

Larval transport and recruitment processes of  
southern rock lobster



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Barry Bruce, David Griffin, Russell Bradford  
– CSIRO Marine and Atmospheric Research



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CSIRO Marine and Atmospheric Research

FRDC 2002/007

Final Report

October 2007

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## NON-TECHNICAL SUMMARY

|          |                                                                     |
|----------|---------------------------------------------------------------------|
| 2002/007 | Larval transport and recruitment processes of southern rock lobster |
|----------|---------------------------------------------------------------------|

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### OBJECTIVES:

1. To examine the relationship between spawning region and settlement success across the range of the SRL fishery – *identify where successfully settling puerulus come from.*
2. To model the effects on settlement, throughout the range of the fishery, of changing spawning output in various areas of the fishery – *provide information on whether manipulating spawning stock biomass in some areas will help to increase recruitment and, hence, yield.*
3. To identify major physical processes contributing to differences in settlement between years and between regions – *help understand whether variations in puerulus settlement result from management changes or environmental effects.*
4. To identify mechanisms for incorporating findings of the project into on-going assessments of recruitment indices and stock status – *how best to develop the model outputs into a form that managers, researchers and industry can use on an on-going basis.*

### NON TECHNICAL SUMMARY:

#### OUTCOMES ACHIEVED TO DATE

1. The broadscale transport processes responsible for the distribution of larvae, the supply of puerulus and the resultant connectivity between regions is much better understood and has been communicated to fishers, managers, researchers and representatives of recreational fishing groups. A primary outcome is the common understanding generated within sectors and authorities that will further improve the high level of cooperation on spawning stock management issues. Information generated by this project is now regularly considered in stock assessment and other management related activities and reports.
2. There is increased understanding across all sectors of the requirements and implications of managing regional egg production from the perspective of maintaining the supply of puerulus.

The southern rock lobster (SRL) fishery is worth over \$100 million annually. It is considered to be fully exploited and catch rates are declining in some regions. Current management practices divide the fishery into seven functionally independent zones and assume that populations within each zone contribute only to local recruitment. However, southern rock lobster larvae are long-lived and have been found considerable distances (100's of kilometres) from shore in areas of southern Australia dominated by west to east current flows. This suggests ample opportunity for transport of larvae from their source to distant regions. Regional recruitment may thus depend on what happens in areas remote from those where the fishery is managed. In addition, there are large variations in egg production throughout the range of the fishery (and in some cases between areas in the same management zone). Given the early life history characteristics of SRL, it is possible that egg production in certain regions is more important in sustaining the fishery than that from others.

The implications of geographically variable egg production, the extent of larval dispersal, factors influencing settlement of puerulus and the effects on these of environmental variability are issues in which managers, researchers and the industry have long shared an interest. These issues have important ramifications for the long-term management of the fishery. In addition, using the level of

puerulus settlement to monitor the health of the fishery; collecting newly settled puerulus from the wild for aquaculture; culturing SRL larvae from eggs and the question of whether reproductive output from SRL in marine reserves may contribute to local recruitment, have further increased the demand for information about early life history stages and the factors influencing their growth, survival, transport and settlement. Understanding larval transport is the key to interpreting patterns of recruitment, connections between regions and the likely benefits/risks of increasing spawning biomass or changing harvesting strategies in these regions. However, the spatial scale over which rock lobster larvae are found and the duration of their early life history make it difficult to study larval transport by directly sampling phyllosoma at sea. Consequently, most published literature relies on speculative conclusions based on sampling over relatively small spatial scales.

The development of models that combine the biological characteristics of rock lobster with simulations of ocean circulation has progressed our understanding of the transport of western and tropical rock lobster larvae in previous FRDC-funded projects (Griffin *et al.* 2001, Pitcher *et al.* 2005). In this project, we have developed these models further and applied them to SRL in order to examine larval transport processes and the connectivity, via larvae supply, between the various management zones in this fishery.

The overall methodology involved the combination of a *biological model* simulating the spawning and planktonic early life history of SRL, *Jasus edwardsii*, with a *hydrodynamic model* that simulated circulation of the ocean.

Model larvae hatch from prescribed locations at prescribed times and individual phyllosoma were allowed to move and grow according to the water velocity and the temperatures respectively that they experience. Water velocity and temperature vary considerably over the range of depths at which phyllosomata are found in the wild, so modelled movement and growth rate take into account their vertical positioning in the water column and the corresponding temperatures that each are exposed to. Different stages have different behaviours and responses to conditions in the wild. The model captures these in stage-specific attributes in vertical distribution, swimming ability and factors influencing growth, settlement and survival.

The model successfully recreated the known spatial and temporal distribution of SRL larvae. The geographic extent over which modelled puerulus settled matched the geographic range of the SRL in Australian waters. Predicted larval duration covered the ranges reported from both aquaculture and field observations. The model output predicts the following for SRL:

Transport of SRL larvae in southern Australia is dominated by an overall easterly displacement from natal spawning sites due primarily to currents that run parallel to the coast from southwest Western Australia to the east coast of Tasmania, particularly near to the shelf break. However, a complex field of eddies and currents in offshore waters over much of southern Australia serves to isolate some larvae from the dominant easterly flow. This results in a net westerly displacement of these larvae and, in some regions, promotes significant levels of self-recruitment despite the lengthy duration of the larval stage.

The main implications of the dominant easterly flows are that the western regions of the fishery – specifically southwest Western Australia, Northern and Southern Zones of South Australia and the Victorian Western Zone are significant sources of successfully settling pueruli for much of the overall fishery. The most important sources of successfully settling pueruli are the South Australian Management Zones and this suggests that careful management of these areas will offer significant benefits across the range of the fishery.

With the exception of southwest Western Australia, all regions receive more pueruli from outside their own boundaries than from self-recruitment. Southwest Western Australia, by virtue of being both the western-most region and being adjacent to the most energetic and consistently located eddy field in southern Australian waters, is predicted to receive nearly all of its settling pueruli from its own waters. Lower, but still significant, levels of self-recruitment are also predicted for both South Australian Zones and in southern Tasmania. Thus setting sustainable harvesting regimes and improving regional spawning stock biomass can have a local impact and does not just serve to benefit distant regions of the fishery.

In terms of average overall success in their contribution of puerulus to the Australian fishery, the nine regions examined were rated by the model in the following order from highest to lowest:

Northern Zone South Australia; Southern Zone South Australia; southwest Western Australia; Western Zone Victoria; Southwest Tasmania; Southeast Tasmania; Northeast Tasmania, Northwest Tasmania, Eastern Zone Victoria.

Two points are worth considering. First, the overall contribution of settling pueruli is dependent on the true levels of egg production in each region. For example, southwest Western Australia has the potential by virtue of its (western) location to be a significant source of pueruli for broad areas of the fishery – particularly the two South Australian Zones and western Victoria. However, this will not manifest in reality if spawning stock biomass in that area is either depleted or naturally low. Second it is worth pointing out that despite the significant differences between regions in their potential to supply successfully settling pueruli, all regions contribute some level of supply and thus the lowest ranked regions should not be seen as unworthy of sustainable management practices.

The model predicts that regions differ significantly in their contribution to successful settlement across the fishery. Thus increasing spawning stock biomass in regions where the contribution to settlement is high, is more likely to have more overall benefit to the fishery than others. However, the same cautionary point applies. All regions contribute to settlement and thus none should be regarded as sacrificial in terms of managing spawning stock biomass. The areas of the fishery including, and to the west of, western Victoria have the greatest potential for contribution to settlement. Thus improving spawning stock biomass in these areas will provide the greatest overall benefits. Some regions have significant, but more localised, benefit relative to the full range of the fishery. Larvae produced in southern Tasmania (both the southwest and southeast regions) contribute significantly to settlement in Tasmanian waters and thus managing spawning stock biomass in these regions is equally important to the overall stability of the Tasmanian fishery. Eastern Victoria and northwest (NW) Tasmania are predicted to have the lowest input to settlement across the range of the fishery. Thus maintaining a stable level of spawning stock biomass may be more effective in terms of benefits accrued to the fishery than programs to greatly increase spawning stock biomass in these areas. However, the relatively minor contribution that NW Tasmania does have, is directed primarily back to Tasmanian waters. Northeast (NE) Tasmania contributes a higher proportion of recruits to the Tasmanian fishery than NW Tasmania and as both regions have depleted spawning stock biomass this suggests that, of these two, improving spawning stock biomass in NE Tasmania would have greater overall potential benefits to the Tasmanian fishery.

The model predicted significant levels of interannual variability in the levels of settlement across southern Australia. However, modelled settlement did not consistently match the observed data. We were unable to demonstrate significant correlations between any simple environmental index and the magnitude of observed or modelled puerulus settlement across southern Australia. This is perhaps not surprising given that the domain of the fishery falls under the influence of several different circulation regimes bounded by the influences of the Leeuwin Current in the west and the East Australian Current in the east. These currents interact in complex ways with the zonal flows of southern Australia and the low energy eddy field south of the Great Australian Bight. We did find significant influences of winter winds in producing the timing of settlement in South Australia. However, there was no robust correlation between the strength of these winds and the magnitude of settlement that could be used for similar recruitment predictions to those seen for western rock lobster (*Panulirus cygnus*). Finding simple correlations between wind speed/direction and settlement across the range of the fishery is also complicated by the different orientation of coastlines across the domain. For example, westerly winds that facilitate onshore winter flows across the GAB, promote largely offshore transport and hence reduce the opportunity for settlement in eastern Tasmania.

Despite the improvements in modelling growth and survival in this model, compared to the models for western rock lobster (Griffin *et al.* 2001) and tropical rock lobster (Pitcher *et al.* 2005), our representation of mortality and the understanding of the processes that influence it are still relatively crude. This currently limits our ability to progress a common understanding of processes contributing to the interannual variability in settlement.

This project provides the first quantitative estimates of larval connectivity between management regions across the range of the SRL fishery. It explains the differences in seasonal settlement signals between South Australia and Tasmanian waters and provides an assessment of the relative contributions each egg production region provides by way of potential puerulus settlement back to the fishery. These findings alone provide benefits for managing spawning stock biomass and making decisions on which areas might best be targeted for accelerating stock rebuilding.

