Contrasting fecundity, size at maturity and reproductive potential of southern rock lobster *Jasus edwardsii* in two South Australian fishing regions

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The annual commercial catch from the Southern Zone of the South Australian rock lobster (*Jasus edwardsii*) fishery is ~1900 tonnes, representing ~50% of total landings from south-east Australia. A single minimum legal size (MLS) of 98.5 mm carapace length (CL) exists across the entire zone. Fecundity (F), size at onset of maturity (SOM) and relative reproductive potential (RRP) of female rock lobsters were investigated in two major fishing regions, i.e. the North Southern Zone (NSZ) and South Southern Zone (SSZ) with a view to providing a basis for future fine-scale spatial management of the resource. F ranged from 45,292 to 466,800 eggs per female and increased proportionally with CL according to the relationship: $F = 0.0584 \times CL^{3.164}$. F was significantly higher in the NSZ compared to the SSZ but was attributed to differences in lobster size between regions. There was no significant difference in the number of eggs $\cdot g^{-1}$ of egg mass between areas. SOM, estimated as the size at which 50% of females reached sexual maturity ($L_{50}$), was higher in the NSZ (104.1 mm CL) compared to SSZ (92.3 mm CL). Approximately 20% of lobsters above the MLS in the commercial catch in the NSZ were under the $L_{50}$ estimate. RRP, as a measure of egg production, was calculated for each size-class from the product of F, SOM and population length–frequency. The modal RRP size-classes in the NSZ were 117.5–122.5 mm CL, while in the SSZ it was 97.5–102.5 mm CL. Only 6% of RRP was contributed by female rock lobsters below the MLS in the NSZ, compared to 34% in the SSZ. Regional differences in SOM and RRP in the Southern Zone of South Australia suggest that different MLSs may be beneficial, particularly if the fishery is to be effectively managed at finer spatial scales.

Keywords: *Jasus edwardsii*; fecundity; maturity; reproduction; South Australia

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INTRODUCTION

Southern rock lobsters, *Jasus edwardsii* (Hutton 1875) are distributed around southern mainland Australia, Tasmania and New Zealand (Smith *et al.*, 1980; Booth *et al.*, 1990). In Australia, the most northerly distribution is Geraldton in Western Australia and Coffs Harbour in northern New South Wales, however the bulk of the population can be found in the south-eastern states of South Australia, Victoria, and Tasmania where they occur in depths from 1 to 200 m. *Jasus edwardsii* generally inhabit bryozoan or aeolianite limestone reefs but are also found on outcrops of igneous rocks such as granite (Phillips *et al.*, 2000).

The annual commercial catch of southern rock lobster in South Australia is ~2400 tonnes, representing ~60% of the total landings from the south-eastern Australian fishery (Linnane *et al.*, 2006). The South Australian fishery is divided into a Northern and Southern Zone, which are each subdivided into Marine Fishing Areas (MFAs) for management purposes (Figure 1). A total of 1900 tonnes (~50% of the total south-eastern fishery) was taken in the Southern Zone in the 2005/2006 season. The zone was managed under a range of input controls such as closed seasons, limited licence entry and spatial closures until 1993, when output controls in the form of a total allowable commercial catch (TACC) were also introduced (Sloan & Crosthwaite, 2007). Fishing is permitted from October to May inclusive and a minimum legal size (MLS) of 98.5 mm carapace length (CL) for all rock lobsters has been in place in the zone since 1970. Commercial fishing can only be undertaken in South Australia using standardized steel-framed pots which are set individually.

The focus of future management for the South Australian rock lobster fishery is a greater emphasis on fine-scale spatial assessment of the resource (Sloan & Crosthwaite, 2007). Specifically, future assessments will focus on key MFAs or sub-groups of MFAs rather than entire zones. An understanding of spatial differences in the reproductive biology of *J. edwardsii* is fundamental to this approach, especially in relation to MLS limits.
Fecundity and size of maturity estimates have been derived for *P. edwardsii* in New Zealand (MacDiarmid, 1989a), Tasmania (Punt & Kennedy, 1997; Gardner et al., 2006) and Victoria (Hobday & Ryan, 1997) where geographical differences were reported. However, despite the importance of the *P. edwardsii* fishery to the region, estimates of these reproductive parameters have never been published from South Australia.

