higher for smaller lobsters.

Objective 2. To assess density-dependent changes in lobster growth

Stochastic modelling of growth was not possible for all sites, as sample sizes were often small and/or the recapture data did not have enough contrast in size bins. The Taroona reserve (release site) and Maatsuyker Island (removal site) had the most recaptures and these involved recaptures of up to five years in duration. In the removal site, although a reasonable sample size was available, most changes in size were within the scale of measurement error of around 3 mm.

The analysis of growth through stochastic modelling was only possible for the Maatsuyker removal site and one release sites, Taroona. For both sites, the growth models before and after translocation were significantly different. At the removal site, there was not enough data to perform the likelihood ratio test for females and contrast growth before and after translocation. Translocated male and female lobsters in the release site (Taroona) had a higher growth rate contrasted with resident lobsters at the removal site (Maatsuyker). At the release site, the growth rate dropped for both males and females after the increase in density. Consequently, the mean growth per year fell for both females, between 0.2 and 0.4 mm year-1, and males, between 1.6 and 1.8 mm year-1. In both cases, the growth reduction was higher for individual at the smaller size group (80 mm CL). At the removal site, males at 110 mm CL increased their mean growth after removals occurred, as females for the three assessed sizes (80, 90 and 105 mm CL).

Objective 3. To describe fine-scale variations in growth off western Tasmania.

Growth estimates at large scale

Growth estimates based on data from commercial operations showed the greatest size increases in the Northern areas and the least in the Southern areas, as has been well established previously. For instance, the mean annual growth of females of 75 mm CL was 19 mm in the NW and 9 mm in the SW. This relative difference between regions increased with size of the lobster.

Size at onset of maturity at large scale

Size at onset of maturity (SOM) had a trend in spatial variation, mostly in the latitudinal gradient, and to a lower extent in longitude. The highest SOM estimates occurred in the NW and NE of TAS, where length at 50% maturity of females was 109 mm CL. In both sides of TAS the SOM gradually decreased, but 50% maturity occurred at the lowest size (70 mm CL) in the SW.

Potential growth span at small scale

The relationship L_{mat}/L_∞ vs. L_{mat} showed the expected pattern of increase of the ratio while L_{mat} increased, with a significant slope ($\beta = 0.009$, $p < 0.001$) and a $R^2 = 0.68$. The relationships K vs. the potential growth (L_m/L_∞) showed that K was higher towards North and consequently the potential growth was also higher towards the same direction. Consistent with this result the asymptotic size was smaller towards North as a consequence of higher K.

Predictions of potential growth span before maturity (L_{mat}/L_∞) were obtained for 270 points around TAS, which were based on estimations of L_{mat} on a small scale. The highest potential growth occurred in the NW region of TAS, with values ranging from 0.7 to 0.96. The Northeast zone showed a slightly lower maximum and a wider range of values, varying between 0.43 and 0.82. The smallest potential growth was observed in the SW region with a minimum and maximum of 0.21 and 0.58 respectively. In contrast, in the SE zone the values fluctuated between 0.43 and 0.74. The East zone had higher values than the West region with maximum values of 0.82 and 0.58 respectively.

Effect of latitude, longitude and depth on potential growth

Latitude, longitude and depth helped explain variation in potential growth, except in the NW area. Variation in potential growth with latitude and longitude reflected a general pattern of high growth rates towards the north. There was a general pattern wherein potential growth in the NW, NE and E zones did not change up to 50 m, while below this depth, the potential growth sharply decreased. In contrast, in the W, SE and a lower extent in the SW zones the potential growth linearly decreased with the increase of the depth across the whole range.

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4. Discussion

Translocated lobsters had higher growth rate of locals at release sites, which indicate that growth compensation occurs in rock lobsters when moved to higher quality habitat. This result had been reported previously but was an unexpected outcome and thus worth confirming with this larger dataset. Compensatory growth has been observed in other animals where growth increases rapidly after a period of depression due to food deprivation (Boersma and Wit 1997; Ali *et al.* 2003).

Growth and colour have been linked together in assessments of compensatory growth (Metcalfe and Monaghan 2001; Alonso-Alvarez *et al.* 2007). Previous studies of translocated lobsters demonstrated a difference in the level of fatty acids between the shallow and deep communities in Tasmania (Chandrapavan *et al.* 2009b) and there was also evidence of fatty acids overshooting that of locals in the translocated lobsters (Chandrapavan *et al.* 2009b), suggested the concurrent change in colour and growth occurred due to improvement in nutrition. Access to better quality of food, including that high in carotenoids may have facilitated the observed compensatory growth.

The analyses conducted here quantified changes in growth in response to both increase and decreases in density following translocation for stock enhancement. Translocated lobsters increased their growth rate relative to both their original site and the resident lobsters in the release site (non-translocated lobsters). This outcome is consistent with change in food availability (Haley *et al.* 2011), but could also be caused by environmental differences such as temperature.

There was some reduction in growth rate of local lobsters at the release area before and after translocation, for both genders, which may be attributed to the sudden increase in density. Crowded conditions can inhibit growth by increasing competition for food (Moorhouse and Macdonald 2011), as seen in changes to moulting frequency and size increment per moult (Cobb *et al.* 1982; Karplus and Barki 2004; Karplus 2005). At the removal site, females and large males increased their mean growth after translocation, which may have been due to reduction in density and reduced competition for resources (Herberholz *et al.* 2007).

Latitudinal changes in SOM and potential growth had a general pattern of increase towards the north. SOM variations have been in part explained by changes in temperature (Pollock 1995b;

Linnane *et al.* 2009). However, the local variation observed in this study suggested that other factors also resulted in differences between sites. The additive model outputs revealed that the potential growth of some zones did not change with depth until a sharp decrease at depths over 50 m. The cause of this change with depth is unknown but may be related to environmental differences, such as temperature, or biological effects such as prey species and/or density. Density of lobsters varies with depth because of different rates of exploitation as a consequence of the fleet behaviour. Shallow waters have received higher fishing pressure relative to deep waters, due to greater market price for shallow water lobsters at some times of the year (Gardner *et al.* 2015). Changes in growth with density have also been observed in SRL in South Australia with a 10% decrease in catch rates leading to growth increase by weight of 2-5% (McGarvey *et al.* 1999). Contrary results of no apparent effect of density on growth was reported from comparisons of SOM between marine reserves and fished areas (Gardner *et al.* 2006). Therefore, these contradicting findings indicate that the effect of density on growth is complex and interacts with other factors such as regional and depth related variation in prey species and availability.

Additional research would be required to understand the mechanisms behind the observed patterns in rock lobster growth; however, for the purposes of managing translocation, quantification of the effect is of most importance because this provides accuracy in model outcomes that affect TAC setting. These refined growth parameters are now documented in Appendix II.

5. Implications

This research has implications through ongoing commercial translocations operations.

These are through:

1) Improved parameterisation and thus accuracy of model projections and TACC setting in the presence of translocation
2) Selection of release sites that result in good growth increases but are smaller distances from removal sites, thus reducing cost of transport.

Translocation increases yield and profitability of the Tasmanian commercial rock lobster fishery, therefore, the main beneficiaries will be owners of quota units in this fishery.

6. Recommendations

Current levels of translocation are small compared to the potential providing an increase of only 50 tonnes or ~ $3 million p.a. Ideally, this opportunity would be more fully utilised for the benefit of the Tasmanian community.

7. Extension and Adoption

This research will be made available to the Tasmanian Rock Lobster Fishermen's Association for planning of translocation operations. It is anticipated this will begin to affect choice of sites in 2016.

8. Project materials developed

This project produced three draft papers that will be submitted to scientific journals (drafts are included in appendices). They will assist in decision making in future translocations. The journal process is important for review and quality assurance of the science that underpins decisions on commercial scale translocation of rock lobsters.

Working titles for these papers are:

Paper 1. Compensatory growth in greener pastures: increased growth in an invertebrate moved to inshore reefs

Paper 2. Translocation of lobsters results in density dependent changes to growth

Paper 3. Spatial variation in potential growth of female southern rock lobster around TAS

9.   Appendices

Appendix I, List of researchers and project staff

IMAS

Bridget S. Green, Caleb Gardner, Klaas Hartmann and Rafael León.

SARDI

Adrian Linnane

DPI VIC

David Hobday

Appendix II. Draft papers associated with each objective

Objective 1. To assess growth compensation in lobsters moved inshore

Compensatory growth in greener pastures: Increased growth in an invertebrate moved to inshore reefs

Bridget S. Green[1], Caleb Gardner[1], David Hobday[2], Adrian Linnane[3]

[1] Institute for Marine and Antarctic Studies, University of Tasmania, Private Bag 49, Tasmania, 7001, Australia.

[2] Primary Industries Research Victoria, Department of Primary industries, PO Box 114, Queenscliff Victoria 3225.

[3] South Australian Research and Development Institute (Aquatic Sciences), PO Box 120, Henley Beach, South Australia 5022, Australia.

Abstract

Compensatory growth is the term used to describe a period of accelerated growth after a period of slower growth, usually occurring when favourable conditions are restored. We examined growth rates in lobsters moved from areas of high density and slow growth to areas of faster growth. We undertook two scales of experiment, one assessing changes in growth along a latitudinal gradient (called latitudinal gradient henceforth) and one assessing change in local areas of faster growth (local gradient). In Tasmania, Australia we moved 25,625 slow growing lobsters from a deep water habitat to eight sites shallow water area along three degrees of latitude, where growth rates of residents were higher. We also moved 4,724 lobsters over shorter distances from deep water to adjacent shallow water in two sites in South Australia and one site in Victoria, Australia. Lobsters grow through annual moulting, and within one moult, the growth of translocated lobsters had improved, exceeding the growth rate of lobsters at both the source location and residents at the new locations. Growth rate increased concurrently with a change in red pigmentation an indicator of change in diet with more carotenoids typical of

shallower water ecosystems. These results raise the interesting issue of why resident lobsters do not grow at faster rates, given that translocated lobsters demonstrated this is possible? They are also useful for parameterising models used to guide translocation operations, which are now being conducted, on a commercial scale.

Keywords: Optimal growth**,** catch-up growth, *Jasus edwardsii***,** assisted migration**,** stock enhancement.

Introduction

Partitioning energy for growth is critical for optimising lifetime reproductive success (Stearns 1976; Roff 1992), and in marine ecosystems is the most important parameter governing biological processes (Andersen and Beyer 2006). Body size is central to reproductive output, individual fitness and survival (Twombly and Tisch 2000). Many organisms grow at a rapid rate from birth until maturity, whereby growth asymptotes as energy is diverted towards reproduction. Causes of variation in growth change between organisms, stocks, and habitats, and remain one of the fundamental mysteries in ecology (Caley and Schwarzkopf 2004). Size matters in ecology, and even more so in fisheries (Froese *et al.* 2008; Cardinale and Hjelm 2012) where there is size-selective removal of parts of the population, leading to shifts in maturation norms, reproductive outputs and long-term sustainability of stocks (Olsen *et al.* 2004; Garcia *et al.* 2012).

In vertebrates, growth of the organism can be constrained by the growth potential of specific tissues (Ricklefs *et al.* 1994), and the division between compensatory storage of readily mobilised nutrient reserves such as lipids and somatic growth such as skeleton (Metcalfe *et al.* 2002). The harshness of environmental conditions can also influence any trade-off between growth and energetic reserves (Post and Parkinson 2001). In crustaceans, growth is discontinuous due to the external rigid cuticle that is replaced intermittently in stepwise moults or ecdysis (Hartnoll 1982). At each moult the old exoskeleton is shed, allowing the animal to expand before new exoskeleton hardens. This increase in size is termed the moult increment, while the intermoult period is the duration between two successive moults. Growth rate in crustaceans is a function of both moult increment and moult frequency (Hartnoll 1982).

Ectotherms are usually larger when temperature is lower (Atkinson 1994) and food availability is higher (Atkinson and Sibly 1997).

Growth rates occurring in the wild are a complex mix of local adaption, maternal effects, their selective agents and local environmental conditions (Caley and Schwarzkopf 2004). The variance in growth rate and reproduction along an environmental cline such as latitude or depth has been documented in a range of organisms (Jensen *et al.* 2000; Yamahira and Conover 2002; Laugen *et al.* 2003; Currie and Schneider 2011; Rosa *et al.* 2012). Variation in growth with latitude does not always occur in a predictable or consistent manner, due to local anomalies (Caley and Schwarzkopf 2004; Linse *et al.* 2006), but has been quantified in many invertebrates, such as crabs (Lardies *et al.* 2010), isopods (Lardies and Bozinovic 2006) and snapping shrimp (Lardies and Wehrtmann 2001).

Jasus edwardsii, an exploited marine crustacean, has a large amount of spatial variation in growth, maximum size, size at maturity, colour and morphometrics throughout the range (Annala and Bycroft 1987; MacDiarmid 1989; Gardner *et al.* 2006; Linnane *et al.* 2008, 2009; Chandrapavan *et al.* 2009a; Green *et al.* 2009). Small, pale, slow growing (SP) lobsters occur in deep water while larger, redder faster-growing (LR) lobsters occur inshore in shallower water (Chandrapavan *et al.* 2009a), throughout its range in Australia. We examine changes in growth rates through an assisted migration of SP lobsters to inshore shallower reefs along a latitudinal gradient when the LR morph resides. We wanted to test whether growth rate of the SP morph was environmentally determined, and if it could be increased to different levels along a latitudinal cline.

Materials and methods

Southern rock lobster

Southern Rock Lobster *Jasus edwardsii* is an exploited spiny lobster with indeterminate growth, which inhabits temperate rocky reefs throughout southern Australia and New Zealand. *J. edwardsii* are relatively site attached (Gardner *et al.* 2003; Linnane *et al.* 2005) with a pelagic larval phase and mixing of stocks through larval dispersal (Booth and Phillips 1994; Chiswell *et al.* 2003). It supports valuable fisheries that are managed through input measures such as size, as well as through individual transferable quota systems.

Study sites

A Before-After Control-Impact (BACI) experiment was undertaken in southeast Tasmania (TAS), Victoria (VIC) South Australia (SA), Australia. In TAS lobsters were translocated from a removal (source) site (Maatsuyker Island) to eight release (transplant) sites (Whale Head, Riedle Bay and Taroona Reserve, Emerald Bay, Ansons Bay, Gull Island, Georges Rocks), along three degrees of latitude (Fig 1). In Victoria the removal and release site were a point offshore and inshore at Port Fairy (Fig. 1). South Australian translocations were from deep to shallow water sites within six few kilometres of each other. Maatsuyker Island is a southern, deep-water (60m-100m), rocky reef, where lobsters grow slowly, are pale in colour (Chandrapavan *et al.* 2009a), size at onset of reproduction (SOM) is small, at around 60mm carapace length (CL) and females rarely reach the minimum legal size of 105mm CL (Gardner *et al.* 2006). This phenotype of lobster is indicative of lobsters from offshore deep water sites in VIC and TAS. While there are sites specific differences, the inshore sites represent shallow rocky reefs where lobsters grow faster and are red in colour (Chandrapavan *et al.* 2009a).

Translocation

Tasmania

In the austral summer from 2005 to 2007, lobsters from Maatsuyker Island were captured and moved to the eight experimental sites (Table 1). Lobsters were caught using 50 steel-framed mesh lobster pots baited with a barracouta head (*Thyrsites atun*) and a jack mackerel (*Trachurus declivis*) and deployed in an area 500 m x 120 m. Pots were emptied twice daily, once at daybreak, then redeployed and emptied again after midday. At capture, *J. edwardsii* were measured and tagged on the ventral surface of the first or second segment of the abdomen with a uniquely coded T-bar tag (Hallmark, Victor Harbour, SA). All rock lobsters for translocation were immediately placed in 2 x 4000 l flow-through tanks aboard the RV "Challenger" under ambient water conditions where they were held until release at the new location (2-3 d). Lobsters were released into an 80 m diameter pen formed by a mesh fence, height 1.5 m of braided nylon mesh (stretched mesh size of 21 mm diagonal) set on the sea floor for 24 h to reduce their initial flight response away from the release site (Mills *et al.* 2006). This reduced dispersal so that recapture surveys could be more targeted to the release location. Release of translocated lobsters onto the reef within the cage occurred at night-time to reduce predator

mortality (van der Meeren 2000). After 24 h, the pen was lifted and the lobsters were able to move unrestricted around the reef.

Victoria

Translocation was conducted during May 2007 when undersize lobsters were captured by participating fishers south of Warrnambool, from waters greater than 50 metres and returned to shore-based holding facilities. When sufficient numbers were available, lobsters were measured and tagged and 135 were released south of Portland at depths between 15 and 20 m (Fig.1). Nineteen translocated lobsters were recaptured at the new site, and their growth was compared to that of 97 resident lobsters captured at the inshore site and 308 resident lobsters from the offshore site.

South Australia

In January 2007, a total of 4589 sub-legal sized speckled/white lobsters (64-158 mm) were caught in depths > 100 m off Southend. A commercial rock lobster fishing vessel and standard baited traps were used to catch all lobsters. To maintain condition, lobsters were held in circulated wells at sea surface temperature aboard the vessel. Lobsters were tagged with white Hallprint T-bar anchor tags using a Dennsion tagfast ® III tag applicator. Tags were inserted ventrally into the anterior oblique muscle between the first and second abdominal sterna. For each lobster the tag number, gender, carapace length, and shell colour (red/brindle/white using a standardised colour chart) were recorded. Approximately 670 lobsters were then translocated to each of three treatment ledges at Ringwood Reef.

Sampling at transplant sites

Tasmania

Sampling took place at the release sites using the same capture method as for the translocated lobsters described above. Sampling occurred mainly between January and March, although there was more frequent sampling in Taroona Reserve. Effort was distributed unevenly at the

different fishing sites. Records were made of CL, tag number, gender and maturational status lobsters for each lobster.

Growth rate of translocated lobsters was calculated as the difference in size between the size at initial capture for translocated and the size at first recapture, divided by the time at liberty. As lobsters grow in salutatory steps as they moult, and timing of moult is not always certain, a fraction of time at large was used to calculate the probability of having moulted between March and November.

South Australia

Translocated lobsters were recaptured by commercial and recreational fisherman during the 2007 and 2008 fishing season of the Southern Zone of the Rock Lobster Fishery (SZRLF). Data recorded on recapture were the same as when first captured.