**KEYWORDS:** southern rock lobster, *Jasus edwardsii*, recruitment, puerulus settlement, spawning stock biomass, larval transport processes, biophysical modelling

## **ACKNOWLEDGMENTS**

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# INTRODUCTION

## Background

The southern rock lobster, *Jasus edwardsii*, (SRL) occurs throughout southern Australia and New Zealand and supports valuable fisheries across its range. The species has a highly protracted oceanic larval phase, called phyllosoma, that may last up to 24 months prior to metamorphosing into puerulus and settling into coastal and shelf habitats (Booth and Phillips 1999). Pueruli then molt after settlement to become juveniles. The long larval duration of SRL is believed to provide ample opportunity for transport of larvae from their source to distant regions. Regional recruitment may thus depend on what happens in areas remote from where local areas of the fishery are managed.

The Australian SRL fishery is divided into seven management zones and although it is generally accepted that recruits to any one zone may come from others, there is currently no information available to assess this and thus provide a more targeted approach to managing spawning stock biomass. Spawning stock biomass in some regions of the fishery has been as low as 8-15% of virgin (Kennedy *et al.* 1994). Improved knowledge of the sources of larvae would assist managers in deciding on management priorities such as in which areas to accelerate stock rebuilding and whether changing harvesting strategies or other measures, such as translocation of stock, in areas where spawning stock biomass is closer to virgin levels is likely to influence recruitment to various other regions of the fishery.

Recruitment and subsequent catch rates in some species of rock lobster, including SRL, have been linked to the number of puerulus that settle (Gardner *et al.* 2001, Breen and Booth 1989, Phillips 1986) and this, in turn, has been linked to offshore oceanographic processes (Clarke and Li 2004, Caputi *et al.* 1995). Understanding larval transport is the key to interpreting patterns of recruitment, connections between regions and the likely benefits/risks of increasing spawning biomass or changing harvesting strategies in these regions.

CSIRO's previous work on SRL concentrated on drawing together existing biological data to establish the distribution of phyllosoma in southern Australia, and establish what oceanographic processes might be important for larval transport (Bruce *et al.* 2000). CSIRO's more recent work on western (WRL) and tropical (TRL) rock lobster successfully developed linked biological + physical oceanographic models that both recreated and explained larval transport for those species (Griffin *et al.* 2001, Pitcher *et al.* 2005).

This current project utilises the combined biological knowledge of Bruce *et al.* (2000) and builds on the modelling skills developed in the projects Griffin *et al.* (2001) and Pitcher *et al.* (2005) to simulate the larval transport and recruitment processes of southern rock lobster.

## Need

This project arose from the need within the SRL fishery to address a series of regional and fishery-wide questions including:

- What areas contribute to successful recruitment within regions of the fishery?
- Will increasing the spawning biomass in regions, where it is currently very low, increase recruitment to the fishery globally, only in certain restricted areas or not at all?
- To what extent are management zones linked via larval transport from both west to east and east to west.
- What drives puerulus settlement across the range of the fishery and can regional and interannual differences in settlement be utilised to assess the health of the stock, and assist in the future with the prediction of catch rates.

These needs have been identified by managers, industry and research providers in Western Australia, South Australia, Victoria and Tasmania. In Tasmania, the Crustacean Research Advisory Group gave this issue their highest priority ranking in the lead up to this project due to its importance in targeting the current management objective aimed at rebuilding egg production.

Addressing these questions will help to ensure the sustainability of the fishery, assess the merits of alternative management strategies for improving recruitment (and hence yield) and provide the basis for possible future predictions of catch rates based on puerulus and/or ocean monitoring.

## **Objectives**

The objectives of this project were:

- To examine the relationship between spawning region and settlement success across the range of the SRL fishery - *identify where successfully settling puerulus come from*;
- To model the effects on settlement, throughout the range of the fishery, of changing spawning output in various areas of the fishery – *provide information on whether increasing spawning stock biomass in some areas will help to increase recruitment and, hence, yield*;
- To identify major physical processes contributing to differences in settlement between years and between regions – *help understand whether variations in puerulus settlement result from management changes or environmental effects*;
- To identify mechanisms for incorporating findings of the project into on-going assessments of recruitment indices and stock status – *how best to develop the model outputs into a form that managers, researchers and industry can use on an on-going basis*;

## **SCOPE OF REPORT**

This project uses a process-based modelling approach to investigate larval transport and recruitment in southern rock lobster. This report details the findings of the project. We will first describe the modelling approach including the parameters used and how they were defined. We then examine the model outputs and predictions and assess these outputs against empirical data (real observations) to assess the credibility of these outputs. Finally, we assess the implications of these results for the management of spawning stock biomass and harvest strategies across the range of the fishery.

# LARVAL TRANSPORT MODEL

## METHODS

### General modelling methodology

The overall methodology involved the combination of a *biological model* simulating the spawning and planktonic early life history of *Jasus edwardsii* with a *hydrodynamic model* (Bluelink) that simulated circulation of the ocean. These two models and their parameters are described separately in the following sections of this report. We refer to the combination of these models as the *larval transport model*. This combined approach is commonly known either as an *Individual Based Model*, or a *Lagrangian Model*, since it models the transport of a population of larvae by simulating and following the movements of many individuals.

The biological model is a further development of that applied to tropical rock lobster, *Panulirus ornatus* (Pitcher *et al.* 2005), which in turn was a development of the model used for western rock lobster, *P. cygnus* (Griffin *et al.* 2001). Rock lobster larvae are called *phyllosoma* (plural = *phyllosomata*) and develop through a series of 11 *stages* (identified by Roman numerals I-XI). In SRL, some stages are separated into sub-stages (called *instars*) identified by alphabetical annotation (eg stages VIII + VIIIa). Model larvae hatch from prescribed locations at prescribed times and individual phyllosoma then move and grow according to the water velocity and the temperatures respectively that they experience. Water velocity and temperature vary considerably over the range of depths at which phyllosomata are found in the wild, so modelled movement and growth rate take into account their vertical positioning in the water column and the corresponding temperatures that each are exposed to. Different stages have different behaviours and responses to conditions in the wild. The model captures these in stage-specific attributes in vertical distribution, swimming ability and factors influencing growth, settlement and survival. Chiswell and Booth (1999) included horizontal swimming ability for late stage phyllosomata in their modelling of *J. edwardsii* larvae off New Zealand, as this best explained the distribution of these stages off the east coast of the North Island. However, in our case, and in lieu of further empirical data supporting their conclusions, our model assumes that phyllosomata have no effective horizontal swimming capacity, but can move vertically. This is generally believed to be the case for most phyllosomata in the various species studied to date (see Phillips and Booth 1994). The last stage in the larval life of a rock lobster is the *puerulus* (pl = *pueruli*), sometimes labelled as stage twelve (XII). This stage can actively swim (Nishida *et al.* 1990, McWilliam and Phillips 1997) but does not feed and has limited energy reserves (Lemmens 1994, Jeffs *et al.* 1999). Accordingly in the model, once phyllosomata have metamorphosed to the puerulus stage, their horizontal movement is no longer totally passive but instead is the sum of the local water velocity and a constant, shore-directed swimming velocity. If model pueruli reach shallow water within a certain time interval (30 d) they are counted as having settled. If they fail to reach land within that time interval, they die.

As in the wild, only a minority of the model phyllosomata successfully metamorphose into pueruli and settle to become juveniles. Many are carried too far from land ever to return, while others succumb to the high rate of predation by planktivorous fish and other zooplankters that is assumed to exist in shelf waters (Kingsford and MacDiarmid 1988, Acosta and Butler 1999). We thus applied different mortality parameters for larvae residing in shelf and offshore waters in the model.

The model domain is large enough to include the entire Australian distribution of *Jasus edwardsii*, while also extending to the west coast of New Zealand. We include the latter for completeness as the eastern boundary to the Tasman Sea. The model output gives some indications of the fate of larvae spawned on New Zealand's west coast but should not be taken as a complete representation of larval transport for that region. A complete assessment of New Zealand waters would require a significant easterly extension of the model's domain, and thus additional model runs, which were not within the scope of this project.

Environmental data for 1993 to 2004 are used, allowing the fate of 10 year-classes of model larvae to be compared over an 11 year period. Each model run follows the fate of 6200 individual larvae spawned across the domain - 62,000 modelled larvae in total. Larvae are tracked for a period up to 28 months after spawning. The choice of 28 months is to ensure that all reported larval duration scenarios are captured within the time period of model runs.

As in the previous projects on the larval transport of western and tropical rock lobster (Griffin *et al.* 2001 and Pitcher *et al.* 2005) we have run the larval transport model many (>120) times with different parameter choices as part of the process of sensitivity testing and minimizing the artefacts of the model's approximations. For simplicity, we have not documented the full evolution of the model's final parameter choices here, but knowledge gained during the evolution of the model is embodied in the final described runs. In this report, we present the parameters used in the final run and the reasons for their choices. The report provides a full description of the transport processes, including larval tracks (trajectories), using year classes hatched in selected years as examples. Our choice of years to illustrate the results in this report was arbitrary as the results for all years are broadly similar. Model outputs for all years are provided on the accompanying CD.

Much of the reporting and extension of the results to industry, other researchers and managers throughout the progress of the project has relied on animations and graphics of model runs. These provide an invaluable tool for illustrating modelled ocean processes as well as the fate of modelled larvae. They provide a useful way of visualizing the circulation systems and model outputs across southern Australia. As in previous projects, we have included these various animations and graphics from the model runs on a CD accompanying this report.

The details of the biological and hydrodynamic models and their parameters are described below.