Similarly, the relative reproductive potential of specific size-classes have been previously estimated for a range of important commercial crustaceans worldwide such as the western rock lobster *Panulirus cygnus* (Morgan, 1972), the European spiny lobster *Palinurus elephas* (Goni et al., 2003a), the American lobster *Homarus americanus* (Campbell & Robinson, 1983) and the European lobster *H. gammarus* (Tully et al., 2001; Agnalt et al., 2006). However, to date, the only published estimates of relative reproductive potential (RRP) for *P. edwardsii* come from the Victorian fishery, where the maximum reproductive potential came from the 105–135 mm CL size-classes (Hobday & Ryan, 1997; Punt & Hobday, 2006) but with contrasting spatial differences between specific fishing zones.

The aim of this study is to describe and compare the relationships between size, fecundity, sexual maturity, and relative reproductive potential of *P. edwardsii* in two major fishing regions in the Southern Zone of the South Australian rock lobster fishery. Results are used to identify appropriate spatial scales for future management of the fishery, especially in relation to MLS limits.

**MATERIALS AND METHODS**

**Study area and data collection**

The Southern Zone rock lobster fishery runs from the mouth of the River Murray in the Coorong area of South Australia to the South Australia/Victoria border (Figure 1). The data used for the study were fishery dependent and came from four MFAs where 99% of the commercial catch is taken annually, i.e. MFAs 51, 55, 56 and 58 (Linnane et al., 2006). Since 1991, scientific observers and commercial fishers from the South Australian rock lobster fishery have collaborated in an at-sea voluntary catch sampling programme. Fishers are requested to count, measure (mm CL), sex and record the reproductive condition of lobsters from up to 3 research pots per fishing trip. In total, 131,521 female rock lobsters were sampled over the period 1991–2004 in MFA 51 (N = 78,48), MFA 55 (N = 48,309), MFA 56 (N = 43,011) and MFA 58 (N = 32,353).

Spatial differences in growth rates between northern and southern regions of the Southern Zone have previously been identified (McGarvey et al., 1999). To examine if this extended to fecundity, size of maturity and RRP, the zone was subdivided into the North Southern Zone (MFAs 51 and 55; NSZ) and South Southern Zone (MFAs 55 and 56; SSZ) for the purpose of this study.

**Fecundity (F)**

The majority of *P. edwardsii* larvae generally hatch from September–November across the range of the species.
(MacDiarmid, 1989b). In South Australia, approximately 30–40% of females caught annually in October are ovigerous (Linnane et al., 2006). A total of 162 ovigerous females were randomly sampled from the Southern Zone in October and November of the 2004/2005 season. Each female was individually measured, tagged, bagged and frozen after collection. On processing, the eggs were removed from the setae and pleopods and any excess water drained before oven drying for 48 h at 50°C (Hobday & Ryan, 1997). Samples containing a large proportion of ruptured eggs after drying were discarded. For each egg mass sample, the total dry weight was determined. Three 0.04 g sub-samples were hydrated in 75% ethanol and enumerated under a dissecting microscope.

For each sub-sample, fecundity (F) was calculated according to the equation:

\[ F = (W_i/W_s) \cdot E \]

where \( W_i \) is the total dry weight, \( W_s \) is the sub-sample weight, and \( E \) is the egg count of the sample. Data from all sub-sample estimates were then fitted, using a SAS non-linear modelling procedure, to the equation:

\[ F = e^{a \cdot CL^{b}} \]

where \( CL \) is the carapace length (mm) and \( a \) and \( b \) are constants.

Regional differences in fecundity were analysed using analysis of covariance where lobster size was a co-variate. Regional differences in the number of eggs \( g^{-1} \) of egg mass were tested using analysis of variance.