Result presented depended on the recapture rates at each of the sites (Table 1). This varied due to sampling effort which was a factor of accessibility limited by weather and remoteness, and catch rate which varied with biomass (Fig. 1).

Results

Growth rate of translocated *J. edwardsii* showed flexibility in growth rates in response to a changed environment. Those lobsters moved from deep water sites inshore to shallow water sites significantly increased growth to a rate that was similar to that of resident inshore lobsters at sites in VIC and SA (Table 2, 3). In TAS, translocated lobsters also significantly increased their growth rate (Table 2, 3 and Fig. 2), and their mean growth was higher than the mean growth of residents.

Growth of lobsters moved to sites along a latitudinal gradient (translocation in TAS), more than 40 km north of the source site exceeded growth of the source (Fig. 2a, b, Table 2, 3, Fig. 3). Growth increased the further north the animals were moved. In TAS, increased growth rate was higher in females, and higher for smaller lobsters (Table 2 and Fig. 2). Colour of lobsters also changed within the first moult from the pale colouration to deep red as reported elsewhere (Chandrapavan *et al.* 2009a).

Discussion

Translocated lobsters exceeded the growth rate of locals in TAS and equalled this rate in SA and VIC. These results indicate that growth compensation occurs in rock lobsters when moved northward and inshore from areas of slow growth and reduced colour to areas where local lobster growth faster and are darker red. Together with an increase in growth rate there was an increase in red colouration, a signal of increased dietary carotenoids. Compensatory growth is thought to occur after a period of growth depression to due food deprivation (Boersma and Wit 1997; Ali *et al.* 2003), and is when animals can achieve a growth rate higher than normal (Boersma and Wit 1997). In the same study on rock lobster a range of biochemical measures were taken to assess whether slow growth was due to undernutrition, and it is likely that it was. Haemolymph parameters included the total haemocyte count, serum protein and electrotypes such as magnesium and potassium (Chandrapavan *et al.* 2010c) and omega-3 long chain fatty acids (Chandrapavan *et al.* 2009b), were different and improved after translocation, suggesting moving to an area of favourable growth. Total lipids however did not increase (Chandrapavan *et al.* 2009b).

Most demonstrations of compensatory growth in marine organisms are in laboratory experiments as it is difficult to tag and recapture enough individuals to observe trends in growth in the wild, and hard to manipulate the conditions that create slow growth to start with [39]. Different growth rates in *Jasus edwardsii* throughout their range and a large-scale fisheries stock enhancement project (Green and Gardner 2009; Green *et al.* 2010; Chandrapavan *et al.* 2010a) have provided a test case for examining growth compensation over a latitudinal gradient offer a natural test. When growth rates are lowered due to reductions in food, ectotherms mature later at smaller sizes (Berrigan and Charnov 1994). As *J. edwardsii* cannot yet be aged, it is not possible to know if they mature later, but the slow growing individuals do mature at much smaller sizes, when related to decreased food quality (Gardner *et al.* 2005).

It is an ongoing curiosity in ecology that most animals do not grow at their maximum rate (Atchley 1984; Alonso-Alvarez *et al.* 2007) given the importance of somatic growth rates to fitness and survival (Roff 1992; Stearns 1992). After periods of deprivation, organisms frequently demonstrate 'catch-up' or 'compensatory growth', whereby their growth rate exceeds what it was previously, and also that of control animals. It generally occurs after periods of undernutrition rather than malnutrition perhaps due to negative impacts early fast growth may have on lifetime reproductive potential (Darwinian fitness). Compensatory growth

commonly occurs after periods of resource deprivation (Mangel and Munch 2005). Growth and colour are frequently linked together in assessments of colour, oxidative stress and compensatory growth (Metcalfe and Monaghan 2001; Alonso-Alvarez *et al.* 2007). Implicit in the understanding of catch-up growth is that growth before the catch-up component was due to a period of undernourishment. Previous studies on the same experiment demonstrated, a difference in the level of fatty acids between the shallow and deep communities in Tasmania (Chandrapavan *et al.* 2009b). These studies also showed evidence of fatty acids overshooting that of locals in the translocated lobsters, which suggested that the concurrent change in colour and growth was due to an improvement in nutrition.

Finches raised in enlarged broads have compensatory growth and this increases oxidative stress (Alonso-Alvarez *et al.* 2007) and also decreases carotenoid levels circulating in the blood stream. The compensatory growth observed in translocated lobsters occurred coincident with a number of changes including an increase in the orange colour from an increase in dietary carotenoids (shallow water habitat has green algae which is the major source of carotenoids through astaxanthin in the marine environment). A trade-off directing energy for somatic growth or storage can occurs when energy is retained for storage as a minimum investment to prevent starvation or for later reproduction, and may vary with patchiness of the food environment (Reznick and Yang 1993; Metcalfe *et al.* 2002). Patterns of allocation and growth compensation may be expected in different environments as resources fluctuate and energy is retained for storage as a minimum investment to prevent starvation (Metcalfe *et al.* 2002). When resources become plentiful, allocation of energy may be prioritised to the restoration of depleted reserves, or straight to somatic growth to restore size through as increase in length or weight (Nicieza and Metcalfe 1997; Metcalfe *et al.* 2002).

Reef habitats in TAS deeper than 40 m do not have sessile macroalgae (Marzinelli *et al.* 2015); which may affect not only carotenoids in the diet of lobsters but also availability of food due to lower productivity.

Additional research would be required to determine the mechanism behind the observed compensatory growth, and the reasons for latitudinal and depth related differences in growth. However, this work suggests that translocated lobsters enhance their growth when food availability increases. This outcome has management and economic implications, as an underutilised fraction of the stock may be made available through translocation, and the consequent stock enhancement may reduce overall exploitation rates.

Table 1. Number of lobsters translocated to each site, each year of the experiment, and number recaptured until 2010.

Area		Site	Translocated			Recaptures	
			Year				
			2005	2006	2007	Resident	Translocated
TAS	1	Whale Head		2000	1500	57	70
	1	Ketchum Island	1800				
	2	Taroona	1800	2000	2000	1601	1177
	2	Reidle Bay (Maria Island)	1800	2000			
	2	Emerald Bay (Maria Island)			2000		
	3	Ansons Bay	1800			17	5
	4	Georges Rocks		2000	1400	7	129
	4	Gull Island		2000	1525		
VIC		Port Fairy			135	97	19
SA	MFA 55	Ringwood Reef			2020	83	287
	MFA 56	Robe			2569	367	322

Table 2. Mean growth for three length classes for translocations for the three states.

Site	Source	Female			Male		
		80	90	105	80	90	110
TAS							
1	Resident	2.9	1.9	0.3	12.2	11.1	9.1
	Translocated	11.4	7.4	1.5	19.4	15.5	7.8
2	Resident	4.1	3.8	3.4	14.2	13.0	10.6
	Translocated	9.5	8.1	5.9	15	13.1	9.4
4	Resident	8.3	7.6	6.4			
	Translocated	12.2	10.7	8.5	25.5	24.0	21
VIC							
Port Fairy	Resident				23.9	21.4	16.4
	Translocated				24.4	20.4	12.3
SA							
MFA 55	Resident	12.8	10.9	8.0	16.5	15.5	13.5
	Translocated	10.3	9.1	7.3	15.0	13.3	9.9
MFA 56	Resident	10.6	8.7	5.9	12.8	11.4	8.6
	Translocated	6.4	5.8	4.8	13.1	11.4	8.2

Table 3   Likelihood ratio test statistics comparing the growth of translocated lobsters to growth at resident and source sites. (n/a - insufficient data or test failed to resolve). A1 = Whale Head, A2 = Taroona Marine Reserve, A3 = Anson Bay and A4 = Georges Rocks.

			Resident				Source		
			χ^2	df	P		χ^2	df	P
TAS	Area 1	Female	n/a				n/a		
		Male	3.54	3	NS		51.18	3	<0.0001
	Area 2	Female	381.2	3	<0.0001		349	3	<0.0001
		Male	26.6	3	<0.0001		258	3	<0.0001
	Area 3	Female	n/a				n/a		
		Male	n/a				n/a		
	Area 4	Female	4.68	3	NS		n/a		
		Male	n/a				n/a		
SA	MFA 55	Female	11.63	3	<0.001				
		Male	11.12	3	<0.05				
	MFA 56	Female	53.39	3	<0.0001				
		Male	n/a						
VIC	Port Fairy Female		n/a				n/a		
		Male	10.00	3	<0.05		12.39	3	<0.001

Site descriptions.

Whale Head (43° 37' 25"S 146° 52' 49"E) is a highly exposed shallow inshore site 23 nm NE of Maatsuyker and is used as the transplant control as it is a shallow site at similar latitude to the source site. The site is dominated by dolorite boulders and macroalgae, and rocky reef extends to 60m depth.

Taroona Reserve is an estuarine rocky reef bounded by large expanses of sand, with an average depth of 7 m, and maximum depth of 15 m. The area is approximately 1.24 km^2 including a surrounding no-take buffer zone. Population density of *J. edwardsii* within the reserve is high (approximately 13 000 individuals), and the reserve has been closed to both commercial and recreational fishing since 10 November 1971 when it was proclaimed as a marine reserve for rock lobster research. Riedle Bay is an inshore exposed rocky reef of granite boulders and macroalgae, with continuous reef to 60m. The average depth is 15m.

Ringwood Reef is characterized by a sea-floor composed by an aeolianite limestone reef matrix, eroded to form ledges, crevices, undercuts and holes. The communities at each site were dominated by encrusting invertebrates (sponges, ascidians, bryozoans), spiny urchins (*Heliocidaris erythrogramma*), red foliose, green foliose (*Caulerpa* sp.), brown branching (*Ecklonia radiata, Macrocystis angustofolia*), and encrusting coralline algae.
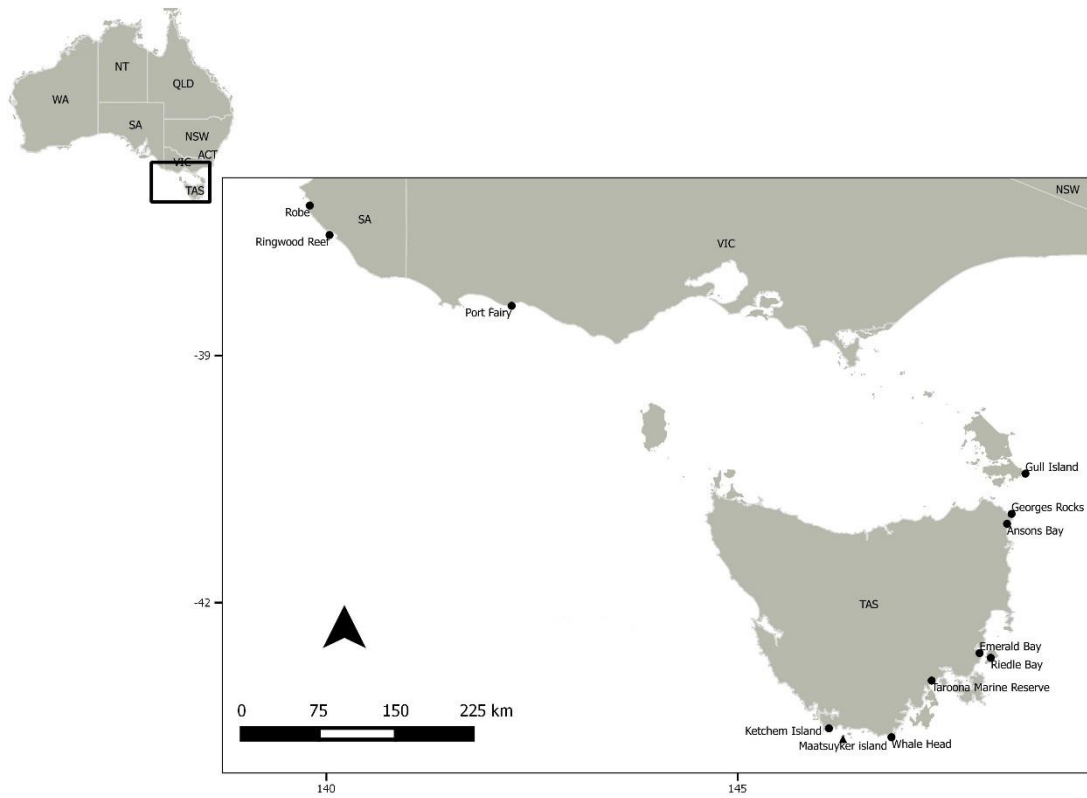
Fig. 1. Sites used for translocation experiments. Removal site (▲) and release sites (●).
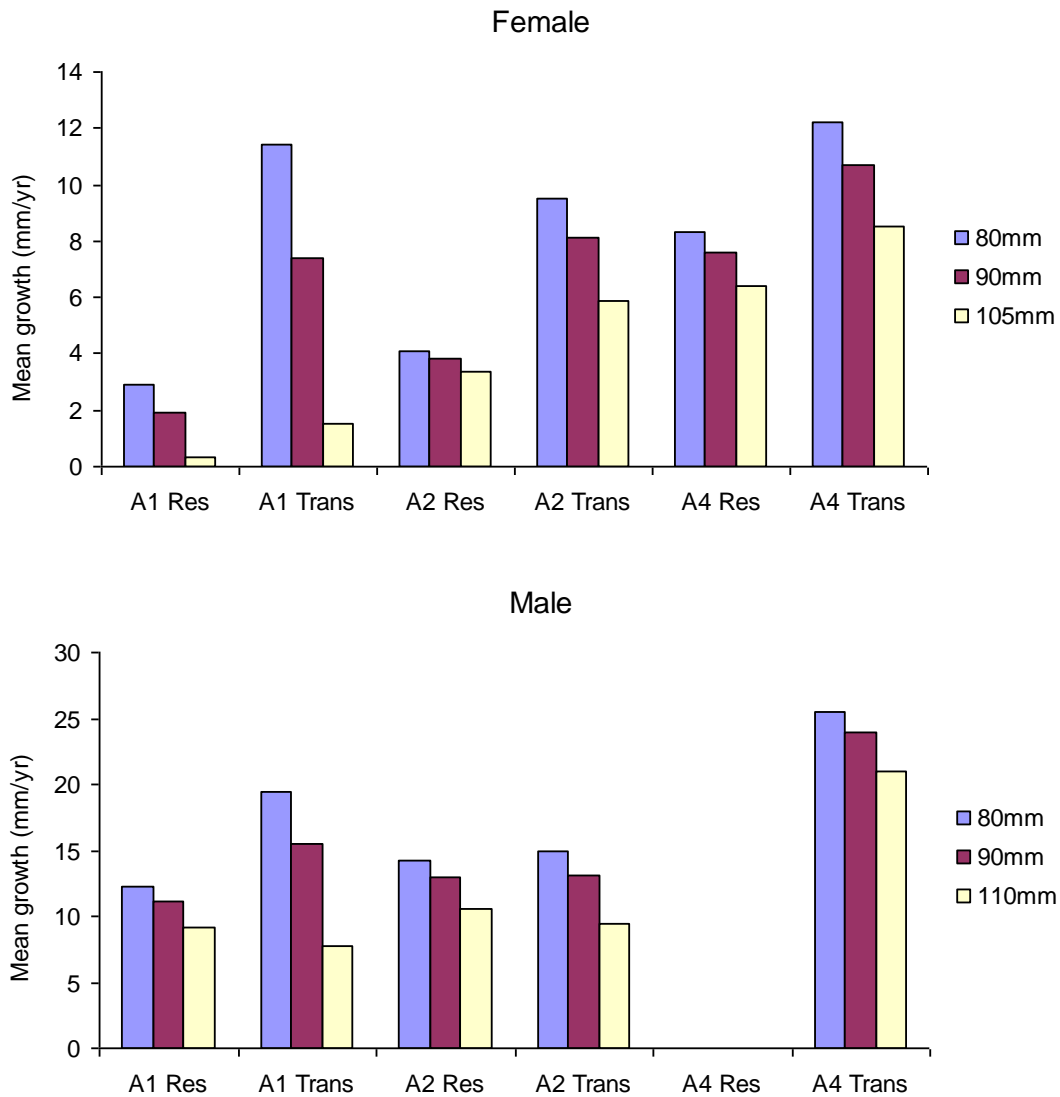
Fig. 2. Mean growth of females and males at three lengths for the Tasmanian translocation areas. Res = Resident, Trans = Translocated, A1 = Whale Head, A2 = Taroona Marine Reserve, A4 = Georges Rocks.
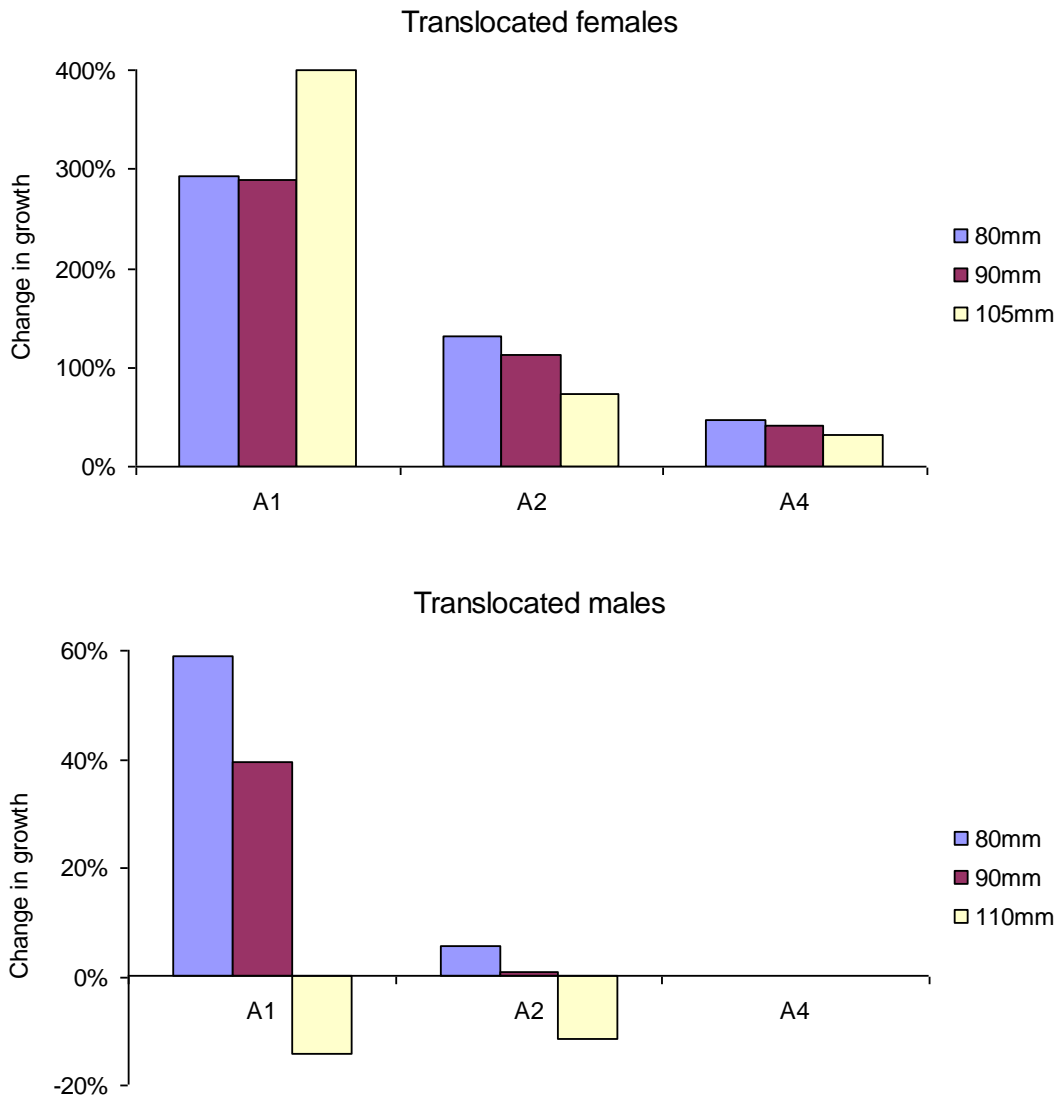
Fig. 3. Percent change in growth of females (top) and males (bottom) at three lengths for the Tasmanian translocation areas. A1 = Whale Head, A2 = Taroona Marine Reserve, A4 = Georges Rocks.