## **Model description**

### ***Biological model***

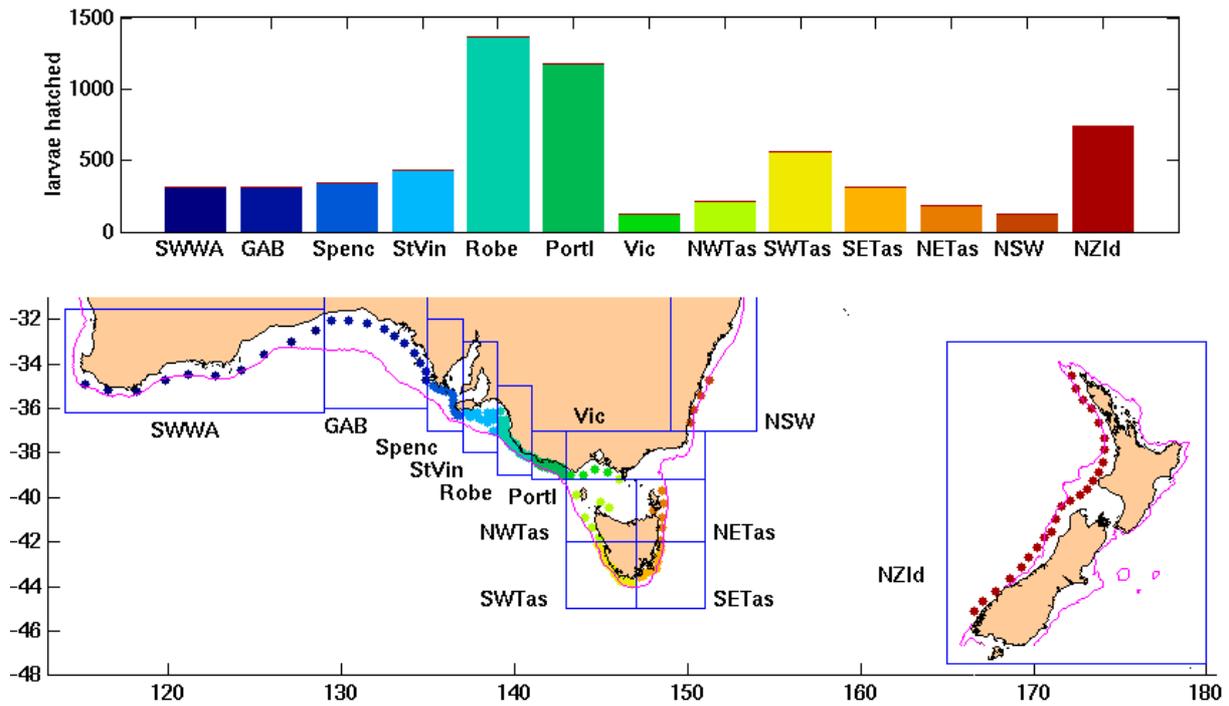
#### ***Hatching***

We have used the term 'hatch' throughout this report to define the start of the pelagic phase.

Model larvae were hatched at the 200 sites within the regions shown in Figure 1. These regions correspond to State Management Zones or to the egg production assessment areas of the fishery, where the latter is undertaken at a higher degree of spatial resolution within individual Zones. The density of hatching sites, and hence number of model larvae produced per region, is based on an approximate representation of the average values of regional egg production over the period 1993-2000<sup>1</sup>. Larvae were hatched every 4 days from 1 September to 30 December (31 instances), giving a total larval release per year of 6200. The choice of sub-regions within State Management Zones to initiate and track larval transport in the model was particularly useful in some areas (eg Tasmania) where significant differences exist in spawning stock biomass across the State.

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<sup>1</sup> Estimates of regional egg production were provided by the co-investigator team: C. Gardner (TAFI), A. Linnane (SARDI), D. Hobday (PIRVic). Estimates were not available for WA – in this case a consensus best-guess estimate was made based on input from co-investigators and R. Melville-Smith (WA Fisheries).



**Figure 1. Model domain showing the number and location of hatching sites and egg production assessment regions for presentation and analysis of results. The 200 m isobath is in pink.**

### *Growth and metamorphosis*

A refinement, used in this project, to the model used for tropical rock lobster (Pitcher *et al.* 2005) is the inclusion of temperature-dependent growth and mortality. We have assumed that the rate at which larvae grow can be approximated by a linear function of water temperature, with growth ceasing at some very cold ‘biological zero’ temperature  $t_0$ . Defining  $T_s$  as the intermolt period of stage  $s$ , we write:

$$1/T_s = g_s(t-t_0) \quad (1)$$

where  $t$  is temperature. For each larval stage, we estimated the growth factor  $g_s$  and biological zero temperature  $t_0$  by fitting (1) to observations of  $T_s$  for *J. edwardsii* larvae reared in tanks of constant temperature. Data published by Tong *et al.* (1997), Tong *et al.* (2000), Ritar (2001), Bermudes (2005) and Kittaka *et al.* (2005) were combined, along with *a priori* estimates that  $T$  is large (200 d) at  $t=10$  °C, to help constrain the fit for stages lacking observations of growth at low temperature. The results of these calculations are best summarised by computing the cumulative totals of the intermolt periods for a range of temperatures, as shown in Figure 2. The intermolt periods of stages VIII and X are greater than the others because these stages each have two instars (Kittaka *et al.* 2005).

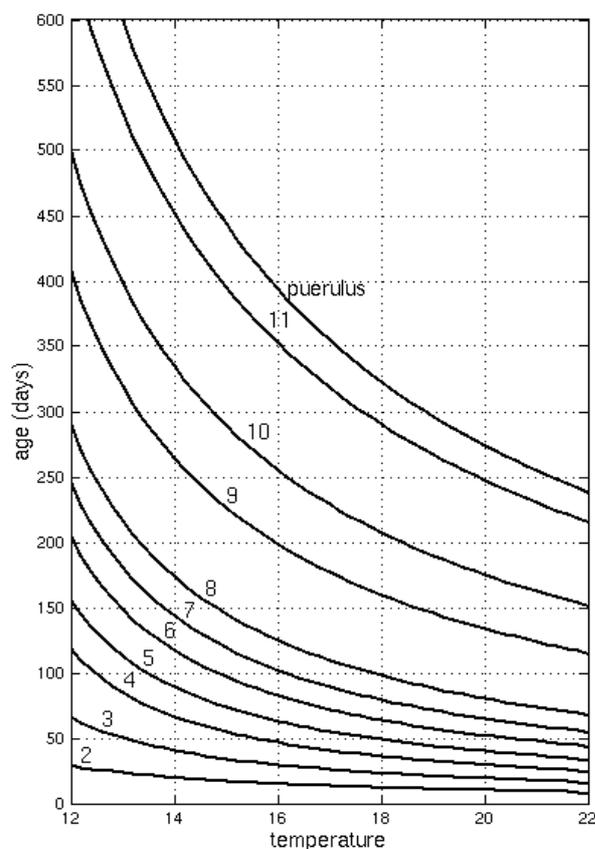
Kittaka *et al.* (2005) observed that, in captivity, both stage X and stage XI phyllosomata could metamorphose to pueruli, so we initially chose to allow model phyllosomata at either of these stages to metamorphose to pueruli. This was modified in one of the final model runs to only allow phyllosomata to metamorphose after they had achieved stage XI.

The growth rates determined from aquaculture observations are not necessarily applicable to what happens in the wild, so we also ran the model with 20% faster and 20% slower growth. By comparing the modelled progression through all stages to field data on stage distribution and occurrence, and the observed annual cycle of puerulus settlement, we were able to identify which growth rate was most realistic.

The real trigger for metamorphosis to the puerulus stage is unknown although the amount of accumulated energy reserves, external stimuli such as contact with lower salinity shelf water,

encounters with the seafloor or being part of a programmed developmental process, have all been suggested as possible cues (Booth and Phillips 1994, McWilliam and Phillips 1997, Jeffs *et al.* 2001). Most *J. edwardsii* pueruli have been caught over continental slope waters (Booth and Stewart 1992, Booth 1994) although in some cases puerulus have been found up to 300 km from shore (Jeffs *et al.* 2001). We allowed modelled phyllosomata to metamorphose if they reached the 2000 m contour over the continental slope, provided they had reached the appropriate stage (X or XI) depending on the model run.

How pueruli know which direction to swim in order to reach shallow water is unknown (Chiswell and Booth 1999), as is how they choose where or when to settle once they reach shallow water. These are subject areas requiring further research. However, we know that pueruli do not feed, thus their energy reserves are limited (Lemmens 1994, Jeffs *et al.* 1999). In the model, we assume that pueruli must reach habitat suitable for settlement within a certain time period after metamorphosis. This period was set at 30 d as per the modelling example of Bestley (2001). Chiswell and Booth (1999) concluded that sustained shoreward swimming speeds of 0.08-0.1 m s<sup>-1</sup> were required to account for the distribution of pueruli inshore of the Wairarapa Eddy off New Zealand's North Island. Accordingly, we assume that puerulus swim at a constant velocity of 0.1 m s<sup>-1</sup> towards shallower water. This would allow pueruli to travel up to approximately 260 km unaided by currents, which is within the swimming range estimated by Jeffs *et al.* (2001) based on lipid analysis of wild-caught specimens. As in the wild, modelled currents are not always conducive to transporting pueruli onshore and, despite their swimming abilities, pueruli may be forced offshore by unfavourable currents. These pueruli may still successfully settle in the model if they are able to make it back to shallow water within the 30 d period. Similar processes no doubt occur in the wild where *J. edwardsii* pueruli have been found up to 300 km from shore (Jeffs *et al.* 2001). Settlement of *J. edwardsii* puerulus has been recorded to depths of at least 50 m (Booth 1994). Correspondingly, any region where the depth is less than 50 m is deemed suitable and triggers settlement in the model.