Size at onset of maturity (SOM)

All 131,521 female lobsters from the voluntary catch sampling programme were used in the estimation of SOM. A female rock lobster was categorized as ‘sexually mature’ if it possessed either eggs or ovigerous setae (Wenner et al., 1974). The percentage of sexually mature female rock lobsters was plotted against carapace length in each 1 mm CL size-class and then fitted, using a SAS non-linear modelling procedure, to the logistic equation:

\[ P_m = \frac{1}{1 + e^{a \cdot b \cdot CL}} \]

where \( P_m \) is the proportion of mature female rock lobsters, \( CL \) is the carapace length, \( e \) is the intersection point of the curve and \( a \) and \( b \) are constants.

Relative reproductive potential (RRP)

The RRP is defined by Morgan (1972) and later modified by Hobday & Ryan (1997) by the relationship:

\[ P_i = C_i f_i \cdot M_i \cdot F_i \]

where \( P_i \) is the RRP for size-class \( i \), \( C_i \) is the sampled proportion in size-class \( i \) of females in the commercial catch, \( M_i \) is the percentage of mature female rock lobsters at size-class \( i \), and \( F_i \) is the fecundity of female rock lobsters at size-class \( i \).

RESULTS

Fecundity

The size-range and numbers of lobsters sampled in each sub-region are provided in Table 1. F was significantly higher in the NSZ compared to the SSZ but this was attributed to the co-variate of lobster size (\( F_{1,161} = 163.57, P < 0.001 \)) (Figure 5) and not region (\( F_{1,161} = 0.04, P = 0.949 \)). Egg mass weight varied from 4.3 to 41.5 g with the power function relating egg mass weight to body size following the relationship: egg mass weight = \((7 \times 10^{-4}) \times CL^{3.103}, R^2 = 0.70; N = 162\).

The maximum number of eggs per female ranged from 45,292 for a 90 mm CL individual to 466,800 for a 141.3 mm CL rock lobster and F was found to vary with CL according to the relationship: \( F = 0.0584 \times CL^{1.1642}, R^2 = 0.71; N = 162 \) (Figure 2A). There was no evidence of differences in size-specific fecundity between the two regions.

The number of eggs \( g^{-1} \) of egg mass varied from 17,515–40,591 eggs \( g^{-1} \) and was related to CL according to the relationship: egg \( g^{-1} = -1.2676 \times CL^2 + 310.78 \times CL + 14335 \) (Table 2; Figure 3). There was no significant difference in the number of eggs \( g^{-1} \) between the NSZ and SSZ (\( F_{1,161} = 0.42, P = 0.51 \)).

Size at onset of maturity (SOM)

The size at which 50% of female rock lobsters were sexually mature (\( L_{50} \)) varied spatially (Table 3; Figure 4). Within the NSZ, \( L_{50} \) occurred at 104.1 mm CL. Fitting of the logistic model to the proportion of mature females in each 5 mm CL size-class in the NSZ resulted in \( R^2 = 0.997 \) from 25 size-classes. More than 95% of female lobsters above 132 mm CL were mature. Based on the size–frequency of commercial catch landings (Figure 5), this suggests that approximately 20% of lobsters above the MLS of 98.5 mm CL in the commercial catch in the NSZ are under the \( L_{50} \) estimation.

Within the SSZ, \( L_{50} \) occurred at 92.3 mm CL. Fitting of the logistic model to the proportion of mature females in each 5 mm CL size-class in the SSZ resulted in \( R^2 = 0.996 \) from 25 size-classes. More than 95% of lobsters above 114 mm CL in the SSZ were mature. Based on the size–frequency of commercial catch landings (Figure 5), 42% of lobsters in the commercial catch are under the MLS of 98.5 mm CL but above the \( L_{50} \) estimation. No female lobsters were found with long setae or eggs below the 62.5 mm CL size-class in either the NSZ or SSZ regions.

Relative reproductive potential (RRP)

As with SOM, size-classes contributing to RRP differed spatially (Figure 5). In the NSZ, the maximum RRP was attributed to the 117.5 (14%) and 122.5 mm CL (14%) size-classes.