Objective 2. To assess density dependent changes in lobster growth

Translocation of lobsters results in density dependent changes to growth

Bridget Green[1], Caleb Gardner[1], Dave Hobday[2], Adrian Linnane[3], Klaas Hartmann[1]

[1] Institute for Marine and Antarctic Studies, University of Tasmania, Private Bag 49, Tasmania, 7001, Australia.

[2] Primary Industries Research Victoria, Department of Primary industries, PO Box 114, Queenscliff Victoria 3225.

[3] South Australian Research and Development Institute (Aquatic Sciences), PO Box 120, Henley Beach, South Australia 5022, Australia.

Abstract

Demographic and market traits of the southern rock lobster, *Jasus edwardsii,* vary throughout its' range, which affects the distribution and production of the fishing industry. Lobsters from deep water tend to be pale (and thus lower value), have slower growth and higher density. We undertook a large-scale experiment to explore whether the yield and value of these deep water lobsters could be increased by translocating individuals to faster growth, shallow habitat. Over 3 years, approximately 26,000 lobsters were captured from a southern, deep water site, Maatsuyker Island, and translocated in lots of 1800 to 2000 individuals to eight inshore shallow water sites along the east coast of Tasmania, ranging from 30 to 300 nautical miles from the capture site. Growth was measured before and after the translocation for residents at the removal site and at one of the release sites, Taroona. Growth at the removal site increased while growth at the release site decreased after 5,800 lobsters were introduced, a pattern consistent with density-dependent effects on growth. These results enable better prediction of the effect of large scale enhancement / translocation programs on productivity. Further, these large scale manipulations of density provide insights into the effects of fishing and stock rebuild strategies in terms of the change in productivity that may result.

Introduction

Growth in crustaceans varies because of internal factors such as hormonal control and external factors such as temperature and food availability (Hartnoll 2001). External environmental factors vary spatially and temporarily and affect growth of crustaceans through changes in moult increments and frequency (Annala and Bycroft 1988; Thomas *et al.* 2000; Comeau and Savoie 2001, 2002). Food availability and quality also varies spatially and is known to be an important influence of spatial patterns in productivity of commercial fisheries (McGarvey *et al.* 1999; Thomas *et al.* 2000; Gendron *et al.* 2001; Hazell *et al.* 2001).

Density also plays a role on changes in crustacean growth but is not as simple process of competition for food (Tuck *et al.* 2000) as both positive and adverse effects have been observed depending on additional factors. Clawed lobsters in culture tend to grow better when they are individually kept than when they are kept in groups due to agonistic interactions (Waddy *et al.* 1995). However, low densities have been found to negatively affect moult increments and frequency in juveniles under culture and enclosure fields conditions (Aiken and Waddy 1978; Wahle *et al.* 2001). Spiny lobsters, can have higher growth at high density in communal rather than individual rearing (Lee and Wickins 1992; Booth and Kittaka 2000); however, in the wild density reduces growth when food is limited (Polovina 1989; Groeneveld 1997; McGarvey *et al.* 1999).

Experimental manipulation of density of lobsters in the wild has not always led to expected outcomes faster growth at lower density. Removal experiments by Ford et al. (1988) led to no detectable differences in growth between increased and reduced density areas although Moohouse and Macdonald (2011) found that removal increased food availability and growth. However, these contradicting outcomes may be a result of practical limitation and/or difficulties in controlling all potential factors associated with growth, which likely interact with density. For instance, the mobility of crustaceans makes it difficult to keep high density in the release sites (Ford *et al.* 1988). Also, differences in type and availability of prey between experimental sites may influence feeding behaviour of resident and moved individuals, which affects their growth (Haley *et al.* 2011).

Southern rock lobster in Tasmania (TAS) have spatial differences in biological traits such as size at onset of maturity (SOM), colouration and growth (Punt *et al.* 1997; Gardner *et al.* 2006; Chandrapavan *et al.* 2009a). The commercial fishing fleet responds to these differences and other spatial differences such as wave exposure so that fishing effort tends to be concentrated in shallow waters where lobsters have darker-red colouration (and thus higher value) plus a reputation for being more robust for live transport (Ford 2001; Bradshaw 2004; Simon *et al.* 2016). As a result, the stock has higher exploitation rate plus low density/ lower exploitation rate and higher density in shallow and deep waters respectively (Semmens *et al.* 2006).

A lobster translocation program has been developed into a commercial operation run on behalf of all commercial quota owners by the industry association in order to increase production in the fishery. This operation capitalises on the high abundance of lobsters in deep water and shifts them to shallow water where they stay and grow faster, thus increasing production of the fishery (Gardner *et al.* 2015). These operations currently move around 100,000 lobsters each year, which results in higher production of around 50 tonnes. The outcome of this process has been estimated and modelled previously assuming growth parameters of local lobsters at removal and release sites, based on pilot-scale field trials (Chandrapavan *et al.* 2010a). That research was extended here to better explore whether changes in the density of lobsters at both removal and release sites alters growth rate, which is possible now due to the larger data on translocated lobsters which was not available to earlier studies.

Materials and methods

Southern rock lobster

Jasus edwardsii is an exploited spiny lobster with indeterminate growth, which inhabits temperate rocky reefs throughout southern Australia and New Zealand. *J. edwardsii* are relatively site attached (Gardner *et al.* 2003; Linnane *et al.* 2005) with a pelagic larval phase and mixing of stocks through larval dispersal (Booth and Phillips 1994; Chiswell *et al.* 2003). Size of maturation varies along with other demographic traits throughout their range (Annala and Bycroft 1987; MacDiarmid 1989; Gardner *et al.* 2006; Linnane *et al.* 2008, 2009; Green *et al.* 2009).

Study sites

This experiment was undertaken in southeast Tasmania (Tas), Australia, with one source site (Maatsuyker Island), and seven transplant sites (Whale Head, Riedle Bay and Taroona Reserve, Emerald Bay, Ansons Bay, Gull Island, Georges Rocks) along four degrees of latitude (**Error! Reference source not found.**).
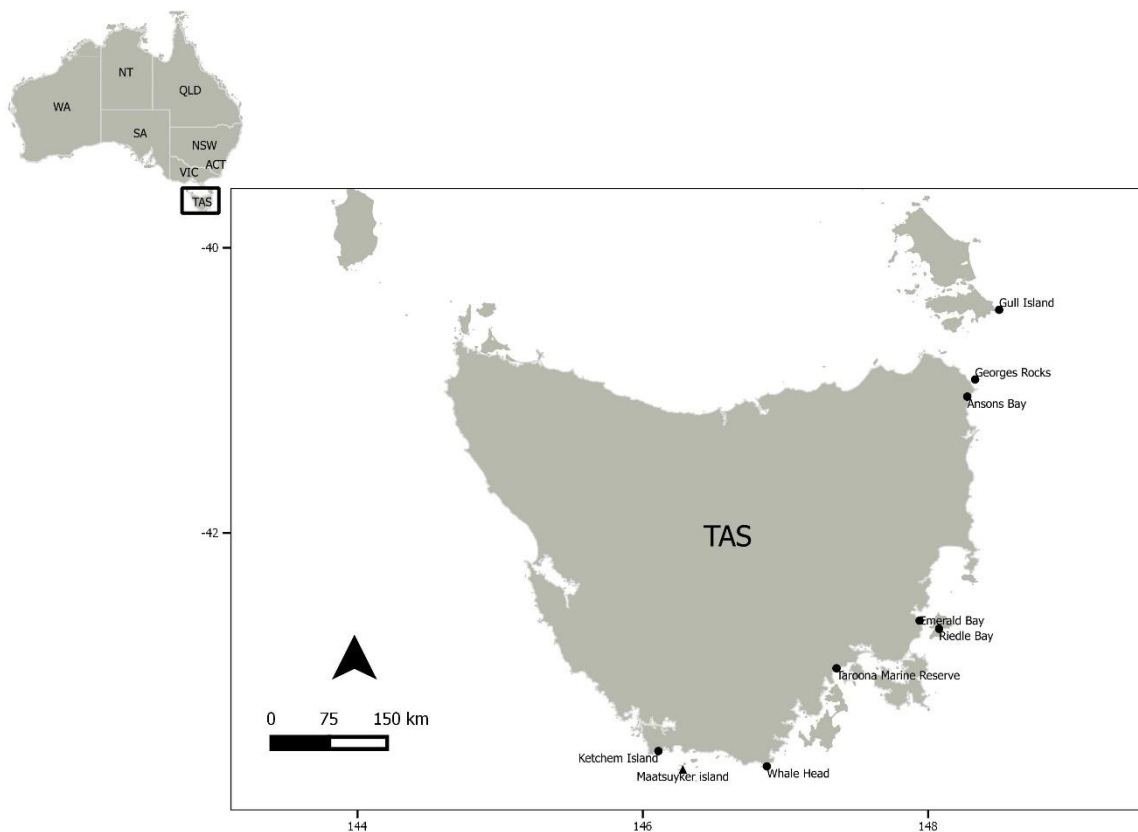
Adequate data for this analysis of density effects was available only for the source (removal) site and one transplant (release) site, which was Taroona Reserve. Maatsuyker Island is a southern, deep-water (60m-100m), rocky reef 12 nm offshore where lobsters grow slowly and are pale in colour (Chandrapavan *et al.* 2009a), with a small SOM, at around 60 mm carapace length (CL) and females rarely reach the minimum legal size of 105-mm (CL) (Gardner *et al.* 2006). Taroona Reserve is an estuarine rocky reef bounded by large expanses of sand, with an average depth of 7 m, and maximum depth of 15 m. The area is approximately 1.24 km^2 including a surrounding no-take buffer zone. The reserve has been closed to both commercial and recreational fishing since November 1971; consequently, population density of *J. edwardsii* within the reserve is high.

Translocation

Translocation occurred in the austral summer from 2005 to 2007, when 2,5625 lobsters, including mature female, were captured from Maatsuyker Island and moved to the eight experimental sites (Table 1).

Table 1. Number of lobsters translocated to each site, each year of the experiment, and number recaptured until 2010.

Area		Site	Translocated			Recaptures	
			Year				
			2005	2006	2007	Resident	Translocated
TAS	1	Whale Head		2000	1500	57	70
	1	Ketchum Island	1800				
	2	Taroona	1800	2000	2000	1601	1177
	2	Reidle Bay (Maria Island)	1800	2000			
	2	Emerald Bay (Maria Island)			2000		
	3	Ansons Bay	1800			17	5
	4	Georges Rocks		2000	1400	7	129
	4	Gull Island		2000	1525		

All translocated lobsters were measured and tagged on the ventral surface of the first or second segment of the abdomen with a uniquely coded T-bar tag (Hallmark, Victor Harbour, South Australia). All rock lobsters for translocation were immediately placed in 2 x 4000 l flow-through tanks aboard the RV "Challenger" under ambient water conditions where they were held until release at the new location 2-3 d later. Lobsters were released at the water surface into an 80 m diameter pen, height 1.5 m with braided nylon mesh (stretched mesh size of 21 mm diagonal) set on the sea floor for 24 h. This didn't perfectly contain all lobsters but did reduce the initial flight response of the majority so that they were retained in the release site which increased recapture rate and thus data for the study (Mills *et al.* 2006). Releases occurred at night to reduce predator mortality upon release (van der Meeren 2000). After 24 h, the cage was lifted and the lobsters were free to disperse over the reef.

Sampling at transplant sites

Later sampling of the transplant sites (Taroona) used baited traps as per the capture method as originally applied to the translocated lobsters. Sampling occurred mainly between January and March, although there was some sampling outside this period. Effort was unevenly distributed at the different fishing sites. All lobsters were measured for carapace length, checked for a tag, and gender and maturational status were recorded.

Growth estimation

To determine the average annual growth rates several stochastic versions of the von Bertalanffy-Fabens growth model were used (Troynikov *et al.* 1998). Inputs to the analyses were carapace lengths at release and recapture and time at liberty. Originally, the von Bertalanffy-Fabens growth model was developed for populations with continuous growth, when a small time at liberty will produce a small length increment. However, rock lobster data demonstrate that for very short time at liberty the increment in size can be zero or significant, depending on whether the lobster has moulted whilst at liberty. In this situation the stochastic von Bertalanffy-Fabens growth model can only use data that have time at liberty more than about 6 months. The outputs of the data parameterisation were annual means and distributions of the length-increments for various lengths at release (80mm, 90mm, 105mm - females and 110mm - males). The deterministic von Bertalanffy-Fabens growth parameters $L\infty$ and k were estimated for each sex at each site. Since the stochastic growth models are in the form of probability density functions the likelihood - ratio test was used for comparison of growth between different sites.

Results

In both removal (Maatsuyker) and release (Taroona) sites, growth models before and after translocation were significantly different (Table 1 and 2, Figs 2-4). Results from the removal site were ambiguous for females as growth increments were very small and data was clustered over a small size range despite the large sample size. Translocated male and female lobsters (post 2005 in Taroona) had a higher growth rate contrasted with resident lobsters in the removal site (pre and post 2005 in Maatsuyker) (Table 3). In the release site (Taroona), the growth rate (*K*) dropped significantly for both males and females after the increase in density (pre 2005 vs.

post 2005, Table 2) consistent with density dependent effects on growth. Consequently, the mean growth per year fell for both females, between 0.2 and 0.4 mm year-1, and males, between 1.6 and 1.8 mm year-1 (Fig. 2, 3 and 5). For both genders, the growth reduction was higher for individuals at the smaller size group (80 mm CL). At the removal site at Maatsuyker Island, growth rate of 110 mm CL males increased consistent with a reduction in density leading to reduced competition for resources (Fig. 4 and Fig. 5).

Table 1.   Likelihood ratio test statistics comparing the growth of resident lobsters before and after 2005. (n/a - insufficient data or test failed to resolve).

		χ^2	df	P
Taroona	Female	6.79	3	<0.01
(release site)	Male	93.36	3	<0.0001
Maatsuyker	Female	n/a		
(removal site)	Male	24.00	3	<0.0001

Table 2. Estimates of the von Bertalanffy growth parameters for density dependent effects. N_{Total} is the total number of first recaptures for the site; T_{min} is the minimum time at liberty used to select recaptures for analysis; $N > T_{min}$ is the number of recaptures at liberty longer than T_{min}; k is the von Bertalanffy growth rate; L_∞ is the von Bertalanffy maximum length. Pre and post are the period before and after removal and release of lobsters from Maatsuyker and to Taroona respectively.