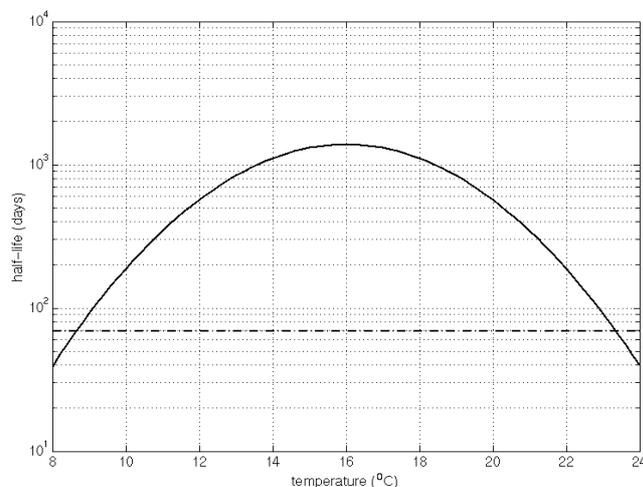


**Figure 2. Modelled dependence of growth rate on temperature, shown as the day of moulting to each phyllosoma stage, for phyllosoma reared at constant temperature.**

## Mortality

The remaining biological process included in the model is a coarse representation of mortality. The same rearing experiments used for estimating the growth rates showed that while growth is faster at high temperatures, so is mortality. We include a symmetric, temperature-dependent, mortality function in the model that results in larvae having a chance of dying at each time-step that depends on the local temperature (see below for details of time steps). The half-life (the time it takes half the population to die) of this process, for constant temperature, is shown in Figure 3. We only wish to simulate the basic regional gradients of mortality, rather than the absolute values, so we scale the mortality rate such that very few larvae die where the water is between 13° C and 19° C. This temperature range brackets where *J. edwardsii* phyllosomata have been most commonly recorded in southern Australia (i.e. the 'phyllosoma water' of Bruce *et al.* 2000). This means that model larvae can survive in the open ocean for longer than each year-class is tracked, which is until the end of the second calendar year following hatching (up to 28 months). This enables larvae to be followed over the full range of duration scenarios reported in the literature (Lesser 1978, Kittaka *et al.* 1988, Booth 1994, Bruce *et al.* 2000, Olsen and Shepherd 2006).

The total rate of mortality in the wild includes predation and starvation. We assume that mortality due to predation in the open ocean is low or negligible compared to that in shelf waters (following the thesis of Cobb *et al.* 1997) and hence drive mortality by the temperature function in offshore waters (Figure 3). For shelf waters, we assume that predation is the significant mortality factor due to the higher number of planktivorous animals in this habitat (Kingsford and MacDiarmid 1988, Acosta and Butler 1999). We have included a basic representation of predation in the model as a constant rate specific to shelf waters <100 m deep. In these areas, the mortality rate is set such that the half-life is just 70 d, in accord with observations that *J. edwardsii* larvae older than that (phyllosoma stages 4-5) are rare in shelf waters (Booth 1994, Bruce *et al.* 2000).



**Figure 3. Mortality rate of model larvae in the open ocean (solid line) and in shelf (<100 m) waters (dashed), expressed as the period for which the chance of survival is 50%.**

Starvation and food availability also have influences on growth and survival, however, in lieu of information on these effects, their interaction and their magnitude, we have chosen not to represent them in the model.

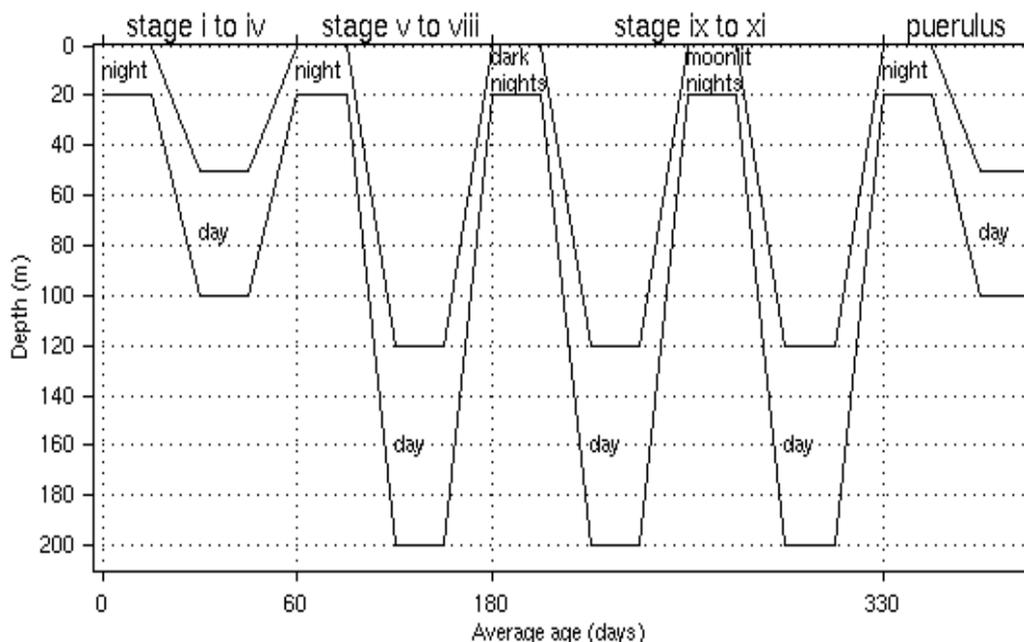
Estimates of mortality and the true spatial and temporal variability in their effects remain some of the most limiting components of the biological model and require further research.

## Vertical migration

Although they have relatively poor horizontal swimming abilities, phyllosomata are generally observed to rise to the surface at night and sink during the day (Booth and Phillips 1994). Diurnal vertical migration has been reported for *J. edwardsii* larvae, but the details are poorly known (Booth

1994, Bruce *et al.* 2000). Currents and temperatures vary markedly with depth so knowing the vertical positioning of the larvae is important for simulating their growth and transport. The vertical behaviour incorporated into the model is drawn from the conclusions of three studies on *J. edwardsii* larvae (Lesser 1978, Booth 1994, Bruce *et al.* 2000), the findings of research carried out as part of this project (Bradford *et al.* 2005 – see Appendix C) and various studies on palinurid larvae in general (Johnson 1960, Rimmer and Phillips 1979, Pollock 1986, Yeung and McGowan 1991, Hernandez *et al.* 2000, Minami *et al.* 2001).

Figure 4 shows the vertical migration of model larvae, as a function of stage. The ‘age’ axis of Figure 4 is indicative only because the age at which model larvae pass through their stages depends on water temperature, and is therefore variable (see above). All model larvae behave the same, and they are assumed to be equally distributed throughout the depth layers shown. We have not made vertical migration depend on the local water temperature, phase of moon, or sea state, since there is no substantive evidence to support such dependencies for *J. edwardsii* despite these factors evidently contributing to vertical migration in some other species (see Rimmer and Phillips 1979). The fraction of a 24 h day spent in the ascended and descended state is not always even as depicted, but varies according to the time of the year and hence day/night-length.



**Figure 4. Vertical migration of model larvae in a ‘standard’ model run.**

### **Hydrodynamic model**

Initial runs of the larval transport model used the same satellite-based estimates of the water velocity and temperature that were used in FRDC projects 1997/139 (Griffin *et al.* 2001) and 2002/008 (Pitcher *et al.* 2005) on western rock lobster and tropical rock lobster respectively (see Griffin *et al.* 2001). This technique proved to be less suitable for the present study region than it was in earlier applications, principally because the currents across much of southern Australia are much weaker, or of narrower width than the earlier-studied regions (Cresswell and Griffin 2004) and thus closer to the detection limit of the satellite techniques. The resolution of the narrow South Australian Current (Ridgway and Condie 2004) and the propagation westwards of eddies that it sheds, are vital to understanding larval transport dynamics in the southern Australian region.

For these reasons, we used a new global hydrodynamic model, *OFAM*, developed by the Bluelink joint project between the CSIRO, Bureau of Meteorology and the Royal Australian Navy. This model provided a finer ( $0.1^\circ = 11$  km, compared with  $0.2^\circ$ ) horizontal resolution than is possible using satellites alone, while also resolving the shelf-edge jet and coastal counter-currents. The Bluelink

model can also more appropriately resolve the vertical gradient of wind-driven transport. The present project is the first application of a Bluelink model to a biological/fisheries related issue. The complete Bluelink system, comprising the OFAM model and the BODAS data-assimilation system are described by Oke *et al.* (2005), Oke *et al.* (2008) and Schiller *et al.* (2008). The first long integration of OFAM using BODAS produced BRAN1, the Bluelink ReANalysis. We performed several experiments using this model run but became unsatisfied with its performance, which was marred by several faults, including a significant warm bias. BRAN2 was not complete in time for our use but a long, free-running (ie, without data-assimilation) run of the model was (with the causes of the warm bias fixed). This model run is known as SPINUP4/5, being an aggregate of the 4<sup>th</sup> and 5<sup>th</sup> long runs of OFAM. The disadvantage of the model having been run without data assimilation is that specific, individual, eddies do not necessarily occur exactly where and when satellite image records position them. That disadvantage is possibly out-weighed, however, by the fact that horizontal mixing processes are probably more realistically modelled by the free-running model. This is because present-generation data assimilation techniques introduce un-physical shocks to the system that trigger spurious small-scale features that possibly inflate the real rates of oceanic mixing.

A brief summary of the major components of the model is provided below.

### *The Bluelink model*

Bluelink *Ocean Forecasting Australia Model (OFAM)* is a 47-layer (10 m resolution in the upper 200 m, then gradually coarsening to a total depth of 5000 m) global implementation of Version 4 of the NOAA Geophysical Fluid Dynamics Laboratory's Modular Ocean Model (Griffies *et al.* 2004). It has resolution grading from 0.1° (in both latitude and longitude) in the Australasian region (16°N-75°S, 90°E-180°E) to 2° in the N Atlantic. The model is forced with atmospheric fluxes of heat and momentum from a combination of the European Center for Medium range Weather Forecasting global reanalysis (ECMWF - ERA40) and the ECMWF operational forecasts, in order to simulate upper-ocean dynamics realistically for the period 1993-2004.

One of the principal advantages of using a global hydrodynamic model is that it has no open boundaries. Hence, linkages between flows in our study region and the large-scale influences such as El Nino and variability of the Subtropical Convergence, are all included much more completely than can be done using a limited-area model. A disadvantage is that running a global model at finer than 0.1° (= ~11 km) resolution is still out of our reach.