Table 1. Summary statistics of lobsters used in the fecundity study for each geographical region of the Southern Zone rock lobster fishery.

<table>
<thead>
<tr>
<th>Region</th>
<th>MFA</th>
<th>N</th>
<th>Mean CL (mm)</th>
<th>SD</th>
<th>Minimum CL (mm)</th>
<th>Maximum CL (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>NSZ</td>
<td>51</td>
<td>55</td>
<td>132.4</td>
<td>8.2</td>
<td>117.2</td>
<td>148.1</td>
</tr>
<tr>
<td>SSZ</td>
<td>56</td>
<td>58</td>
<td>116.7</td>
<td>9.3</td>
<td>86.6</td>
<td>130.0</td>
</tr>
</tbody>
</table>
whereas the maximum RRP in the SSZ was attributed to the size-classes between 97.5 (21%) and 102.5 mm CL (21%). Only, 6% of total RRP came from rock lobsters below the MLS in the NSZ, whereas 34% of RRP came from below the MLS in the SSZ.

Table 2. Estimates of mean eggs \( \cdot \) g\(^{-1} \) egg mass for each geographical region of the Southern Zone rock lobster fishery.

<table>
<thead>
<tr>
<th>Sub-zone</th>
<th>Mean eggs ( \cdot ) g(^{-1} )</th>
<th>SD</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>NSZ</td>
<td>33.342.7</td>
<td>4.280.85</td>
<td>21,593.4</td>
<td>40,591.7</td>
</tr>
<tr>
<td>SSZ</td>
<td>32.895.9</td>
<td>3.717.15</td>
<td>17,515.3</td>
<td>40,183.4</td>
</tr>
</tbody>
</table>

The modal size-classes in the distributions of the commercial catches in the NSZ were 97.5 – 117.5 mm CL (58%). In the SSZ, it was 92.5 to 102.5 mm CL (60%).

DISCUSSION

*J. edwardsii* generally breed from April – November across their geographical range. Mating occurs from April – July, with female rock lobsters brooding eggs for approximately 3 – 4 months over the winter season (MacDiarmid, 1989a). The relationship between size and fecundity of *J. edwardsii* in South Australia is consistent with that from other regions such as Victoria (Hobday & Ryan, 1997), Tasmania (Punt & Kennedy, 1997) and New Zealand (MacDiarmid, 1989a) (Figure 2B) although estimates from South Australia were lower than other fisheries. Limitations associated with fishery dependent estimates of size–fecundity relationships however, should be noted. Specifically, lobster catchability can vary by both size and sex (Miller, 1990; Frusher & Hoening, 2001) depending on a variety of factors such as environmental or behavioural variability (Morgan, 1974; Addison, 1995). In South Australia, female lobsters <70 and >140 mm CL are rarely caught (Linnane et al., 2006) which is consistent with the size selectivity of trap caught spiny lobsters in other fisheries (e.g. Goni, 2003b). As a result, data required to estimate fecundity in larger size-classes (>150 mm CL) are limited. The spatial differences in fecundity observed between northern and southern regions of the Southern Zone were a function of lobster size and reflect differences in growth between these regions. Specifically, growth rates are higher in the NSZ compared to the SSZ (McGarvey et al., 1999) and fecundity, therefore, is greater in northern areas where females develop larger pleopods enabling them to carry more eggs.

![Fig. 2](image1.png)

Fig. 2. (A) Size–fecundity relationship with fitted power model for all regions combined within the Southern Zone; and (B) comparison of size–fecundity relationship from previous studies fitted to the length range of samples from South Australia (this study), Sources are: Victoria (Hobday & Ryan, 1997), Tasmania (Punt & Kennedy, 1997) and New Zealand (MacDiarmid, 1989a).

![Fig. 3](image2.png)

Fig. 3. Number of eggs \( \cdot \) g\(^{-1} \) of egg mass against carapace length for female Southern Zone lobsters. Equations of fitted line are provided in the text.