Site	Sex	Data source	N_{Total}	T_{min} (yr)	$N > T_{min}$	Distribution model	k	L_∞ (mm)
Release (Taroona)	Male	Pre 2005	2537	0.6	1293	Weibull	0.186	192.9
		Post 2005	761	0.6	575	Weibull	0.151	192.4
	Female	Pre 2005	1899	0.6	1321	Gamma	0.099	145.4
		Post 2005	245	0.6	203	Gamma	0.073	157.0
Removal (Maatsuyker)	Male	Pre 2005	462	0.6	299	Gamma	0.149	130.0
		Post 2005	314	0.6	176	Weibull	0.147	134.6
	Female	Pre 2005	238	2.0	79	Gamma	0.051	105.7
		Post 2005	392	0.6	392	Weibull	0.015	137.7

Release site before translocation - female

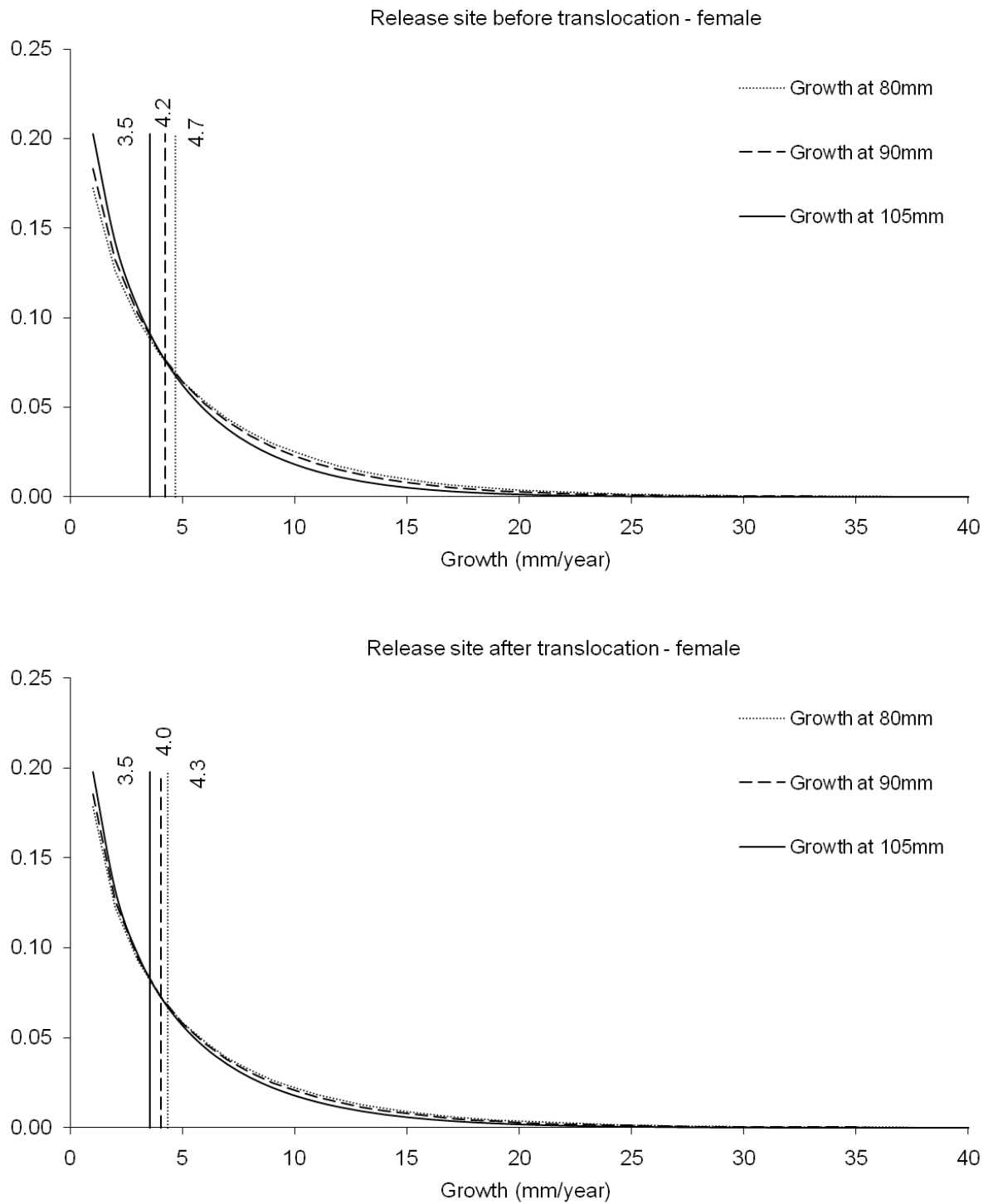## Release site after translocation - female

Fig. 2. Probability density function of annual growth increments at three lengths for females at the Taroona release site before and after translocation. Vertical lines indicate the mean annual growth at each length.
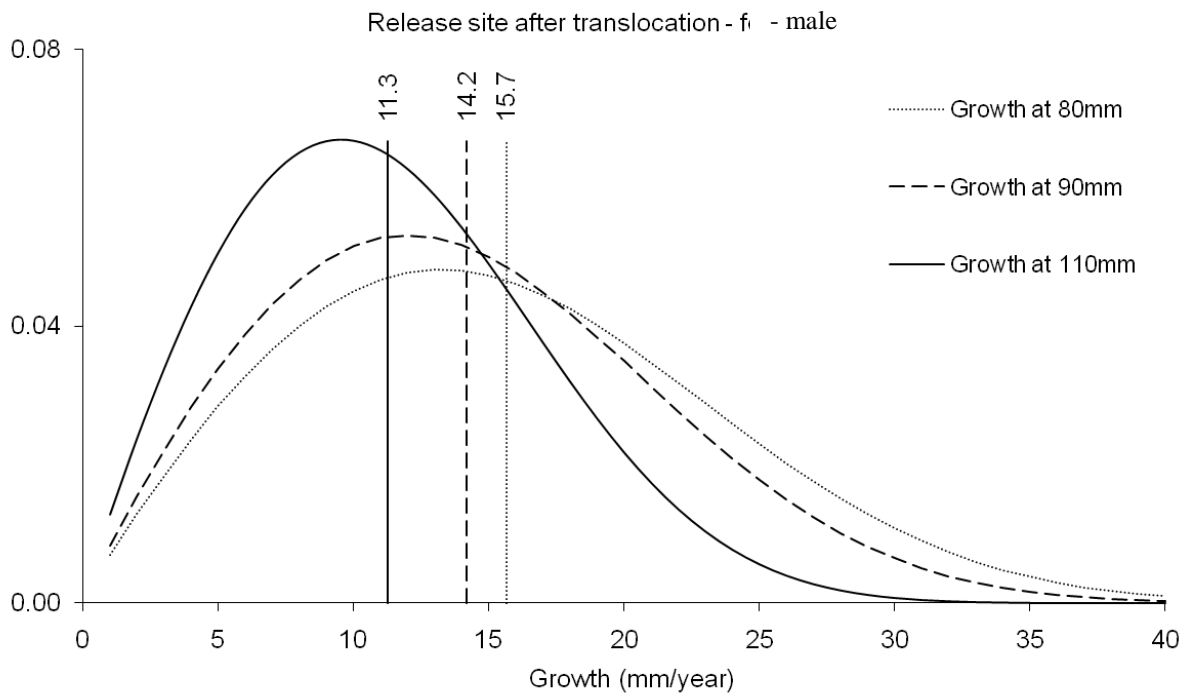
Fig. 3. Probability density function of annual growth increments at three lengths for males at the Taroona release site before and after translocation. Vertical lines indicate the mean annual growth at each length.
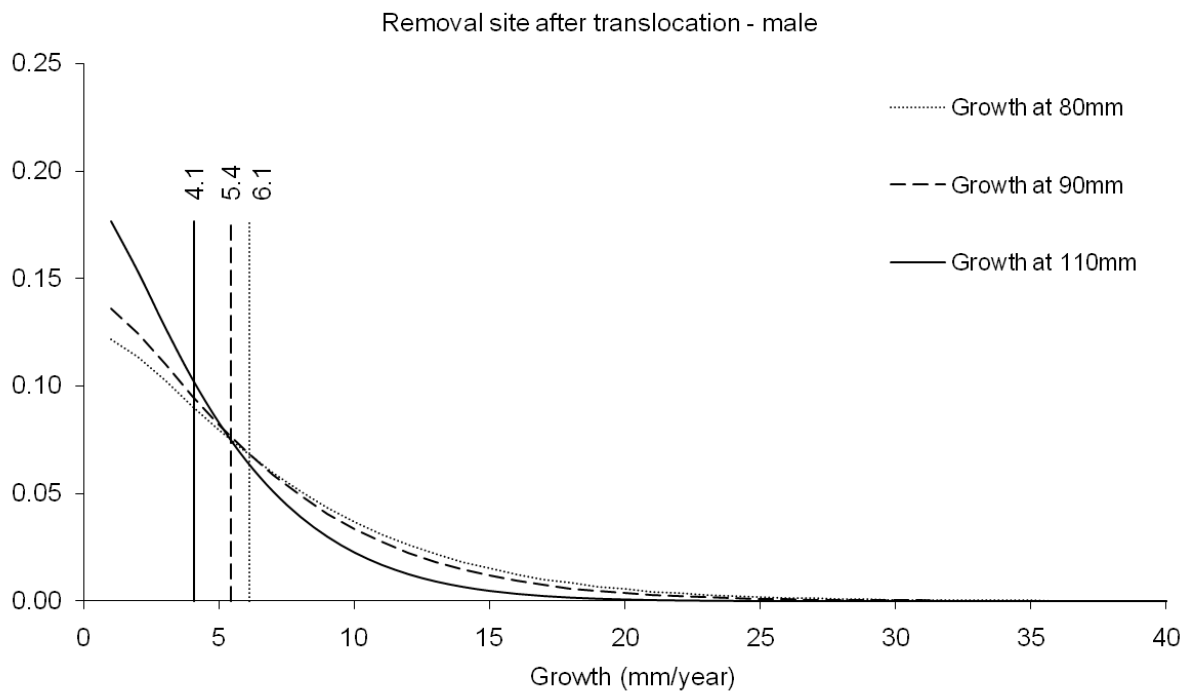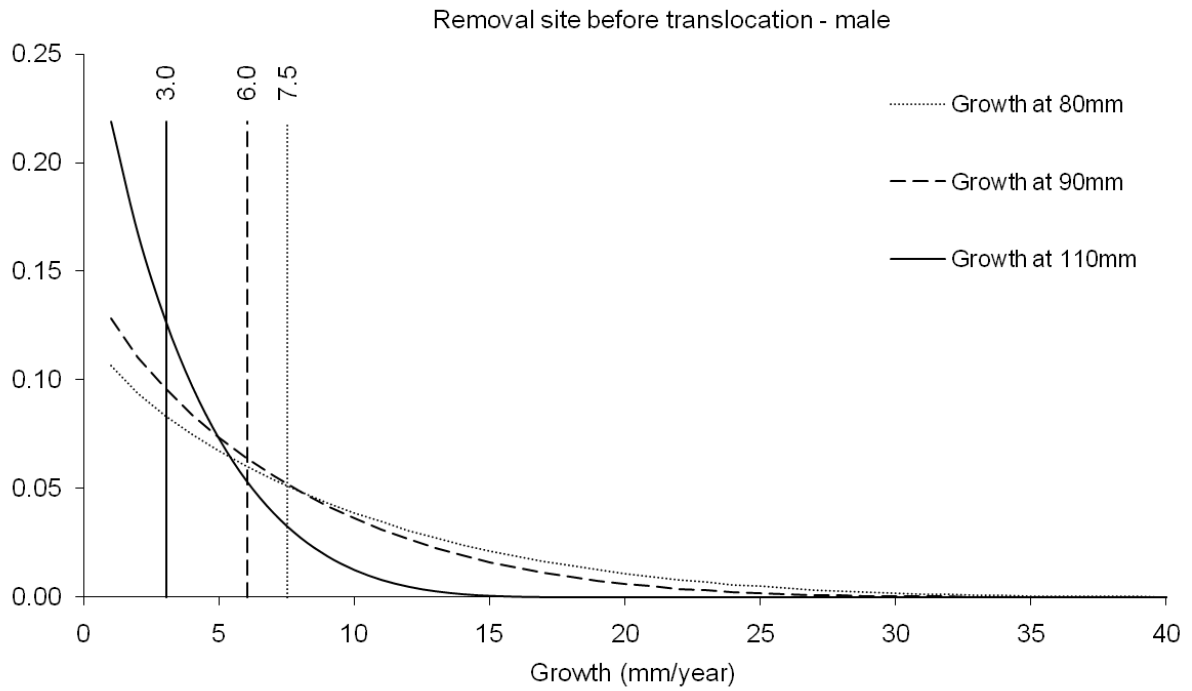
Fig. 4 Probability density function of annual growth increments at three lengths for males at the Maatsuyker removal site before and after translocation. Vertical lines indicate the mean annual growth at each length.
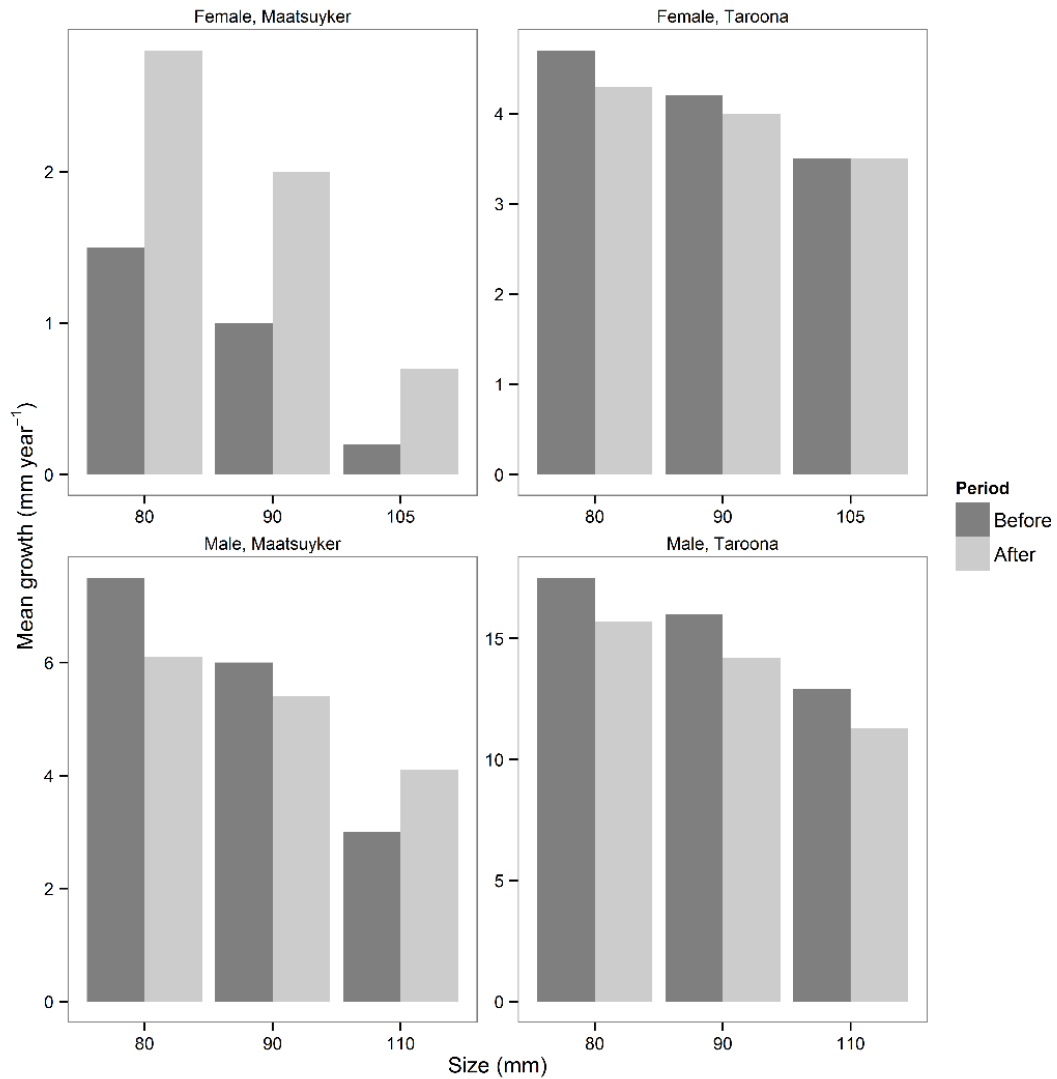
Fig. 5. Mean growth (mm year^{-1}) at three lengths for the Maatsuyker (removal site) and Taroona (release site) before and after the translocations.

Discussion

Density-dependent changes to demographic parameters, are not a new concept in marine populations and have been examined in a range of fish and fisheries species for growth (Dixon and Day 2004), mortality (Hixon and Carr 1997) and reproduction (Gardner *et al.* 2006). Theoretical demonstrations of density dependence are common, including for reproductive traits (Ernande *et al.* 2004), mortality (Beverton and Iles 1992). This study clearly demonstrates density-dependent changes in growth in response to both increase and decreases in density following translocation for stock enhancement.

Translocated lobsters increased their growth rate relative to the resident ones in the removal area (non-translocated lobsters). This result suggests an influence of improved environmental conditions, possibly food availability, in the release area. This outcome is consistent with that expected where greater food availability positively affects growth of lobsters in the wild (Haley *et al.* 2011).

Lobsters at the release site had lower growth rate after translocation, for both female and male, which may be attributed to the sudden increase in density. Crowded conditions have been observed to cause an increase in agonistic interactions with large individuals inhibiting the growth of smaller ones through competing for food (Moorhouse and Macdonald 2011), so that moult frequency and size increment is reduced (Cobb *et al.* 1982; Karplus and Barki 2004; Karplus 2005). In the removal area, females and large males increased their mean growth after density reduction, which may have released interference competition, making food more available (Herberholz *et al.* 2007).

Even though it was not possible to model growth for all release sites, there was enough information to conclude a significant effect of density on growth. One plausible mechanism by which density acts is access interference to food amongst crowded individuals. The scale of the observed reduction in growth was modest and only occurred in an area closed to fishing with unusually high lobster density. Parameterisation of this effect is helpful for modelling of translocation although the scale of density-dependent reduction in growth observed here was so modest that it is seems unlikely to have any impact in areas where stocks are already depleted from natural levels through removals by fishing.

Objective 3. To describe fine scale variations in growth of lobsters off western Tasmania

Fine scale spatial variation in growth of southern rock lobster around TAS

Rafael León[1], Caleb Gardner[1], Bridget Green[1], Klaas Hartmann[1], Adrian Linnane[2]

[1]Institute for Marine and Antarctic Studies, University of Tasmania, Private Bag 49, Tasmania, 7001, Australia.

[2]SARDI Aquatic Sciences, Hamra Avenue, West Beach, South Australia.

Abstract

Stocks of marine resources tend to be spatially heterogeneous in their biological traits, which has management and economic implications. Spatial heterogeneity in the growth of Southern Rock Lobster (SRL) in Tasmania Australia has led to commercial translocation operations where lobsters are moved from slow to fast growth areas to increase sustainable harvests. These operations currently use coarse scale information on growth to manage where lobsters are taken from and where they are released. Finer spatial information on growth rate would assist planning of translocation and improve results because it may be possible to identify ideal areas for release that involve smaller travel distances. To assist with finding ideal, small-scale sites for release of lobsters, we estimated growth coefficients on a large scale (because of data limitation) and size at 50% onset of maturity (L_{mat}) on a smaller scale. We used the potential growth span before maturity, represented by the ratio L_{mat}/L_∞, as a proxy for growth at small-scale. We also fitted a Generalized Additive Model (GAM) to investigate the effect of the geographical location and depth on growth. SRL reached first maturity and L_∞ at largest size in the north with potential growth before maturity greatest in the north. The effect of depth was also examined with no changes in potential growth up to 50 m of deep, while below this depth it sharply decreased. Estimation of potential growth appears to provide a feasible method for identifying locations and depths that would refine translocation operations.