To represent the random component of the unresolved sub-gridscale physical processes, a random-walk simulation is included in the larval advection model, at the scale of the individual larva. The median random velocity is 0.05 m s<sup>-1</sup> plus 15% of the local current speed, as resolved by the model. Results are not sensitive to this inclusion but we make it for completeness. The sum of the random and model-resolved velocities are used with a 4<sup>th</sup>-order Runge-Kutta integration scheme (Hofmann *et al.* 1991) to advance the positions of all model larvae 5 times per day. Tests of this scheme show that it does an excellent job of making sure that where the flow is circular, for example, particles complete many closed loops similar to the observed trajectories of satellite-tracked drifters in the study area (Cresswell 2000).

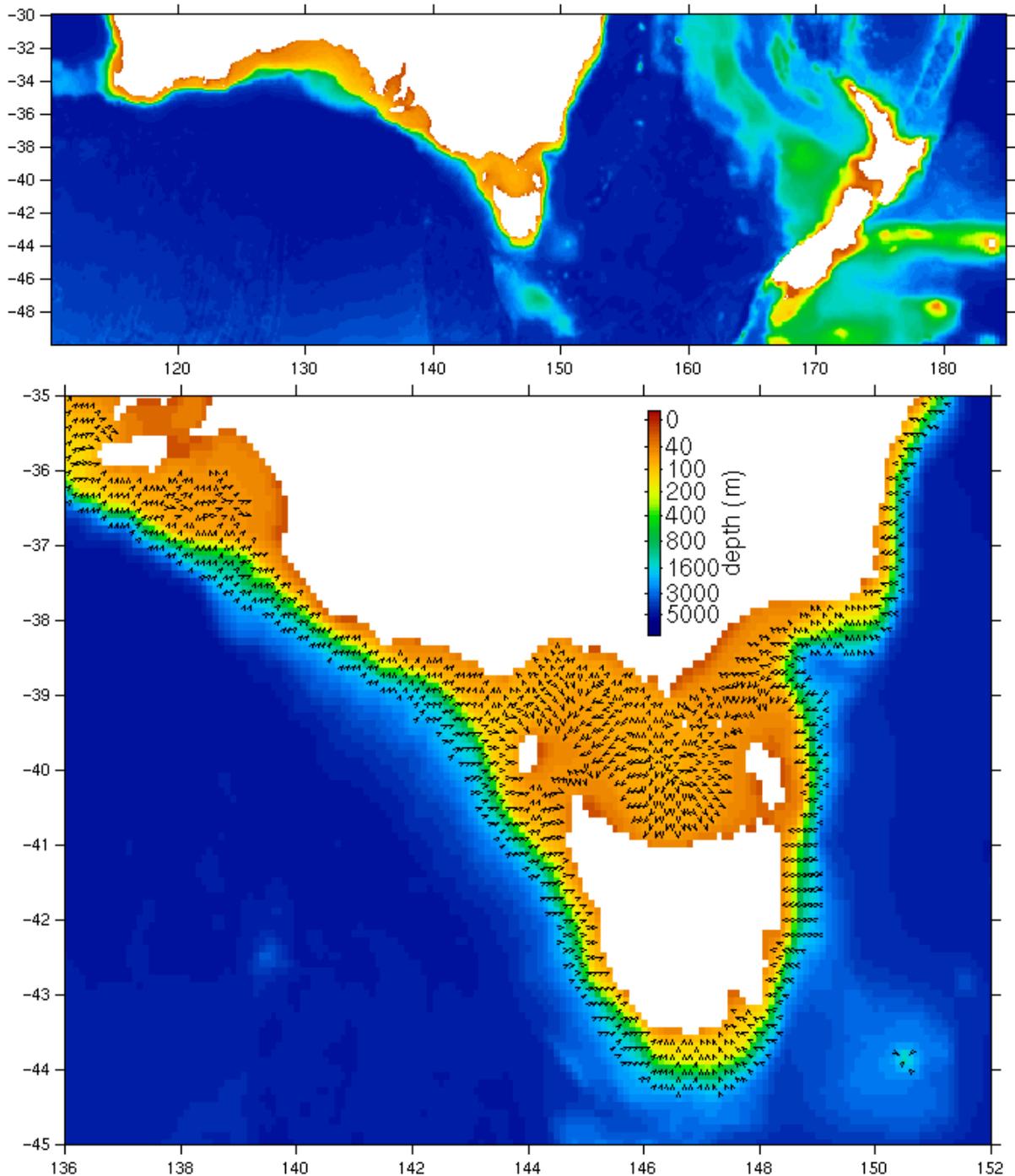
Running the hydrodynamic model was the biggest single job undertaken to date by the CSIRO-BoM NEC SX6 Supercomputer and took many months to run. For this reason, the larval transport model was run offline using stored daily outputs so that many experiments with various biological parameters could be performed. The complete archive of the daily-averaged fields of all model state variables occupies about six Terabytes of storage.

### *Bathymetry and 'depth effects'*

The bathymetry (Figure 5) in the model is based on a combination of data products from Geoscience Australia and the US Navy, with some alterations to prevent numerical problems. For example, the model requires a minimum of two layers everywhere. As the vertical resolution is comprised of 10 m layers in the upper 200 m, the water depth near the coast must be at least 20 m (i.e. two x 10 m layers), and gaps between islands must be at least two cells (i.e. 2 x ~11 km = ~22 km) wide. Depths greater than 5000 m are truncated at 5000 m.

For computational efficiency, and recognising that the vertical positions of larvae are certainly not known to fully exploit the 10 m vertical resolution of the model, layer-averages of the model's velocity and temperature fields were computed, for just the depth ranges assumed to be occupied by the larvae (Figure 4). A subtlety of this calculation is that the velocities in the bottom-most layer are reduced by 30% and rotated 45° to the right in recognition of the fact that the bottom Ekman layer is under-represented in the model. To deal with the situation of larvae that are in water too shallow for them to complete a full diel migration, the layer-averaging computation uses the bottom-most values of velocity and temperature where required.

A major disadvantage of the satellite-derived ocean currents used in the earlier studies is that the geostrophic approximation, that is the basis on which velocity is determined from sealevel, breaks down in shallow water. The result is that the onshore component of velocity is greater than it is in reality, leading to larvae being cast ashore ('beached') in places where the real current might simply turn to flow alongshore. The same issue sometimes arises when using the currents estimated by the Bluelink model but to a much lesser extent because current velocities are constrained properly by the coastline. When it does occur, beaching of larvae is reduced by returning phyllosoma-stage larvae downslope if they enter water less than 50 m deep. If beaching persists, the larvae are tagged as dead.

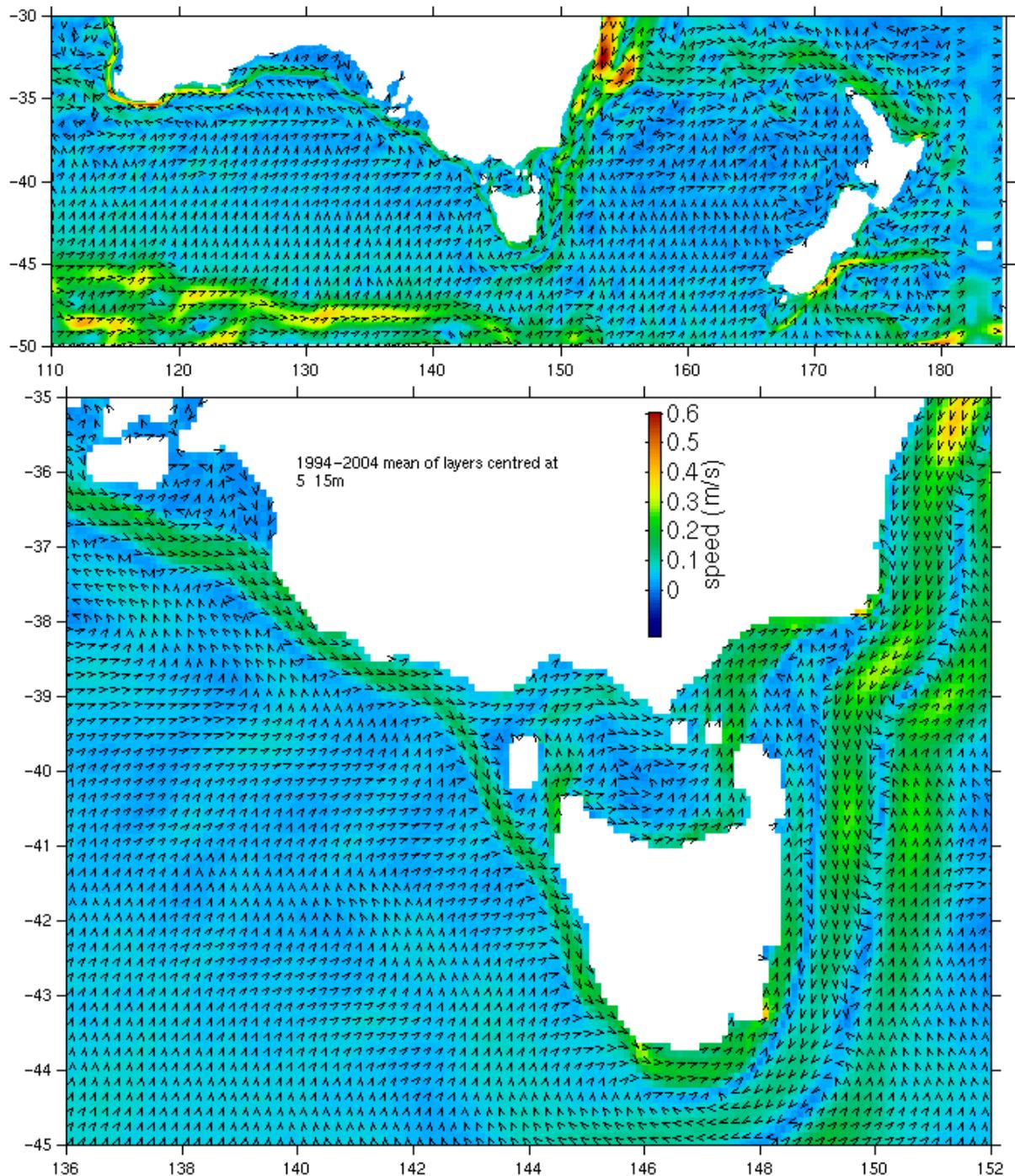


**Figure 5. Model bathymetry for the whole domain of the larval transport simulations (top), and for the SA-Tas region (bottom). Black arrow heads show the local upslope directions between the isobaths triggering metamorphosis (2000 m) and settlement of puerulus (50 m).**