![Fig. 4](image3.png)

Fig. 4. The \( L_{50} \) logistic curves for the proportion of mature female rock lobsters as a function of carapace length sampled from the North Southern Zone (NSZ) and South Southern Zone (SSZ) regions of the South Australian rock lobster fishery.

Table 3. Parameters for logistic function \( (P_m = \frac{L}{1 + e^{a-b CL}}) \) fitted to catch sampling data for each geographical region of the Southern Zone rock lobster fishery.

<table>
<thead>
<tr>
<th>Region</th>
<th>( N )</th>
<th>( a  )</th>
<th>( b  )</th>
<th>( L_{50} ) (mm CL)</th>
</tr>
</thead>
<tbody>
<tr>
<td>NSZ</td>
<td>56.157</td>
<td>-14.08</td>
<td>0.19</td>
<td>104.1</td>
</tr>
<tr>
<td>SSZ</td>
<td>75.384</td>
<td>-9.75</td>
<td>0.09</td>
<td>92.3</td>
</tr>
</tbody>
</table>
While fecundity increased with body size in all areas, maximum reproductive yield (eggs per gram of egg mass) appeared to be reached at intermediate sizes as observed in *Panulirus argus* (Bertelsen & Matthews, 2001) and *Palinurus elephas* (Goni et al., 2003a). Egg size was not recorded in the current study but there is evidence to suggest that it increases with female size in at least some species of spiny lobster (Goni et al., 2003a). This has implications for *J. edwardsii* larval quality where larger females appear to produce larger, more viable larvae (Smith & Ritar, 2007).

Spatial differences in SOM appear to be influenced by a range of factors including temperature (Annala & Bycroft, 1987), growth rates (Hobday & Ryan, 1997) density dependence (Beyers & Goosen, 1987; MacDiarmid, 1989b) and food availability (Melville-Smith et al., 1995). In south-eastern Australia and New Zealand, SOM for *J. edwardsii* increases with latitude ranging from 41 mm CL in south-west Tasmania (Gardner et al., 2006) to 122 mm CL in New Zealand (Annala et al., 1980; MacDiarmid, 1989b). Estimates from South Australia are closest to intermediate figures from Victoria where the SOM of 90 mm CL recorded in the Western Zone of Victoria (Hobday & Ryan, 1997) is comparable with that of 92.3 mm CL from the SSZ.

In spiny lobsters at least, SOM appears to be age, rather than size specific (Wenner, 1974; Beyers & Goosen, 1987). Therefore, where growth rates are fast, as in the NSZ, SOM is reached at a larger size. Goni et al. (2003a) suggested that for *P. elephas*, lower population densities at specific sites off Corsica resulted in lower competition for food (Kanciruk, 1980) or shelter (Polovina, 1989) thereby resulting in faster growth rates and larger SOM. Similarly in the North Island of New Zealand, female SOM was higher on the lower density west coast compared to the higher density east coast (MacDiarmid, 1989a). In South Australia, spatial differences in catch per unit of effort (CPUE) estimates provide some support for this hypothesis. Commercial CPUE rates (lobsters · potlift⁻¹) are consistently lower in the NSZ compared to the SSZ (Linnane et al., 2006), suggesting that the density of rock lobsters in northern MFAs is lower than southern regions. It should be noted however that a recent study in Tasmania between fished and unfished areas found no difference in SOM between regions despite substantial differences in density (Gardner et al., 2006). Clearly, the effects of density on SOM in *J. edwardsii* are unclear and more research is warranted.