Keywords: potential growth, size at onset of maturity, spatial management, latitudinal and depth gradient, translocation, *Jasus edwardsii*.

Introduction

The stocks of marine resources tend to be spatially heterogeneous in their biological traits, such as growth and the size at onset of maturity (SOM). The growth of Southern Rock Lobster (SRL) in Tasmania (TAS) varies over gradients of latitude and depth, with a general pattern of fastest growth in the north and shallower habitat (Punt *et al.* 1997; Linnane *et al.* 2009; Chandrapavan *et al.* 2010b). Similarly, SOM changes from north to south in TAS, with females of SRL reaching the first maturity at 100-105 mm of carapace length (CL) and 60-65 mm in the north and south respectively (Gardner *et al.* 2006). Additionally, SRL varies in its coloration with depth, with lobsters from shallow waters having darker red colouration (Chandrapavan *et al.* 2009a).

Biological heterogeneity may have implications for management, especially when stocks that are managed as a single unit and spatial variation at a smaller scale are not considered. For instance, the use of a single size limit zone in the Tasmanian SRL fishery despite the large spatial variation in growth results in a substantial loss of yield relative to what could be obtained with regional size limits (Hartmann *et al.* 2013; Gardner *et al.* 2014). The spatial heterogeneity in biological traits and spatial differences in operating conditions for the fleet in terms of wave exposure means that some regions tend to receive more effort and become more depleted (Ford 2001). In particular, there is concentration of fishing effort in shallower waters and on the east coast, while deeper water habitats on the west coast have lower exploitation rates (Bradshaw 2004). This distribution of effort may potentially dissipate rent when it results in localised growth overfishing. There are also problems of congestion externalities (e.g. competition, gear interference) despite the individual quota system in place because there are incentives to be the first to reach highly valued lobsters and fish when the catch rate is higher rather than waiting for periods when price is higher (Emery *et al.* 2014).

One approach to managing spatial differences in biology involves translocation of lobsters between regions and was approved by the Government of Tasmania for commercial scale operations managed by an industry group representing all quota owners in the fishery (Gardner *et al.* 2015). This translocation currently involves capture and transport of 100,000 undersized lobsters from deep to shallow waters each year, following economic and biological feasibility research (Gardner and Van Putten 2008a,b). After five years, amongst other positive outcomes,

the translocated lobsters changed colour and increased their growth rates (Chandrapavan *et al.* 2009b, 2010a).

SRL translocation in TAS was guided by a population dynamic model that described growth rates, sex and size-structure of the stock in 11 statistical sub-zones (Punt *et al.* 1997; Gardner *et al.* 2015). However, given the large spatial scale of the statistical sub-zones, the full potential of the translocation operations may not be captured. A particular concern of industry is that there may sites within the larger sub-zones that have ideal traits for promoting fast growth of lobsters but are not currently being used.

Finer scale information on growth and maturity of lobsters is also of interest for better understanding these biological processes. Spatial patterns are surprisingly different for the same species in New Zealand where size at first maturity increases towards the south (Annala *et al.* 1980) while it increases towards the North in Australia (Gardner *et al.* 2006). These contradicting outputs suggest that other factors different from temperature may affect the population dynamics, possibly local variation in food availability (Skewes *et al.* 1997; McGarvey *et al.* 1999; Mayfield *et al.* 2000; O'Malley *et al.* 2012).

Analysis of finer spatial scale information on growth rate was limited in this study by the availability of suitable data despite around 40,000 tag recaptures from several decades of research efforts. This was because of issues such as the distribution of tags and the size range required enabling growth curves to be fitted. In contrast, maturity data was available with a larger number of animals with better spatial coverage, which enabled to estimate the size at first maturity to be estimated at a much finer spatial scale. Fortunately, there is a well-established relationship between growth coefficients and size at first maturity (Beverton 1992; Froese and Binohlan 2000) and this was used to estimate potential growth at a finer spatial scale in this fishery.

Methods

Data

This study included southern rock lobster data from South Australia (SA) and TAS (TAS), which was compiled from databases maintained by South Australia Research and Development Institute (SARDI) and the Institute for Marine and Antarctic Studies, University of Tasmania, respectively. These databases contain comprehensive tag-recapture data from commercial

fishing operations including carapace length, sex, maturity stage (for females), date of tagging/recapture and latitude/longitude. These coordinates were projected to the Universal Transversal Mercator (UTM) coordinate system. Data was used from 1973 to 2014 for SA and from 1993 to 2014 for TAS.

Growth estimation

The Faben's parametrization of the von Bertalanffy growth function (VBGF) was used to determine growth coefficients. This approach avoids the difficulties of unknowing the age at-first-capture in crustacean because this is based on the moulting increment and intermoult period from tag-recapture (Chang *et al.* 2012). The estimated growth increase in a particular period is given by

$$\Delta \hat{L} = (L_\infty - L_t)(1 - e^{-K\Delta t})$$

where $\Delta \hat{L}$ is the expected change in length over the period Δt for an animal with an initial length of L_t, K and L_∞ are the growth rate and asymptotic length respectively.

The data from both fisheries comprise an extended period over which tag-recapture data has been collected; hence, there were numerous records of specimens with multiple recaptures. This issue may cause bias on growth estimates (Wahle and Fogarty 2006), and we addressed this using just the first recapture to fit the growth models. Also, even though there is concern about using the VBGF in crustaceans, as their growth is discontinuous and this function assumes continuous growth, VBGF has been successfully used to estimate growth in crustaceans and gives a medium to high biological reality in average growth estimations (Chang *et al.* 2012). In this study, this function was used to estimate growth for females at a large spatial scale, based on a 90x90 km and 90x45 km blocks. In each case, estimation was carried out for a unique size group (64 -198 mm), because sample size became insufficient while we split the data into more specific size categories. Hence, growth coefficients were estimated for seven sites in TAS. We kept the same CL size group to calculate growth coefficients with data from SA, based on a 20x20 km blocks and data was sufficient to obtain estimation in nine sites.

Size at onset of maturity

The proportion of mature females at different sizes was modelled at the same scale than growth was estimated (90x90 km and 20 x20 km blocks for TAS and SA respectively) with a logistic function

$$P_{mat} = \frac{e^{(a+bx)}}{1 + e^{(a+bx)}}$$

Where P_{mat} is the proportion of mature females, x is females' size, a and b are model coefficients. This function was also used to estimate the size at which 50% of the females were mature $L_{mat} = -\,^{a}\!/_{b}$.

Additionally, new values of size at maturity were calculated at a small scale (1.5-3.0 km). They were used to predict values of potential growth as described below. When estimating L∞ at a small scale, two issues arose. The first was of nearly separated data, with smallest female specimens immature and largest specimens mature, especially in the northern blocks, which produces non-convergence. Second at some southern sites, almost 100% of females were mature with immature females apparently too small to be captured effectively in traps. The separation issue was addressed by fitting the model using penalised maximum likelihood (Heinze and Schemper 2002) with the R package logistf (Heinze *et al.* 2013). The large proportion of mature female was solved by using only sub-blocks with at least 20% of the females immature.

Potential growth

The ratio L_{mat}/L_∞ was used as an approach to growth, as this represents the proportion of the potential growth span covered before maturation, henceforth potential growth. This ratio has better properties than separate values of L_{mat} and L_∞ when studying relations between growth and sexual maturity (Beverton 1992; Froese and Binohlan 2000; He and Stewart 2001). A linear model between this ratio and L_{mat} was fitted to predict the potential growth from estimates of L_{mat} at a small spatial scale (1.5-3.0 km). Also, the relationship between K growth coefficient vs. the ratio L_m/L_∞ and K vs. the asymptotic size (L_∞) was described, as they aid the interpretation of the potential growth and its relation with the SOM (He and Stewart 2001).

Effect of latitude, longitude and depth on potential growth

The relationship between potential growth and depth, latitude and longitude did not show a clear linear pattern. Therefore, an Additive Model was fitted with a smoothing function for each explanatory variable. Interactions between latitude and longitude and each one of these with depth did not improve the quality of the model; however, the interaction between depth and spatial location as a factor did. The Akaike information criterion (AIC), Generalised cross-validation score (GCV), explained deviance and parsimony were used as a guideline to choose a model; thus, the selected model was:

$$L_{mat}/L_\infty = \alpha + f_1(Depth) \times Location + f_2(East) + f_3(North)$$

Where α is the intercept; *Location* is the categorical geographical area with the levels, W, SW, SE, E and NE; *East* and *North* are the projected longitude and latitude respectively, and f represents a smoothing function. The estimation of the smoothers was done using Cubic Spline and accurate p-values were obtained by bootstrapping (Keele 2008).

Results

Growth estimates at large scale

As has been well established previously, growth was greatest in the Northern zones and least in Southern zones (Fig. 1, Table 1). For instance, the mean annual growth increment for females of 75 mm CL was 19 mm in the NW and 16 mm in the Northeast. This latitudinal change was less on the East coast than the West coast (Table 1). Slowest growth occurred in the extreme SW of TAS, at 9 mm for females of 75 mm CL. There was not sufficient data to estimate growth at the middle W and SE coast of TAS.

Table 1. Growth coefficients and size at first maturity for blocks 90x90 km in TAS.

Location	L_∞		K		L_{mat}	
	Estimated	SE	Estimated	SE	Estimated	SE
Upper-NW-A	152.08	4.15	0.00081	7.80E-05	109.18	0.12
Upper-NW-B	149.51	3.69	0.00082	7.36E-05	109.38	0.11
SW	185.82	20.24	0.00026	5.83E-05	70.24	0.48
Lower-E	128.43	4.77	0.00071	1.10E-04	106.76	0.16
Upper-E	143.57	8.16	0.00046	7.39E-05	72.35	0.62
Lower-NE	163.57	22.92	0.00045	1.84E-04	109.26	0.24
Upper-NE	150.63	6.95	0.00067	1.10E-04	109.48	0.14

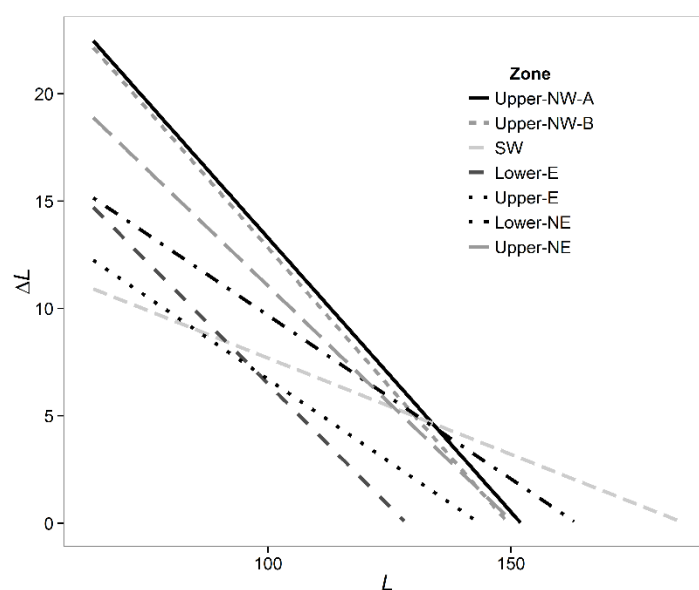Fig. 1. Expected length change (ΔL) for a given initial length (L) in a time interval of 365 days.

Size at onset of maturity at large scale

Size at the onset of maturity (SOM) showed a marked spatial variation, mostly in the latitudinal gradient, and to a lesser extent in longitude. The highest SOM estimates occurred in the NW and NE of TAS, where females reached first maturity at 109 mm CL. In both sides of TAS the SOM gradually decreased, but females reached maturity at the lowest size (70 mm CL) in the SW.

Potential growth span at small scale

The relationship L_{mat}/L_∞ vs. L_{mat} was explored using data from both TAS and SA to increase the available data and contrast. The ratio showed the expected pattern of an increase in the ratio while L_{mat} increased, with a significant slope ($\beta = 0.009, p < 0.001$) and a $R^2 = 0.68$. Values were similar for data from SA and the North of TAS, which are all relatively fast growth areas, while lower values were observed in the South and East of TAS (the two lower points in the scatterplot, Fig. 2).
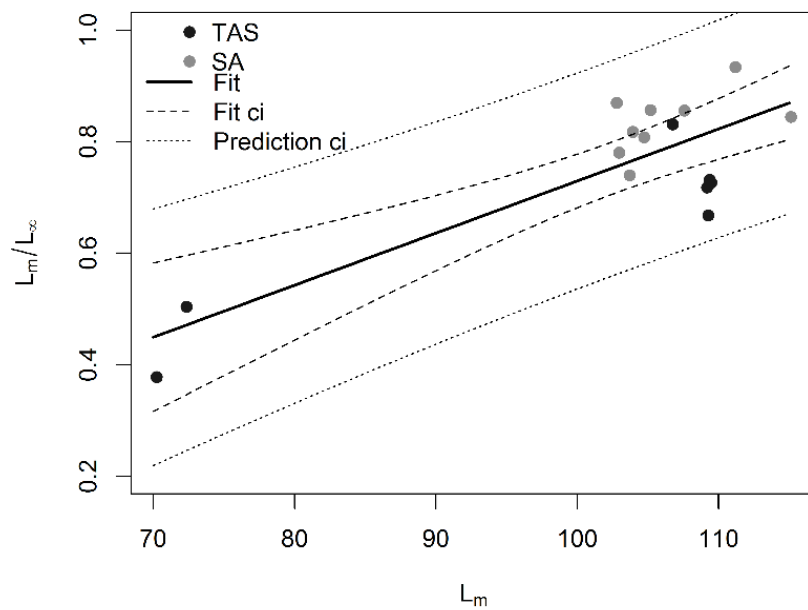

Fig. 2. Linear model describing the relationship between size at first maturity (L_m) and potential growth span before maturity (L_m/L_∞).
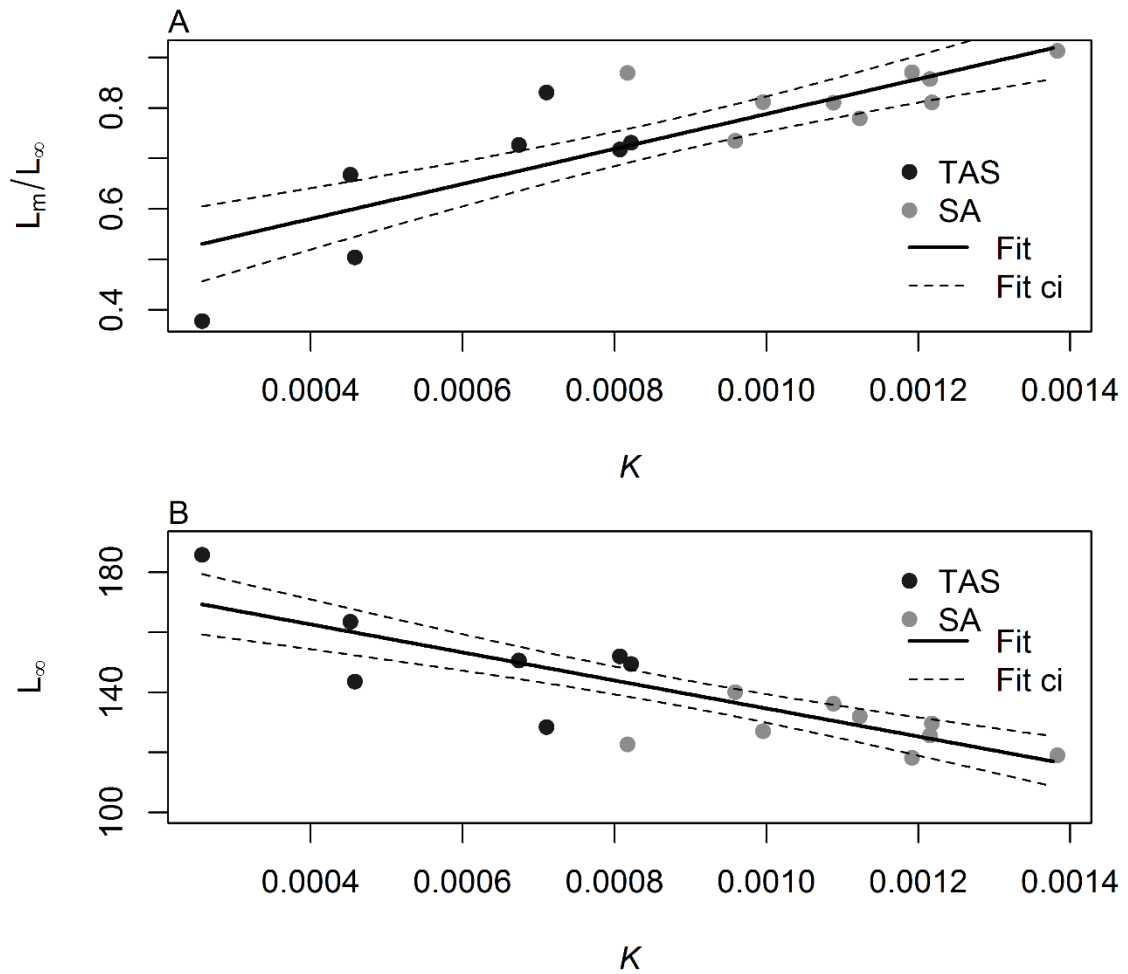
Fig. 2. Linear model describing the relationship between (A) K growth coefficient vs. potential growth span before maturity (L_m/L_∞) and (B) vs. the asymptotic size (L_∞).