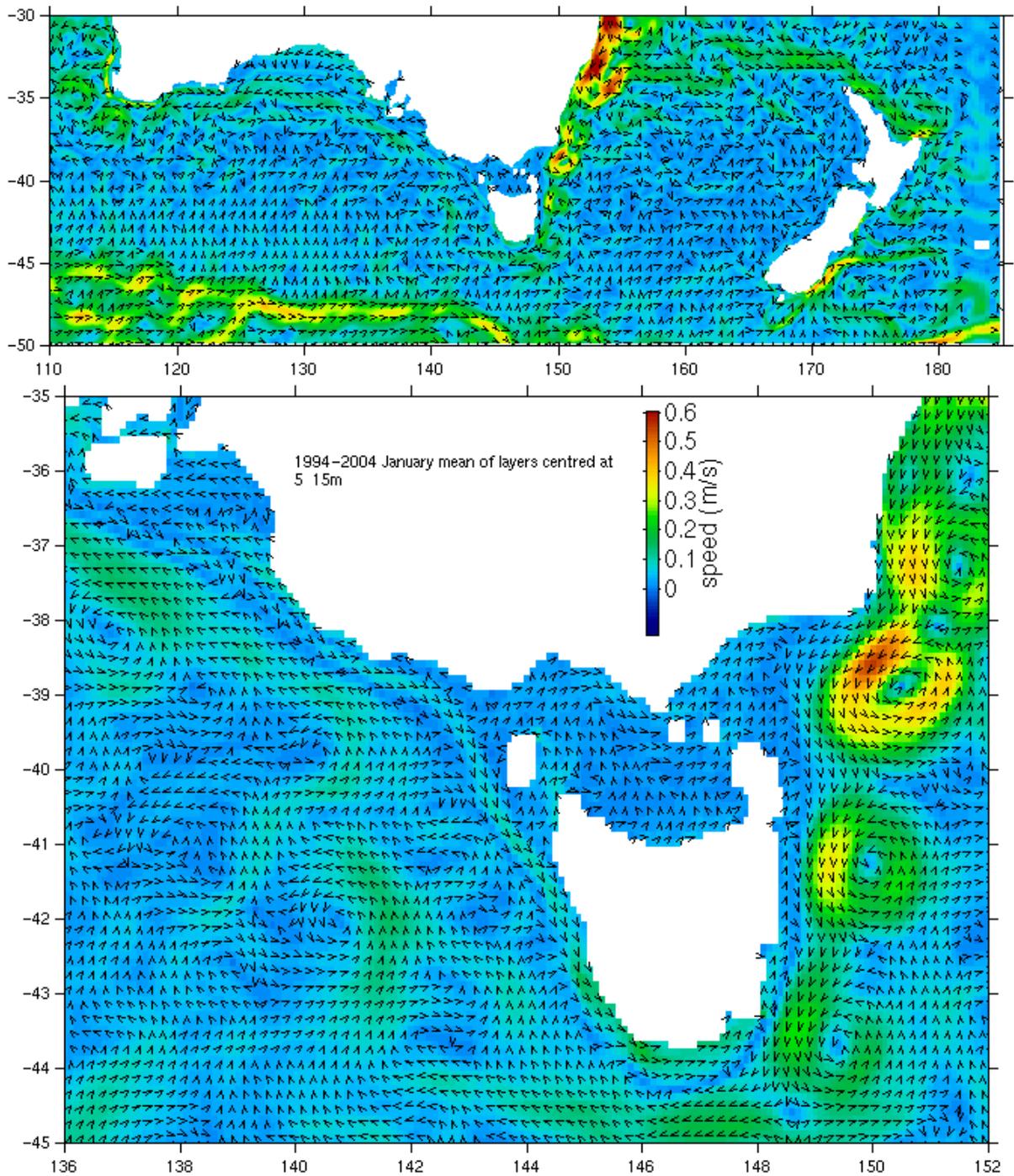
### *Ocean currents and temperatures*

A major difference between the present study and modelling larval transport off WA (Griffin *et al.* 2001) is the relative importance of the mean flow (Figure 6) and seasonal variations (Figures 7 and 8) in zonal (along-shelf) current velocities in southern Australia, compared with the influence of eddies (Figure 9) on the west and east coasts. The Leeuwin Current is second only to the East Australian Current, in Australian waters, with respect to the strength of its eddy field. These eddies are sufficiently energetic to generate velocities typically 10 times those of the mean geostrophic field and are thus dominant features of the circulation. However, in the SRL study region and, particularly for waters of the Great Australian Bight, the eddy field is much weaker, the result being that the mean

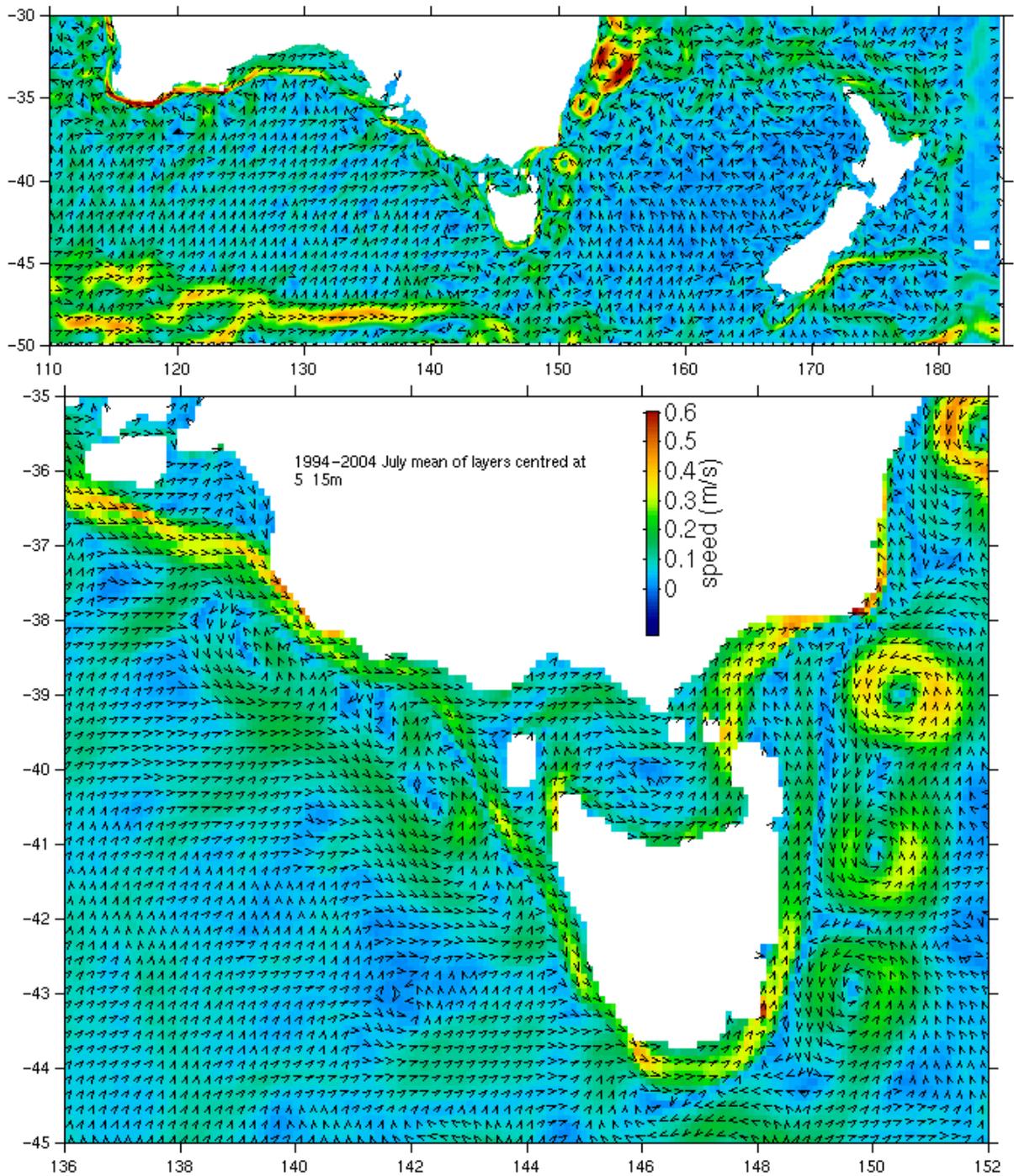
geostrophic field forms a more important component in simulating circulation dynamics in the area. The uncertainties in estimating the mean flow were the reasons why the results of initial attempts to apply the WA rock lobster larval transport model to SRL by Bestley (2001) were limited compared to what we have now achieved in this project.