Annala (1991) and Waddy & Aiken (1991) suggest that variations in SOM are also environmentally driven. This can be evidenced in South Australia where local environmental and oceanographic conditions are temporally and spatially variable. Specifically, during summer the predominant south-easterly winds result in an upwelling of nutrient-rich, cold water (11–12°C) which intrudes onto the continental shelf (Schahinger, 1987). This coldwater upwelling, known locally as the Bonney upwelling, tends to be confined to southern regions of South Australia and only occasionally impacts northern regions (McClatchie et al., 2006). The result is a temperature gradient, leading to higher water temperature (Lewis, 1981), growth rates (McGarvey et al., 1999) and presumably SOM in the NSZ compared to the SSZ. This supports findings from both Tasmania and Victoria where regional differences in SOM are correlated to differences in water temperature due to changes in latitude or localized upwelling events (Hobday & Ryan, 1997; Gardner et al., 2006). However, while SOM may be positively correlated to water temperature in some regions, in others such as New Zealand, it is negatively related and appears unrelated to age (Annala et al., 1980). Environmental factors driving spatial variability in SOM have also been reported for clawed lobster species such as the European lobster (*Ligurian-Cubedo et al., 2003*), and the Norwegian lobster *Nephrops norvegicus* (Tuck et al., 2000). In addition to population density and environmental factors, other mechanisms driving spatial variation in SOM in lobsters have been suggested but remain largely unclear. These include habitat type (Howard, 1980), fishing pressure (Ligurian-Cubedo et al., 2003) and social interactions (Thomas et al., 2003).

Although there was no evidence from the current study to suggest a seasonal loss of setae, the data underpinning estimates of SOM are nonetheless fishery dependent and therefore limited to the months of October to May inclusive in South Australia. This may have implications for estimates. For example, in Tasmania SOM in two regions differed significantly between months, suggesting that a seasonal process was influencing results (Gardner et al., 2006). While the nature of the driving processes is unclear, suggested causes were movement or catchability, both of which vary seasonally and in relation to maturity of females (Ziegler et al., 2002; Gardner et al., 2003).

Size at maturity and fecundity were utilized to estimate the RRP, as an indicator of the relative contribution specific size-classes make to total egg production. RRP has direct relevance to management outcomes, especially in relation to
MLS limits. It is generally accepted that limits should be set at a size that allows individuals to reproduce at least once before reaching their exploitable size (Chubb, 2000). This study has shown that in the SSZ of South Australia, 34% of egg production is provided by size-classes below the MLS of 98.5 mm CL. Within this region, it is generally the females, which are at or above the MLS of 98.5 mm CL that provide the greatest RRP. In this situation, it is likely that some individuals will indeed reproduce at least once before entering the exploitable biomass.

The protection provided to female lobsters by the MLS was not as significant in the NSZ however. In this region, size-classes below the MLS provided only 6% of egg production, with the maximum RRP coming from size-classes within the 117–122 mm CL range. In addition, approximately 20% of lobsters in the commercial catch in the NSZ were under the size at 50% maturity. Under this scenario, few female rock lobsters will have reproduced before entering the fishable biomass and the protection afforded to them by the current MLS of 98.5 mm CL is therefore limited.

A presumption of current management strategies in relation to MLS limits, is that local population egg production contributes to local recruitment. However, J. edwardsii larvae are long lived (at least 12–22 months) and have been found at various depths and considerable distances (100 s of kilometres) away from inshore spawning sites (Booth, 1994; Booth & Ovenden, 2000). This suggests that larvae have ample opportunity to be transported from their source to other regions and questions the usefulness of different MLS limits over small spatial scales. Using a combination of biological and hydrodynamic modelling, Bruce et al. (2007) simulated the planktonic early life history of J. edwardsii across its geographical range. In relation to sources of recruiting pueruli to the Southern Zone, the study predicted that while the most significant levels of recruitment occur from regions west of the zone, some degree of self-recruitment is predicted in most years. Importantly, the study found that the Southern Zone of South Australia had the highest levels of egg production in southern Australia and as a result, was an important source of pueruli for much of the overall southeastern fishery.

In conclusion, the spatial differences in SOM and RRP highlighted here indicate that a review of size limits may be required if this management tool is to be utilized on a regional basis within the Southern Zone rock lobster fishery. Such an approach has potential benefits in terms of increased recruitment not just locally in the Southern Zone, but indeed in other fishery jurisdictions across the geographical range of J. edwardsii.

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