The relationship between K and the potential growth (L_m/L_∞) showed that K was higher towards North and consequently the potential growth was also higher towards the same direction (Fig. 3A). Consistent with this result the asymptotic size was smaller towards North as a consequence of higher K (Fig. 3B)

Predictions of potential growth span before maturity (L_{mat}/L_∞) were obtained for 270 points around TAS (Fig. 4), which were based on estimations of L_{mat} at a small scale. The highest potential growth occurred in the NW region of TAS, with values ranging from 0.7 to 0.96. The Northeast zone had a slightly lower maximum and a wider range of values, varying between 0.43 and 0.82. The smallest potential growth was observed in the SW region with a minimum and maximum of 0.21 and 0.58 respectively. In contrast, the SE zone the values fluctuated between 0.43 and 0.74. The East zone showed higher values than the West region with

maximum values of 0.82 and 0.58 respectively. Many anomalous sites were identified at this small scale, which are locations with higher or lower potential growth than would be predicted by latitude, longitude or depth alone (Fig. 4).
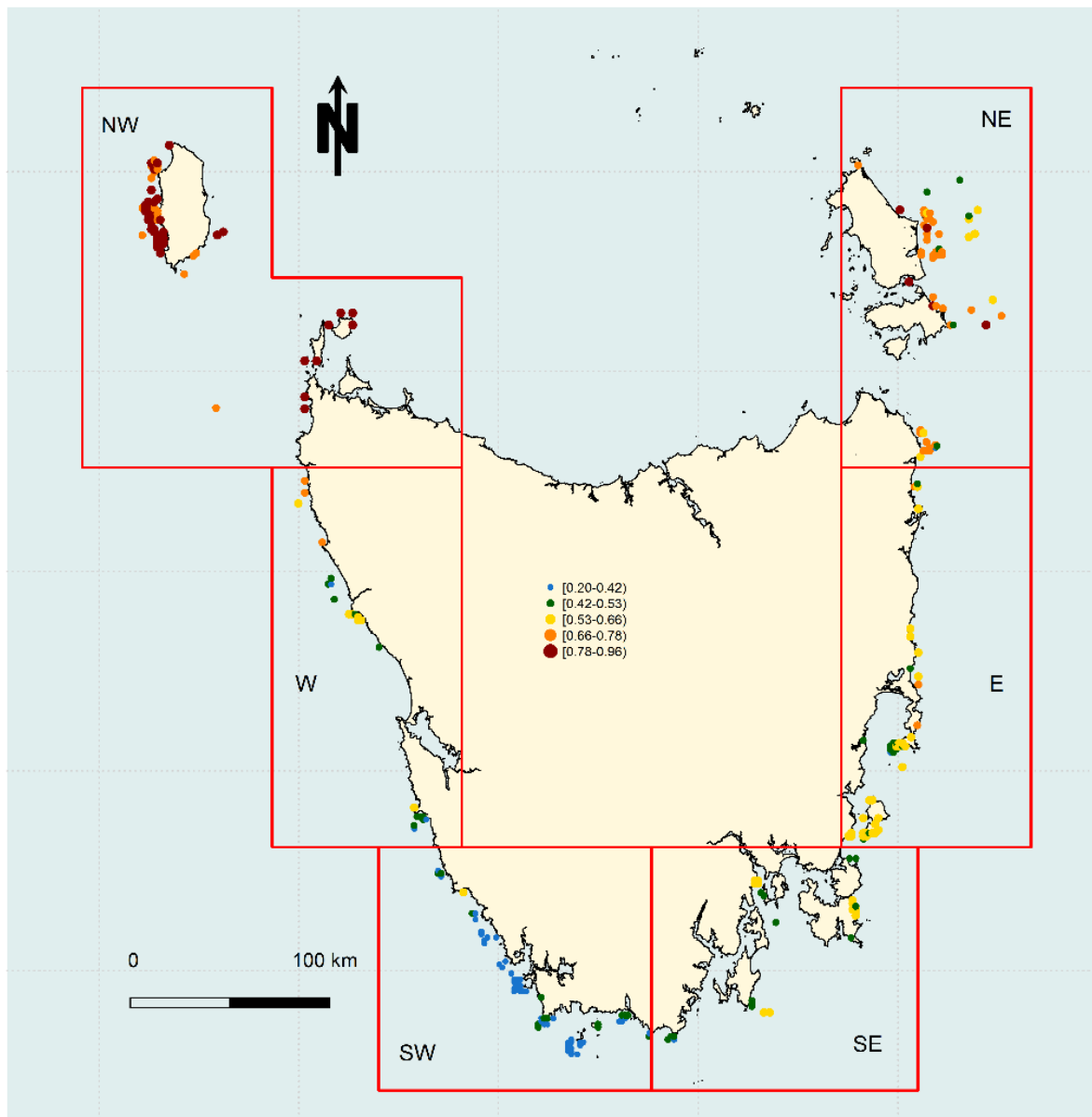

Fig. 4. Spatial distribution of different values of potential growth around TAS.

Effect of latitude, longitude and depth on potential growth

Latitude, longitude and depth significantly affected potential growth, except in the NW area (Table 2). The relatively high estimated degree of freedom in most of the covariates revealed that changes on the potential growth were highly non-linear, except in the W and SE zones (Fig.

5). The variation of potential growth with changes in latitude and longitude reflected a general pattern of high growth rates towards the north. For instance, in the relation between longitude (East) and potential growth (Fig. 5) low and high longitude reflected what happened in the NW and NE zones respectively, and mid-longitude revealed what happened in the south extreme of TAS.

There was a general pattern wherein the NW, NE and E zones where the potential growth did not change up to 50 m and below this depth, the potential growth sharply decreased. In contrast, in the W, SE and a lower extent in the SW zones the potential growth linearly decreased with the increase of the depth across the whole depth range examined.

Table 2. Parametric coefficient and smooth terms' significance of the additive model describing the relationship between depth, latitude and longitude versus potential growth span before maturity. Explained deviance (R^2) = 90%, EDF = Estimated degree of freedom for the smoother.

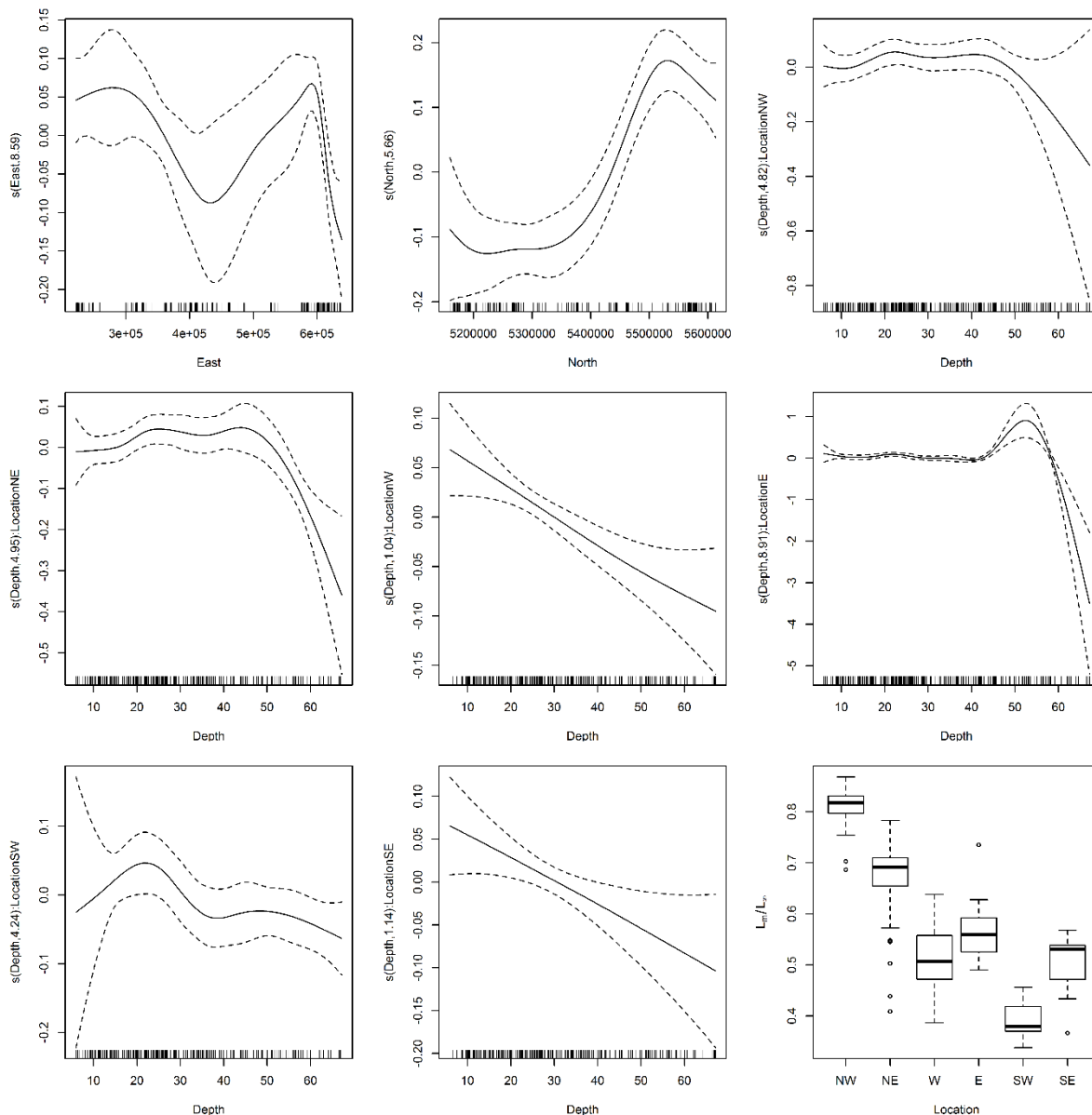| Parametric coefficient	Estimate	SE	t-value	p-value
Intercept	0.59	0.01	97.95	< 0.001
Smooth terms:	edf	Ref.df	F	p-value
East (longitude)	8.59	8.89	7.91	< 0.001
North (latitude)	5.66	6.81	17.33	< 0.001
Depth:NW	4.82	5.86	1.74	0.115
Depth:NE	4.95	5.97	5.42	< 0.001
Depth:W	1.04	1.29	11.62	< 0.001
Depth:E	8.91	8.99	4.65	< 0.001
Depth:SW	4.24	4.95	3.32	0.007
Depth:SE	1.14	1.48	3.79	0.037

Fig. 5. Contribution of latitude, longitude and depth by different geographical zones on changes of potential growth span before maturity.

Discussion

Potential growth (L_{mat}/L_∞) and SOM had a significant positive linear relationship, with lobsters reaching sexual maturity at a high size when their potential growth was high and vice versa. Marine organisms may increase potential growth by increasing K and consequently having a small L_∞, or by increasing T_{mat} (time at first maturity) with the consequent delay of first reproduction (He and Stewart 2001). The positive relation of SOM and growth was consistent with evidence for other spiny lobsters that showed that SOM is age rather than size specific (Beyers and Goosen 1987; Pollock and Goosen 1991). Therefore, SRL seemed to have

increased its potential growth by increasing K rather than delaying the first reproduction, which was supported by a smaller K in the SW than the value estimated in the NW and NE zones. Maturity based on age was also consistent with the significant positive and negative relationship between K and L_{mat}/L_∞ and K vs. L_∞ respectively, distinctive in species that increase L_{mat}/L_∞ by increasing K (He and Stewart 2001). The observed large K from lobsters from the north has management implications as it means a rapid approach to L_∞ so that female SRL may reach the minimum legal size and be harvested in these locations without an opportunity for reproduction.

The local variation observed in SOM and potential growth in this study gave some insight into factors affecting these other than the previously reported influence of latitude (Pollock 1995a; Linnane *et al.* 2009). The additive model outputs revealed that the potential growth of some zones did not change in shallow waters, but sharply decreased at depths over 50 m. Depth may be a proxy for temperature, diet, and density. Conflicting conclusions on the effect of density on SOM and growth of SRL have been reported in the literature previously. McGarvey et al. (1999) concluded that a 10% decrease in catch rates of SRL in SA led to growth increase by weight of 2-5%. However, no differences were found in comparisons of SOM between lobsters from high density locations in marine reserve, and areas accessible to the fishery, with lower density (Gardner *et al.* 2006). These contradicting findings and the fine scale variation shown in this study suggests that SRL density may interact with other factors to influence SOM and growth depending on the geographic region.

Food availability varies with depth and density and may explain temporal and spatial changes in growth of South African rock lobster (Skewes *et al.* 1997; Mayfield *et al.* 2000; O'Malley *et al.* 2012). In TAS, the abrupt drop in potential growth over 50 m of depth may be also related to the food availability, in particular the shift in community from macroalgae dominated ecosystem to sponges and other filter feeders.

Current information on drivers of SOM and growth are based on studies using field data from research or commercial potting operations (Annala *et al.* 1980; Gardner *et al.* 2006; Linnane *et al.* 2009), which not necessarily follow a survey design well suited for determining these underlying factors affecting biological traits. Therefore, surveying other possible factors affecting growth and manipulative studies altering the density may give an insight of covariates contributing to variance in growth rate. Regardless of the specific factors driving SOM and growth, their spatial differences documented here at a fine-scale will enable better targeting of SRL translocation sites.

Appendix 1. Model selection criteria. AIC = Akaike information criterion, GCV = Generalised cross validation score. As a general guideline a good model, relative to others, should have a low AIC and GCV, a high explained deviance and should be simple. In bold the selected model.

| Model	AIC	GCV	Explained Deviance
Depth x Location North South	**-719.08**	**0.0038**	**90.5**
Depth x Location North x South	-720.12	0.0038	90
Depth x North Depth x South North South	-707.71	0.0040	89.2
North x South Depth x North Depth x South	-750.85	0.0034	91.7

Appendix 2. Growth coefficients and size at first maturity for blocks 20x20 km in South Australia.

Block	L_∞		K		L_{mat}	
	Estimate	se	Estimate	se	Estimate	se
E22N7	136.28	2.73	0.0011	1.40E-04	115.12	2.41
E23N6	129.59	1.48	0.0012	9.55E-05	104.73	1.98
E23N7	140.13	4.94	0.0010	1.56E-04	103.72	1.80
E24N5	127.12	2.79	0.0010	1.25E-04	103.94	1.91
E24N6	131.94	3.16	0.0011	1.45E-04	102.96	1.64
E25N4	119.05	1.85	0.0014	1.50E-04	111.19	2.05
E25N5	118.21	2.34	0.0012	1.62E-04	102.79	1.80
E26N3	123.33	3.53	0.0008	1.03E-04	105.18	2.16
E9N16	125.68	1.74	0.0012	1.11E-04	107.59	1.75

Appendix 3. Detailed maps of estimates of potential growth span before maturity around TAS.

Legend:
- [0.43-0.65)
- [0.65-0.68)
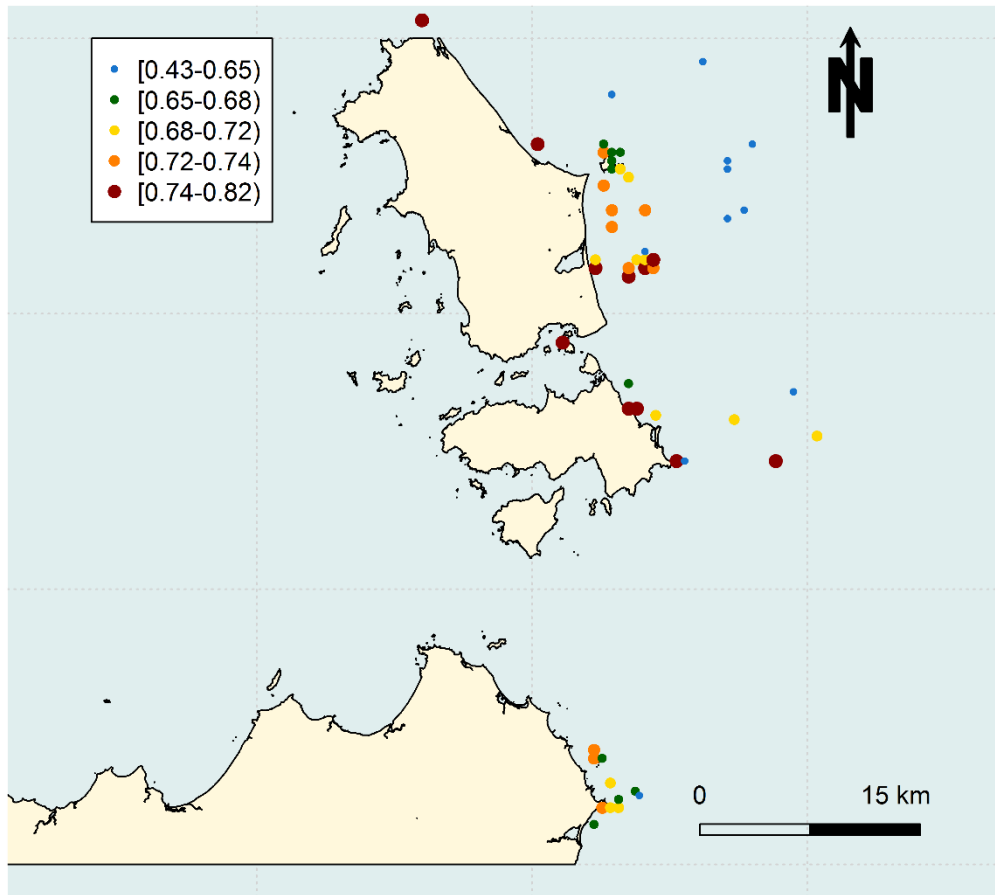- [0.68-0.72)
- [0.72-0.74)
- [0.74-0.82)