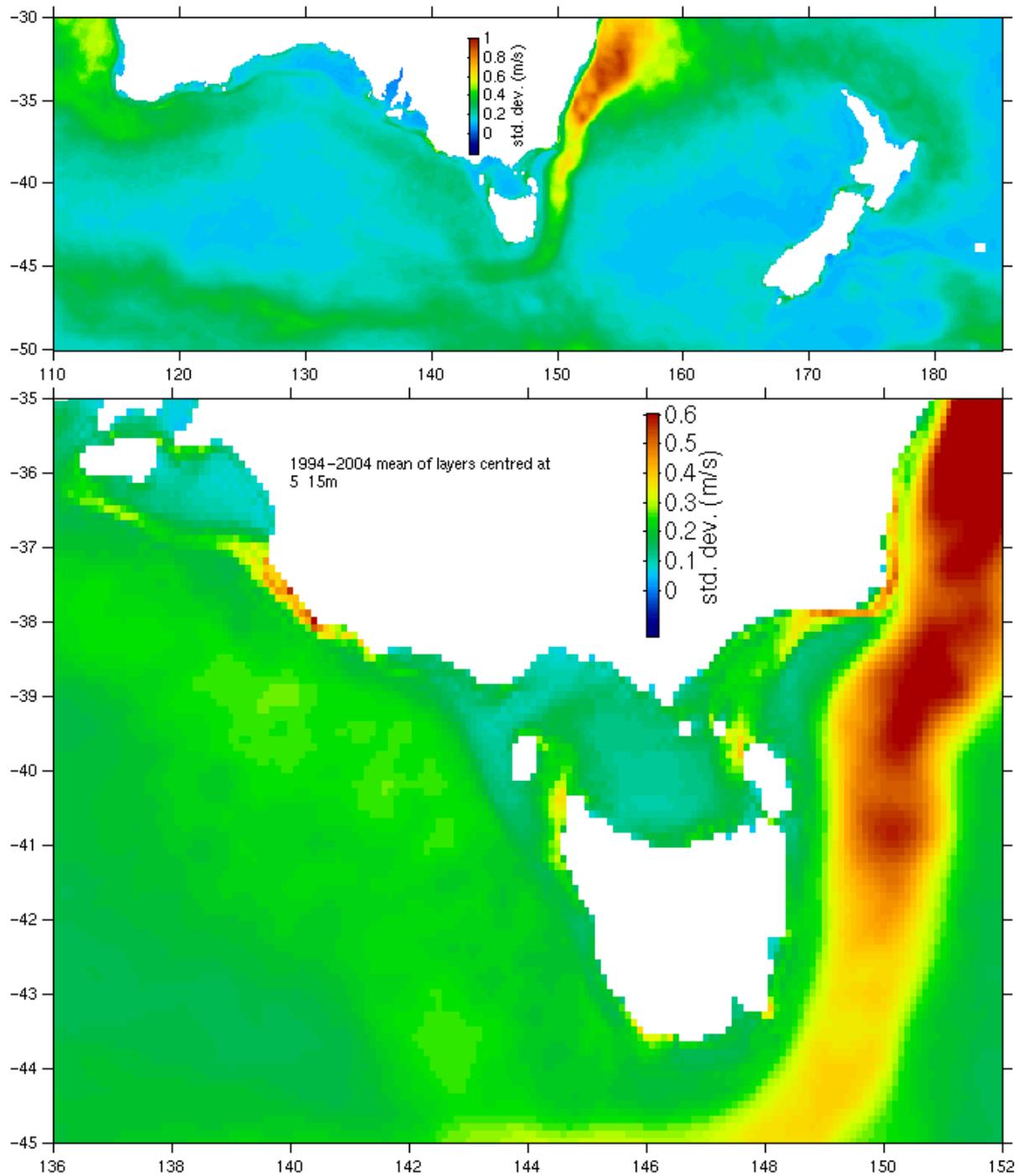
**Figure 6.** The model's estimate of the magnitude (see scale) and direction (arrow heads) of the 1994-2004 vector mean flow velocity in the upper 20 m. The seasonal flow of the South Australian Current across the GAB dominates the annual mean near the shelf edge in this region. This flow appears as a continuation of the Leewin Current extending from WA and with the Zeehan current along the west and southern coasts of Tasmania. The bottom figure provides more detail of the average annual mean flow in the south-east region including the estimated mean path of EAC derived eddies and the overflow of EAC water south and west of Tasmania.



**Figure 7. The model's estimate of the magnitude (see scale) and direction (arrow heads) of the summer (January) vector mean flow velocity in the upper 20 m. The SAC is weak and shelf flows in the South Australian region become north-westward.**



**Figure 8.** The model's estimate of the magnitude (see scale) and direction (arrow heads) of the winter (July) vector mean flow velocity in the upper 20 m. The strength of the SAC is obvious along the shelf edge across the GAB and extends into the Zeehan Current off western Tasmania (see inset).



**Figure 9.** The model's estimate of the 1994-2004 standard deviation of the flow velocity in the upper 20 m. Note the influence of energetic flows (i.e. larger standard deviations) and in particular that of the eddy fields off eastern and Western Australia compared to the less energetic regions of much of southern Australia.

## RESULTS + DISCUSSION

This section is structured in the following manner. Outputs from the larval transport model are firstly compared and discussed with respect to known field data on larval development, distribution and puerulus settlement. We then describe and discuss the trajectories of modelled larvae to examine the connectivity of regions across southern Australia and the contribution to recruitment provided by different zones in the fishery. We have chosen, for expediency and to reduce the complexity of the report, to focus on the outputs of the final model runs. The larval transport model evolved through the establishment of over 120 separate experimental runs and describing each in turn is unwarranted in the context of this report. We do, however, present details of the sensitivity of selected parameters to test the veracity and robustness of model predictions.

The performance of the Bluelink hydrodynamic model with respect to its skill in reproducing known circulation features and time-specific events is briefly reviewed in Appendix C. A more detailed analysis of the Bluelink model is currently being performed as part of the Bluelink project and will be reported elsewhere.

### Comparisons of larval transport model predictions to empirical data sets

The veracity of the larval transport model was tested by comparing several model outputs to available empirical (field) data sets, specifically, the observed:

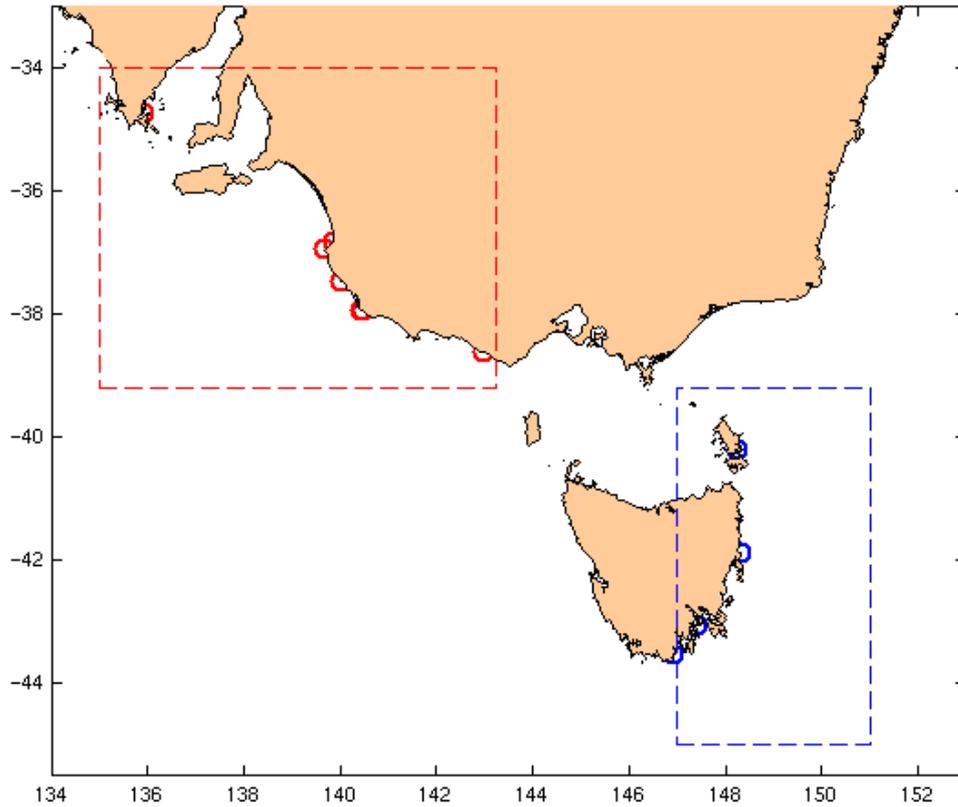
- seasonal occurrence of phyllosoma stages;
- timing of puerulus settlement over a ‘standard’ year;
- seasonal and interannual rates of settlement over the period 1993-2004;
- spatial distribution of phyllosoma across southern Australia and the Tasman Sea;

### **Sensitivity analyses – growth parameters**

The temperature-dependence of growth used in the model is based on data from laboratory experiments and we refer to model results using these growth parameters as ‘*standard growth runs*’. As we had no *a-priori* knowledge of how accurately these data reflected growth in the wild, we also ran the larval transport model using a 20% faster and a 20% slower growth parameter than predicted from the laboratory data. We refer to these as ‘*fast growth runs*’ and ‘*slow growth runs*’ respectively. The outputs of all three (fast, standard and slow) model runs were compared to field data in order to assess the most appropriate choice of growth parameter. These comparisons are detailed below.

### **Seasonal occurrence of phyllosoma stages**

To test if the modelled progression of larvae through their 11 phyllosoma stages agreed with the field data compiled by Bruce *et al.* (2000), we computed, for both model and field observations, the average and range of the day-numbers on which larval stages were present. This analysis was performed for the region off eastern Tasmania delineated by the blue box in Figure 10. This region was chosen because it delineated the area from where most of the data in Bruce *et al.* (2000) originated. Model data from a second region, off South Australia – see the red box in Figure 10, was also analysed but there were too few field data from that region to make a similar comparison. We explore the differences between the model outputs for these two areas to examine the regional impact of temperature differences on stage progression predicted by the model. These two regions are also used to compare modelled and observed patterns of puerulus settlement in a subsequent section.