0   15 km
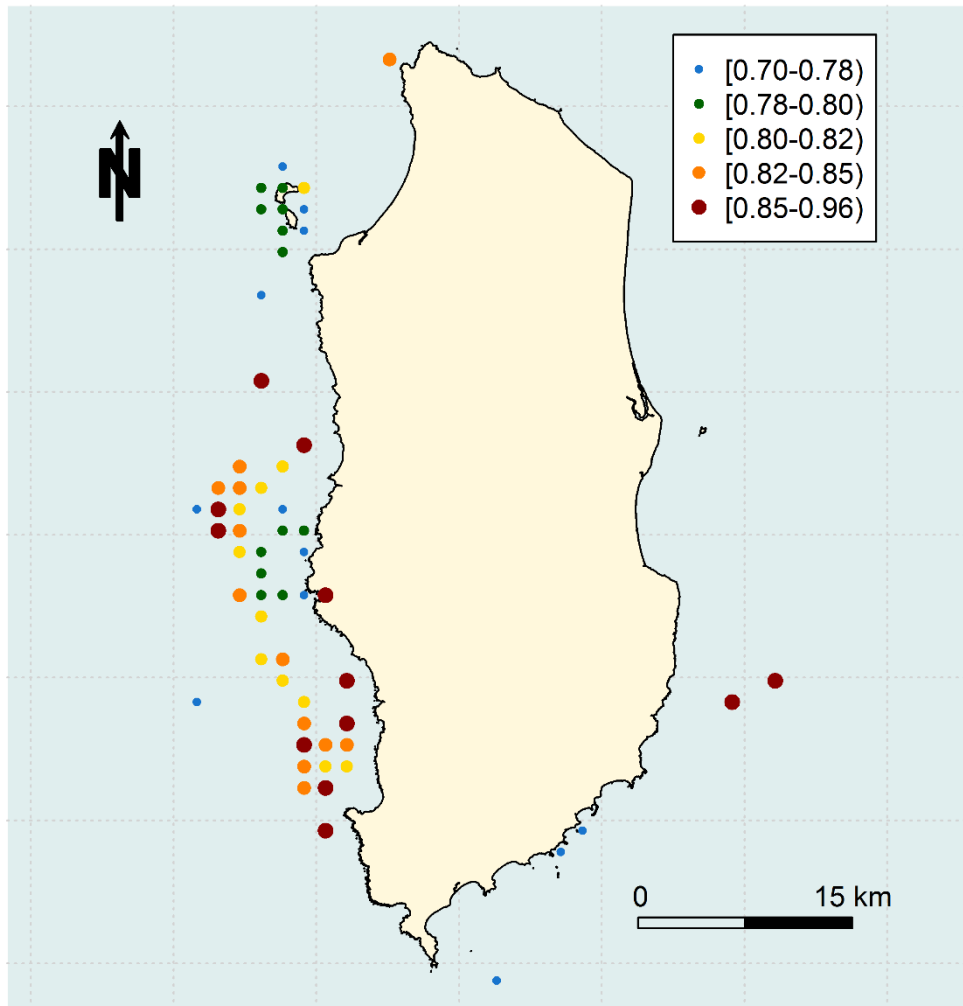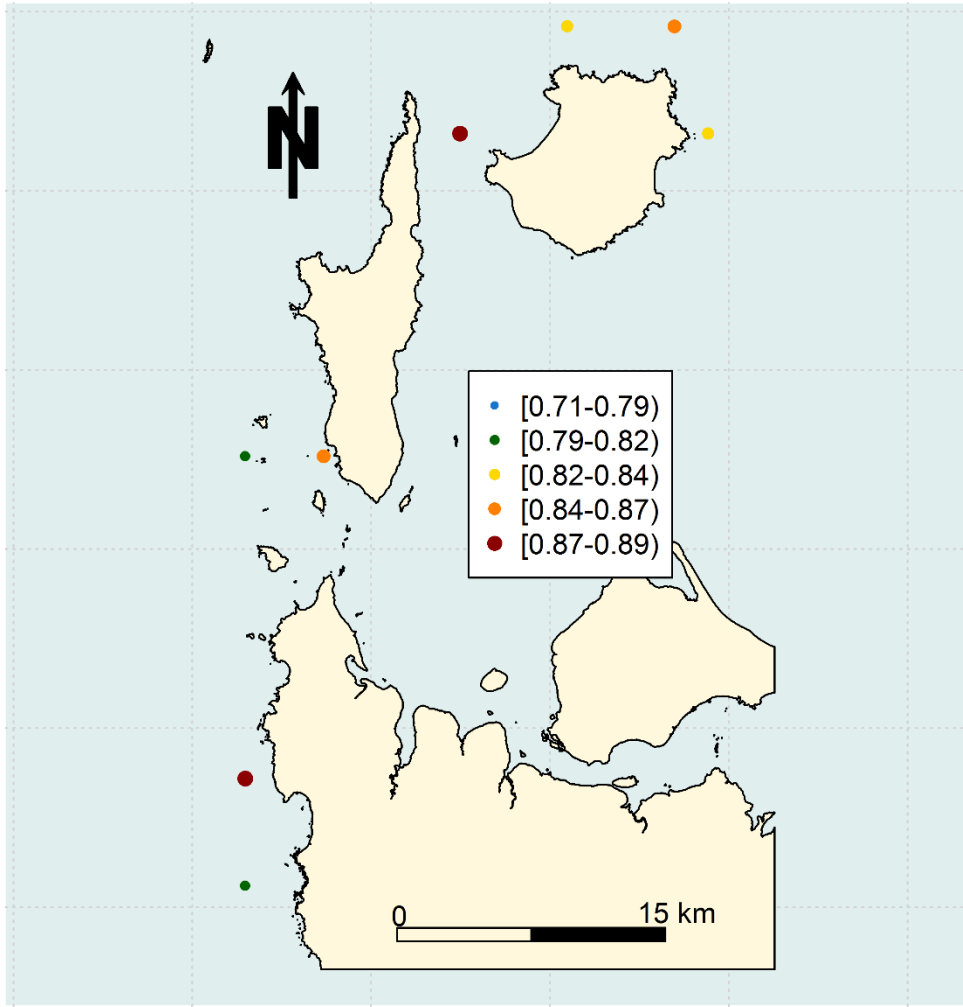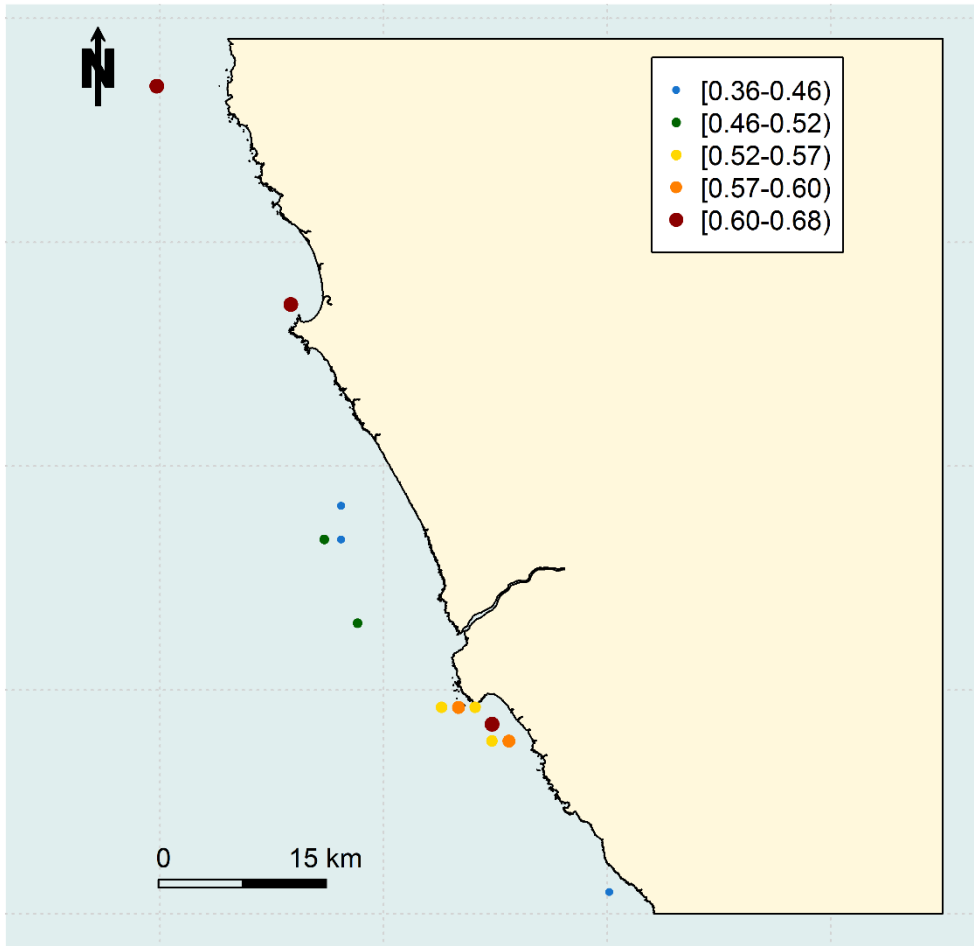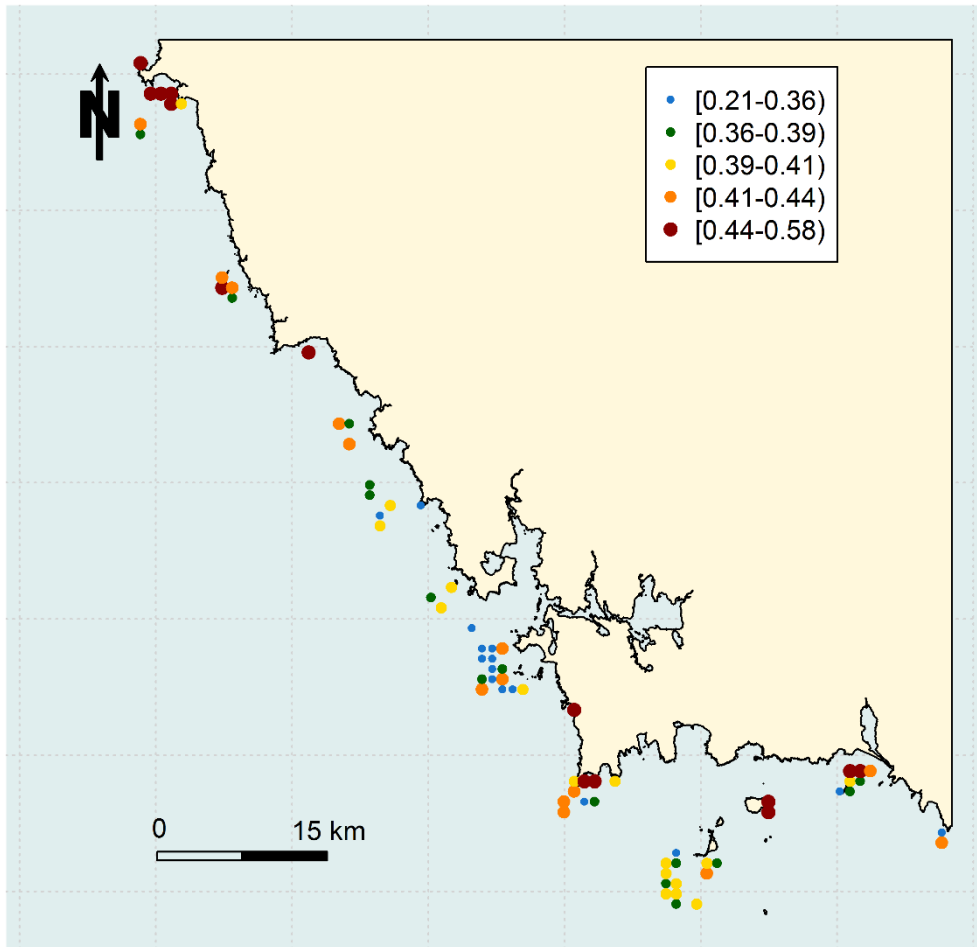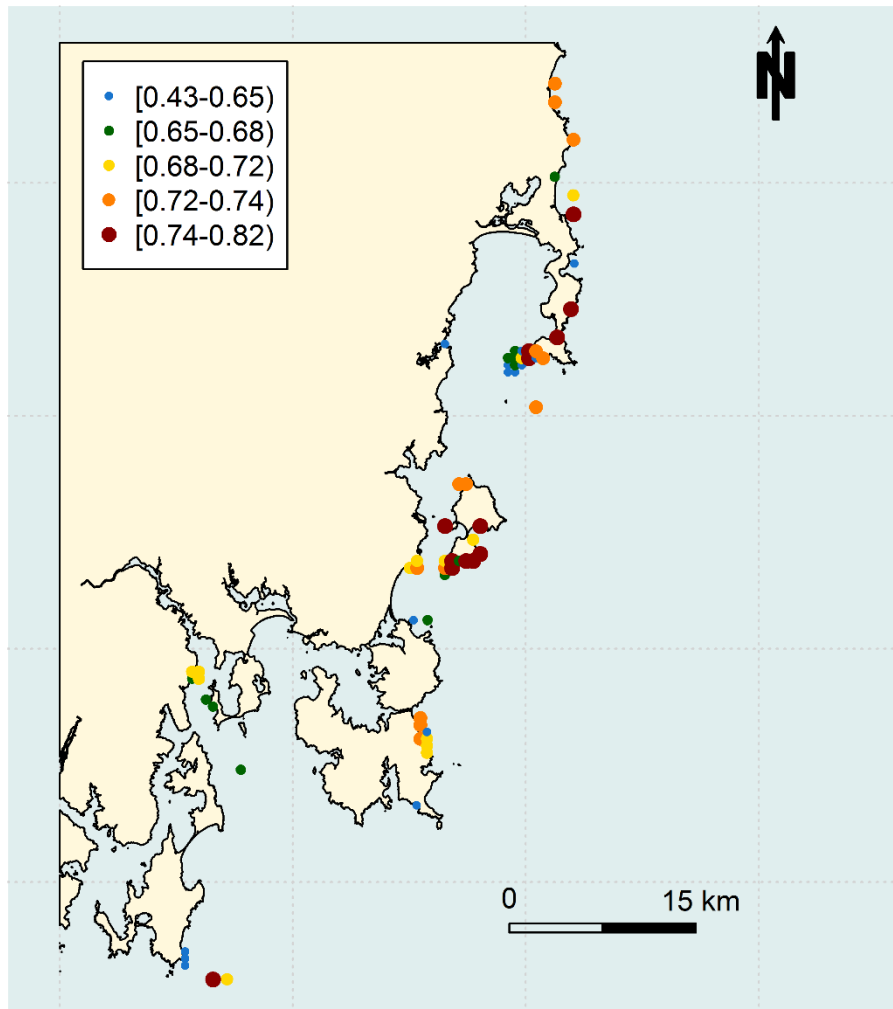
10. References

Aiken, D.E. and Waddy, S.L. (1978) Space, density and growth of lobster. *Proceedings of the annual meeting - World Mariculture Society* **9**, 461–467.

Ali, M., Nicieza, A. and Wootton, R.J. (2003) Compensatory growth in fishes: A response to growth depression. *Fish and Fisheries* **4**, 147–190.

Alonso-Alvarez, C., Bertrand, S., Faivre, B. and Sorci, G. (2007) Increased susceptibility to oxidative damage as a cost of accelerated somatic growth in zebra finches. *Functional Ecology* **21**, 873–879.

Andersen, K.H. and Beyer, J.E. (2006) Asymptotic size determines species abundance in the marine size spectrum. *American Naturalist* **168**, 54–61.

Annala, J.H. and Bycroft, B.L. (1987) Fecundity of the New Zealand Red Rock Lobster, _Jasus edwardsii_ . *New Zealand Journal of Marine and Freshwater Research* **21** , 591–597.

Annala, J.H. and Bycroft, B.L. (1988) Growth of rock lobsters (Jasus edwardsii) in Fiordland, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **22**, 29–42.

Annala, J.H., McKoy, J.L., Booth, J.D. and Pike, R.B. (1980) Size at the onset of sexual maturity in female Jasus edwardsii (Decapoda: Palinuridae) in New Zealand. *New Zealand journal of Marine and freshwater research* **14**, 217–227.

Atchley, W.R. (1984) Ontogeny, timing of development, and genetic variance-covariances structure. *The American Naturalist* **123**, 519–540.

Atkinson, D. (1994) Temperature and organism size-A biological law for ectotherms? *Advances in Ecological Research* **3**, 1–58.

Atkinson, D. and Sibly, R.M. (1997) Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends in Ecology and Evolution* **12**, 235–239.

Berrigan, D. and Charnov, E.L. (1994) Reaction norms for age and size at maturity in response to tempertature: a puzzle for life historians. *Oik* **70**, 474–478.

Beverton, R.J.H. (1992) Patterns of reproductive parameters in some marine teleost fishes. *Journal of Fish Biology* **41**, 137–160.

Beverton, R.J.H. and Iles, T.C. (1992) Mortality rates of 0-group plaice (Platessa platessa l.), dab (Limanda limanda l.) and turbot (Scophthalmus maxlmus l.) in european waters: III. Density-dependence of mortality rates of 0-group plaice and some demographic implications. *Netherlands Journal of Sea Research* **29**, 61–79.

Beyers, C.J.D.B. and Goosen, P.C. (1987) Variations in fecundity and size at sexual maturity of female rock lobster Jasus lalandii in the Benguela ecosystem. *South African Journal Of Marine Science* **5**, 513–521.

Boersma, B. and Wit, J.M. (1997) Catch-up Growth. *Endocrine Reviews* **18**, 646–661.

Booth, J.D. and Kittaka, J. (2000) Spiny lobster growout. In: *Spiny Lobsters: Fisheries and Culture*. (eds B.F. Phillips and J. Kittaka), 2nd edn. Blackwell Science, Oxford.

Booth, J.D. and Phillips, B.F. (1994) Early life history of spiny lobster. *Crustaceana* **66**, 271–294.

Bradshaw, M. (2004) A combination of state and market through ITQs in the Tasmanian commercial rock lobster fishery: The tail wagging the dog? *Fisheries Research* **67**, 99–109.

Caley, M.J. and Schwarzkopf, L. (2004) Complex growth rate evolution in a latitudinally widespread species. *Evolution* **58**, 862–869.

Cardinale, M. and Hjelm, J. (2012) Size matters: Short term loss and long term gain in a size-selective fishery. *Marine Policy* **36**, 903–906.

Chandrapavan, A., Gardner, C. and Green, B.S. (2010a) Growth rate of adult rock lobsters Jasus edwardsii increased through translocation. *Fisheries Research* **105**, 244–247.

Chandrapavan, A., Gardner, C. and Green, B.S. (2010b) Growth rate of adult rock lobsters Jasus edwardsii increased through translocation. *Fisheries Research* **105**, 244–247.

Chandrapavan, A., Gardner, C. and Green, B.S. (2010c) Haemolymph condition of deep-water southern rock lobsters (Jasus edwardsii) translocated to inshore reefs. *Marine and Freshwater Behaviour and Physiology* **43**.

Chandrapavan, A., Gardner, C., Linnane, A. and Hobday, D. (2009a) Colour variation in the southern rock lobster Jasus edwardsii and its economic impact on the commercial industry. *The Royal Society of New Zealand* **43**, 537–545.

Chandrapavan, A., Guest, M.A., Nichols, P.D. and Gardner, C. (2009b) Translocating southern rock lobsters (Jasus edwardsii) from deep-water to shallow inshore water enhances nutritional condition through omega-3 long-chain polyunsaturated fatty acid content. *Journal of Experimental Marine Biology and Ecology* **375**, 9–15.

Chang, Y.J., Sun, C.L., Chen, Y. and Yeh, S.Z. (2012) Modelling the growth of crustacean species. *Reviews in Fish Biology and Fisheries* **22**, 157–187.

Chiswell, S.M., Wilkin, J., Booth, J.D. and Stanton, B. (2003) Trans-Tasman Sea larval transport: Is Australia a source for New Zealand rock lobsters? *Marine Ecology Progress Series* **247**, 173–182.

Cobb, J.S., Tamm, G.R. and Wang, D. (1982) Behavioral mechanisms influencing molt frequency in the American lobster, Homarus americanus Milne Edwards. *Journal of Experimental Marine Biology and Ecology* **62**, 185–200.

Comeau, M. and Savoie, F. (2001) Growth increment and molt frequency of the american lobster (*Homarus americanus*) in the southwestern Gulf of St. Lawrence. *Journal of Crustacean Biology* **21**, 923–936.

Comeau, M. and Savoie, F. (2002) Maturity and Reproductive Cycle of the Female American Lobster, Homarus Americanus, in the Southern Gulf of St. Lawrence, Canada. *Journal of Crustacean Biology* **22**, 762–774.

Currie, J.J. and Schneider, D.C. (2011) Spatial scaling from latitudinal gradients: Size-specific fecundity in the American lobster Homarus americanus. *Marine Ecology Progress Series* **439**, 193–201.

Dixon, C.D. and Day, R.W. (2004) Growth responses in emergent greenlip abalone to density reductions and translocations. *Journal of Shellfish Research* **23**, 1223–1228.

Emery, T.J., Hartmann, K., Green, B.S., Gardner, C. and Tisdell, J. (2014) Fishing for revenue: how leasing quota can be hazardous to your health. *ICES Journal of Marine Science*, 1–12.

Ernande, B., Dieckmann, U. and Heino, M. (2004) Adaptive changes in harvested populations: plasticity and evolution of age and size at maturation. *Proceedings. Biological sciences / The Royal Society* **271**, 415–23.

Ford, R.F., Phillips, B.F. and Joll, L.M. (1988) Experimental Manipulation of Population-Density and Its Effects on Growth and Mortality of Juvenile Western Rock Lobsters, Panulirus-Cygnus George. *Fishery Bulletin* **86**, 773–787.

Ford, W. (2001) Restructuring the Tasmanian rock-lobster fishery—the effect of two years of management under individual transferable quotas. *Marine Freshwater Research* **52**, 1641–1648.

Froese, R. and Binohlan, C. (2000) Empirical relationships to estimate asymptotic length, length at first maturity and length at maximum yield per recruit in fishes, with a simple method to evaluate length

frequency data. *Journal of Fish Biology* **56**, 758–773.

Froese, R., Stern-Pirlot, A., Winker, H. and Gascuel, D. (2008) Size matters: How single-species management can contribute to ecosystem-based fisheries management. *Fisheries Research* **92**, 231–241.

Garcia, S.M., Kolding, J., Rice, J., et al. (2012) Reconsidering the consequences of selective fisheries. *Science* **335**, 1045–1047.

Gardner, C., Frusher, S., Barrett, N., Haddon, M. and Buxton, C. (2006) Spatial variation in size at onset of maturity of female southern rock lobster Jasus edwardsii around Tasmania, Australia. *Scientia Marina* **70**, 423–430.

Gardner, C., Frusher, S., Haddon, M. and Buxton, C. (2003) Movements of the southern rock lobster Jasus edwardsii in Tasmania, Australia. *Bulletin of Marine Science* **73**, 653–671.

Gardner, C., Hartmann, K., Punt, A.E., Jennings, S. and Green, B. (2015) Bio-economics of commercial scale translocation of southern rock lobster. *Fisheries Research* **162**, 29–36.

Gardner, C., Hartmann, K., Punt, E. and Hoshino, E. (2014) Fewer eggs from larger size limits: Counterintuitive outcomes in a spatially heterogeneous fisher. *ICES Journal of Marine Science* **72**, 1–8.

Gardner, C., Mills, D. and Frusher, S. (2005) Does pleopod setation provide a measure of maturity in female southern rock lobsters Jasus edwardsii? *Scientia Marina* **69**, 123–131.

Gardner, C. and Van Putten, E.I. (2008a) Biological modeling of translocation as a management tool for a rock lobster fishery. *Reviews in Fisheries Science* **16**, 81–90.

Gardner, C. and Van Putten, E.I. (2008b) The economic feasibility of translocating rock lobsters to increase yield. *Reviews in Fisheries Science* **16**, 154–163.

Gendron, L., Fradette, P. and Godbout, G. (2001) The importance of rock crab (Cancer irroratus) for growth, condition and ovary development of adult American lobster (Homarus americanus). *Journal of Experimental Marine Biology and Ecology* **262**, 221–241.

Green, B.S. and Gardner, C. (2009) Surviving a sea-change: survival of southern rock lobster (Jasus edwardsii) translocated to a site of fast growth. *ICES Journal of Marine Science* **66**, 656–664.

Green, B.S., Gardner, C. and Kennedy, R.B. (2009) Generalised linear modelling of fecundity at length in southern rock lobsters, Jasus edwardsii. *Marine Biology* **156**, 1941–1947.

Green, B.S., Gardner, C., Linnane, A. and Hawthorne, P.J. (2010) The Good, the Bad and the Recovery in an Assisted Migration. *PLoS ONE* **5**.

Groeneveld, J.C. (1997) Growth of spiny lobster Palinurus gilchristi (Decapoda: Palinuridae) off South Africa. *South African Journal of Marine Science* **18**, 19–29.

Haley, C.N., Blamey, L.K., Atkinson, L.J. and Branch, G.M. (2011) Dietary change of the rock lobster Jasus lalandii after an "invasive" geographic shift: Effects of size, density and food availability. *Estuarine, Coastal and Shelf Science* **93**, 160–170.

Hartmann, K., Gardner, C. and Hobday, D. (2013) Fishery Assessment Report. 59.

Hartnoll, R.G. (1982) Growth. In: *The Biology of Crustacea: Volume 2 Embryology, morphology and menetics*. (eds D.E. Bliss and L.G. Abele). Academic Press, New York, pp 111–196.

Hartnoll, R.G. (2001) Growth in Crustacea - Twenty years on. *Hydrobiologia* **449**, 111–122.

Hazell, A.R.W., Schoeman, D.S. and Noffke, M.N. (2001) Do fluctuations in the somatic growth rate of rock lobster (asus lalandii) encompass all size classes A re assessment of juvenile growth. *Fishery bulletin* **100**, 510–518.

He, J.X. and Stewart, D.J. (2001) Age and Size at first reproduction of fishes: Predictive models based only on growth trajectories. *Ecology* **82**, 784–791.

Heinze, G., Ploner, M., Dunkler, D. and Southworth, H. (2013) logistf: Firth's bias reduced logistic regression. R package.

Heinze, G. and Schemper, M. (2002) A solution to the problem of separation in logistic regression. *Statistics in Medicine* **21**, 2409–2419.

Herberholz, J., Mccurdy, C. and Edwards, D.H. (2007) Direct benefits of social dominance in juvenile crayfish. *Biological Bulletin* **213**, 21–27.

Hixon, M.A. and Carr, M.H. (1997) `Synergistic predation, density dependence, and population regulation in Marine Fish. *Science* **277**, 946–949.

Jensen, A.J., Forseth, T. and Johnsen, B.O. (2000) Latitudinal variation in growth of young brown trout Salmo trutta. *Journal of animal ecology* **69**, 1010–1020.

Karplus, I. (2005) Social control of growth in Macrobrachium rosenbergii (De Man): A review and prospects for future research. *Aquaculture Research* **36**, 238–254.

Karplus, I. and Barki, A. (2004) Social control of growth in the redclaw crayfish, Cherax quadricarinatus: Testing the sensory modalities involved. *Aquaculture* **242**, 321–333.

Keele, L.J. (2008) *Semiparametric Regression for the Social Sciences*. John Willey & Sons Ltd, Chichester.

Lardies, M.A., Arias, M.B. and Bacigalupe, L.D. (2010) Phenotypic covariance matrix in life-history traits along a latitudinal gradient: A study case in a geographically widespread crab on the coast of Chile. *Marine Ecology Progress Series* **412**, 179–187.

Lardies, M.A. and Bozinovic, F. (2006) Geographic covariation between metabolic rate and life-history traits. *Evolutionary Ecology Research* **8**, 455–470.

Lardies, M.A. and Wehrtmann, I.S. (2001) Latitudinal variation in the reproductive biology of Betaeus truncatus (Decapoda: Alpheidae) along the Chilean coast. *Ophelia* **55**, 55–67.

Laugen, a T., Laurila, a, Rasanen, K. and Merila, J. (2003) Latitudinal countergradient variation in the common frog (Rana temporaria) development rates - evidence for local adaptation. *Journal of Evolutionary Biology* **16**, 996–1005.

Lee, D.O.C. and Wickins, J.F. (1992) *Crustacean Farming*. Blackwell Scientific Publications, Oxford.

Linnane, a. J., Penny, S.S. and Ward, T.M. (2008) Contrasting fecundity, size at maturity and reproductive potential of southern rock lobster Jasus edwardsii in two South Australian fishing regions. *Journal of the Marine Biological Association of the UK* **88**, 583–589.

Linnane, A., Dimmlich, W. and Ward, T. (2005) Movement patterns of the southern rock lobster, Jasus edwardsii, off South Australia. *New Zealand Journal of Marine and Freshwater Research* **39**, 335–346.

Linnane, A., Penny, S., Hawthorne, P. and Hoare, M. (2009) Spatial differences in size of maturity and reproductive potential between inshore and offshore fisheries for southern rock lobster (Jasus edwardsii) in South Australia. *Fisheries Research* **96**, 238–243.

Linse, K., Barnes, D.K.A. and Enderlein, P. (2006) Body size and growth of benthic invertebrates along an Antarctic latitudinal gradient. *Deep-Sea Research Part Ii-Topical Studies in Oceanography* **53**, 921–931.

MacDiarmid, A.B. (1989) Size at onset of maturity and size-dependent reproductive output of female and male spiny lobsters Jasus edwardsii (Hutton) (Decapoda, Palinuridae) in northern New Zealand. *Journal of Experimental Marine Biology and Ecology* **127**, 229–243.

Mangel, M. and Munch, S.B. (2005) A Life-History Perspective on Short- and Long-Term Consequences of Compensatory Growth. *The American Naturalist* **166**, E155–E176.

Marzinelli, E.M., Williams, S.B., Babcock, R.C., et al. (2015) Large-Scale Geographic Variation in Distribution and Abundance of Australian Deep-Water Kelp Forests. *Plos One* **10**, e0118390.

Mayfield, S., Branch, G.M. and Cockcroft, A.C. (2000) Relationships among diet, growth rate, and food availability for the South African rock lobster, Jasus lalandii (Decapoda, Palinuridea). *Crustaceana* **73**, 815–834.

McGarvey, R., Ferguson, G.J. and Prescott, J.H. (1999) Spatial variation in mean growth rates at size of southern rock lobster, Jasus edwardsii, in South Australian waters. *Marine Freshwater ResearchResearch* **50**, 333–42.

van der Meeren, G.I. (2000) Predation on hatchery-reared lobsters released in the wild. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 1794–1803.

Metcalfe, N.B., Bull, C.D. and Mangel, M. (2002) Seasonal variation in catch-up growth reveals state-dependent somatic allocations in salmon. *Evolutionary Ecology Research* **4**, 871–881.

Metcalfe, N.B. and Monaghan, P. (2001) Compensation for a bad start: Grow now, pay later? *Trends in Ecology and Evolution* **16**, 254–260.

Mills, D.J., Gardner, C. and Johnson, C.R. (2006) Experimental reseeding of juvenile spiny lobsters (Jasus edwardsii): Comparing survival and movement of wild and naive lobsters at multiple sites. *Aquaculture* **254**, 256–268.

Moorhouse, T.P. and Macdonald, D.W. (2011) Immigration rates of signal crayfish (Pacifastacus leniusculus) in response to manual control measures. *Freshwater Biology* **56**, 993–1001.

Nicieza, A.G. and Metcalfe, N.B. (1997) Growth Compensation in Juvenile Atlantic Salmon: Responses to Depressed Temperature and Food Availability. *Ecology* **78**, 2385–2400.

O'Malley, J., Drazen, J., Popp, B., Gier, E. and Toonen, R. (2012) Spatial variability in growth and prey availability of lobsters in the northwestern Hawaiian Islands. *Marine Ecology Progress Series* **449**, 211–220.

Olsen, E.M., Heino, M., Lilly, G.R., Morgan, M.J.J., Brattey, J., Ernande, B. and Dieckmann, U. (2004) Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature* **428**, 932–935.

Pollock, D.E. (1995a) Changes in maturation ages and sizes in crustacean and fish populations . *S.Afr.J.mar.Sci.* **15** , 99–103.

Pollock, D.E. (1995b) Notes on Phenotypic and Genotypic Variability in Lobsters. *Crustaceana* **68**, 193–202.

Pollock, D.E. and Goosen, P.C. (1991) Reproductive dynamics of two Jasus species in the South Atlantic region. *South African Journal of Marine Science* **10**, 141–147.

Polovina, J.J. (1989) Density dependence in spiny lobster, Panulirus marginatus, in the Northwestern Hawaiian Islands. *Canadian Journal of Fisheries and Aquatic Sciences* **46**, 660–665.

Post, J.R. and Parkinson, E.A. (2001) Energy allocation strategy in young fish: Allometry and survival. *Ecology* **82**, 1040–1051.

Punt, A.E., Kennedy, R.B. and Frusher, S.D. (1997) Estimating the size-transition matrix for Tasmanian rock lobster, Jasus edwardsii. *Marine and Freshwater Research* **48**, 981.

Reznick, D. and Yang, A.P. (1993) The influence of fluctuating resources on life history: Patterns of allocation and plasticity in female guppies. *Ecology* **74**, 2011–2019.

Ricklefs, R.E., Shea, R.E. and Choi, I.-H. (1994) Inverse relationship between functional maturity and exponential growth rate of avian skeletal muscle: A constraint on evolutionary response. *Evolution* **48**, 1080–1088.

Roff, D.A. (1992) *The evolution of life histories: Theory and analysis*. Chapman & Hall, New York.

Rosa, R., Gonzalez, L., Dierssen, H.M. and Seibel, B.A. (2012) Environmental determinants of latitudinal size-trends in cephalopods. *Marine Ecology Progress Series* **464**, 153–165.

Semmens, J., Haddon, M. and Mackinnon, C. (2006) Tasmanian rock lobster fishery 2004/05, Fishery assessment report. Tasmanian Aquaculture and Fisheries Institute. Hobart, Australia.

Simon, C.J., Mendo, T.C., Green, B.S. and Gardner, C. (2016) Predicting transport survival of brindle and red rock lobsters Jasus edwardsii using haemolymph biochemistry and behaviour traits. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* **201**, 101–109.

Skewes, T.D., Pitcher, C.R. and Dennis, D.M. (1997) Growth of ornate rock lobsters, Panulirus ornatus, in Torres Strait, Australia. *Marine and Freshwater Research* **48**, 497–501.

Stearns, S.C. (1976) Life-history tactics: A review of the ideas. *The Quarterly Review of Biology* **51**, 3–47.

Stearns, S.C. (1992) The Evolution of Life Histories.

Thomas, C.W., Crear, B.J. and Hart, P.R. (2000) The effect of temperature on survival, growth, feeding and metabolic activity of the southern rock lobster, Jasus edwardsii. *Aquaculture* **185**, 73–84.

Troynikov, V.S., Day, R.W. and Leorke, A.M. (1998) Estimation of seasonal growth parameters using a stochastic Gompertz model for tagging data. *Journal of Shellfish Research* **17**, 833–838.

Tuck, I.D., Chapman, C.J., Atkinson, R.J.A. and Chapman, T. (2000) Population biology of the Norway lobster, Nephrops norvegicus (L.) in the Firth of Clyde, Scotland II: fecundity and size at onset of sexual maturity. *ICES Journal of Marine Science* **57**, 1227–1239.

Twombly, S. and Tisch, N. (2000) Body size regulation in copepod crustaceans. *Oecologia* **122**, 318–326.

Waddy, S.L., Aiken, D.E. and De Kleijn, D.P.V. (1995) Control of growth and reproduction. In: *Biology of the Lobster, Homarus americanus*. (ed J.R. Factor). Academic Press, New York.

Wahle, R.A. and Fogarty, M.J. (2006) Growth and development: Understanding and modelling growth variability in lobsters. In: *Lobsters: Biology, Management, Aquaculture & Fisheries*. (ed B.F. Phillips). Blackwell Publishing, Oxford, UK, pp 1–44.

Wahle, R.A., Tully, O. and O 'Donovan, V. (2001) Environmentally mediated crowding effects on growth, survival and metabolic rate of juvenile American lobsters (Homarus americanus). *Marine and Freshwater Research* **52**, 1157–1166.

Yamahira, K. and Conover, D. (2002) Intra- Vs . Interspecific Latitudinal Variation in Growth: Adaptation To Temperature or Seasonality ? *Ecology* **83**, 1252–1262.

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IMAS Waterfront Building
20 Castray Esplanade
Battery Point Tasmania Australia
Telephone: +61 3 6226 6379

Postal address:
Private Bag 129, Hobart TAS 7001

IMAS Taroona
Nubeena Crescent
Taroona Tasmania Australia
Telephone: +61 3 6227 7277

Postal address:
Private Bag 49, Hobart TAS 7001

www.imas.utas.edu.au

IMAS Launceston
Old School Road
Newnham Tasmania Australia
Telephone: +61 3 6324 3801

Postal address:
Private Bag 1370 Launceston TAS 7250