**Figure 10: Areas used for comparison between field data (larval stage progression + puerulus settlement data) and model outputs. Open semi-circles on the coast give the locations of puerulus collectors used for settlement comparisons.**

For the field data of Bruce *et al.* (2000), we used only those net samples in which *J. edwardsii* larvae were found, and computed, for each stage, the average day-number ( $\bar{D}$ ) as follows:

$$\bar{D} = \sum_j (n.d) / \sum_j (n) \quad (2)$$

where  $n$  is the density (number of phyllosomata per volume filtered) and  $d$  the day-number of capture. The day-number of capture is modified following Bruce *et al.* (2000) to separate the multiple cohorts of larvae that are observed in the water at any one time. However, in this case, we have used day-number starting 1 January of the year of hatching rather than the linear-day conversion of Bruce *et al.* (2000). Most hatching of *J. edwardsii* occurs in the latter months of a calendar year (i.e. September – December = Julian days 270-365). For our purposes then, the day-number of a stage 1 larva captured on 1 November is 305 but for one caught on 1 January, the day-number is 1+365=366. Late stage phyllosomata (e.g. Stage 10) caught on 1 January that could not have come from the previous spring-early summer hatching are assigned day number 365+365 +1 = 731. Note that estimated ‘true’ age (or linear day age) would require subtracting the Julian day number of hatching. Naturally this is unknown for each individual larva in the field. Bruce *et al.* (2000) used Julian day-number 280 as day 1 for purposes of calculating linear (or estimated ‘true’) age as this was the day number when stage 1 larvae first appeared in large numbers in field sampling. Thus the linear day-number (estimated true age) of a stage 1 phyllosoma on day-number 305, using the methodology of Bruce *et al.* (2000) would be 305-280 = 25 d. By equivalent calculations, the estimated true age of a stage 5 phyllosoma on day-number 450 would be 450-280 = 170 d.

The data of Bruce *et al.* (2000) is based on sampling effort that was very unevenly distributed throughout the year, so our estimates of  $\bar{D}$  almost certainly include errors for stages that occur in months of little or no sampling. To reduce the effects of this uneven sampling intensity,  $n$  and  $d$  in equation (2) are averages of the individual field sample data within 10 d wide ‘bins’.

For the model data, the actual hatching date of each larva is known so there is no uncertainty of its age as there is with the field data. However, for consistency of approach, we estimate  $\check{D}$  for the model larvae (rather than average age), by finding, for all the model larvae within the region of interest, the average and range of the day-number on which the larva is half way through each stage.

### ***Model outputs***

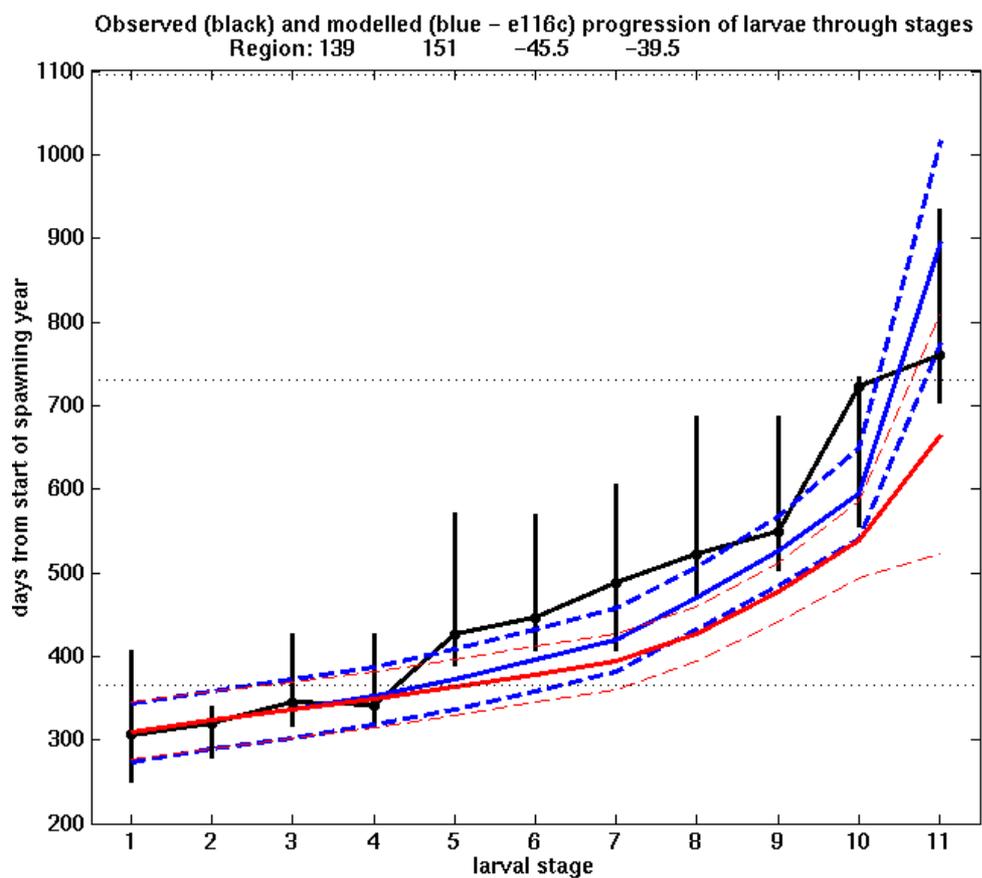
Results are presented for each of the model runs (fast, standard, slow growth) and are displayed in two graphical formats. First, the progression of stage is plotted against total day-number (after spawning). These plots show the model predictions for both eastern Tasmania and South Australia, and compare them to the field data from eastern Tasmania. The second plot shows the occurrence and normalised abundance of each larval stage over an annual cycle (a calendar year). In this latter case, for simplicity, the model predictions and field data are only plotted for Tasmania.

### ***Fast growth run***

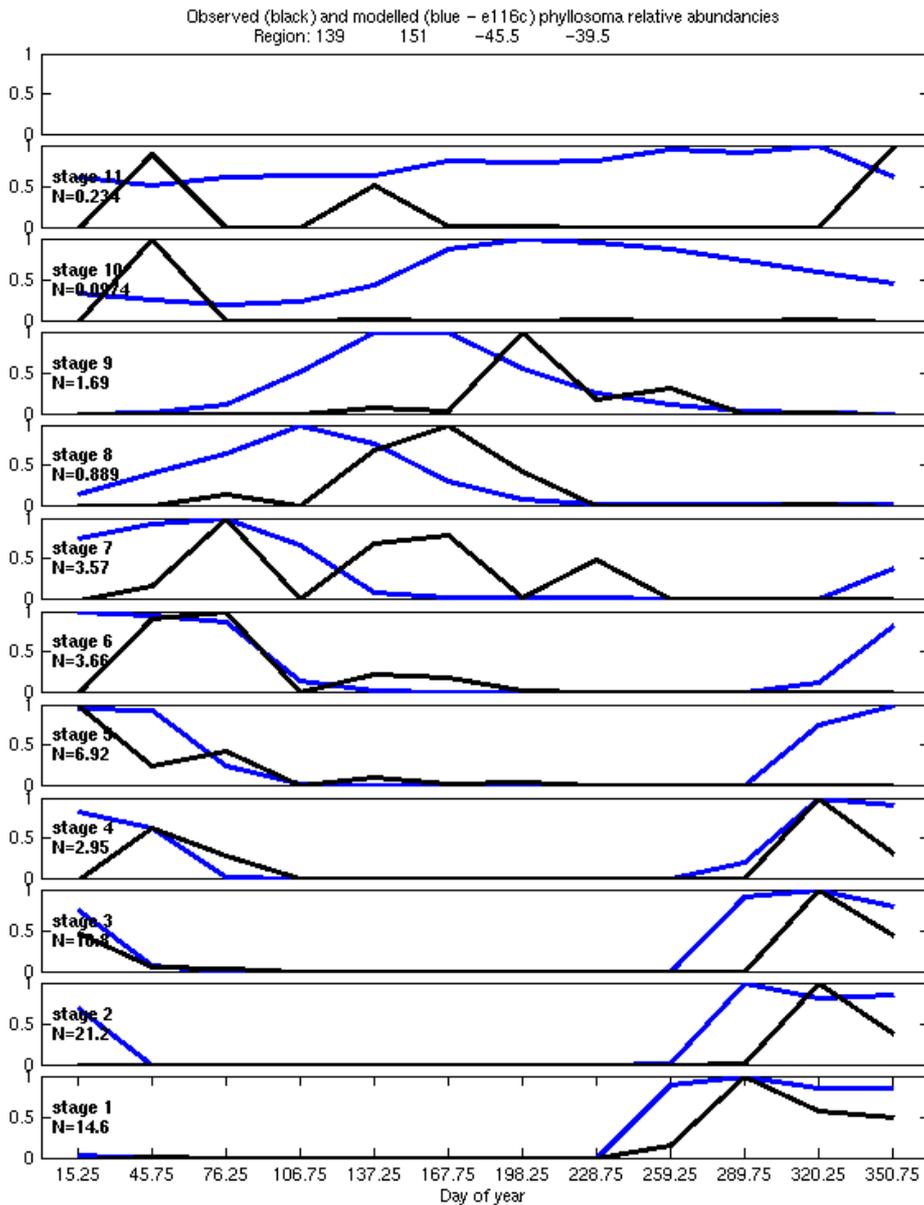
Model predictions from the fast growth run agree with observed data for stages 1 to 4 (Figure 11). The model predictions deviate from observed for stages 5 to 8, the model larvae being more advanced than is observed. Model stages 9 to 11 are largely within the range of field data, although the model may be slightly under-estimating growth rate by stage 10/11. Modelled stage 10/11 phyllosomata are present in the water column from January to October, covering much of the observed settlement period in Tasmania.

Model predictions indicate that larvae grow at a more rapid rate in SA waters. Modelled stage 10/11 phyllosomata are present in the water column from June, just prior to the main observed winter settlement period in that region.

Examining stages over a calendar year (Figure 12) suggest a similar pattern. The predicted temporal occurrence of stages matches the Tasmanian observations for stages 1 to 4. The model's predictions for the occurrence of stages 5 to 8 in the field is earlier than observed. However, the timing of late stage larvae is similar between predicted and observed, due obviously to the presence of late stage larvae at nearly all times of the year.



**Figure 11: Fast growth - modelled versus observed seasonal occurrence of phyllosoma stages. Black = observed field data from Bruce *et al.* (2000) – points are the average, vertical bars indicate range. Blue = model predictions (solid line = average and range boundaries marked by dashed lines) for the eastern Tasmanian region denoted by the blue box in Figure 10; red = model predictions (solid line = average and range boundaries marked by dashed lines) for the South Australia region denoted by the red box in Figure 10. Dotted horizontal lines denote the start of calendar years (i.e. 1 January).**

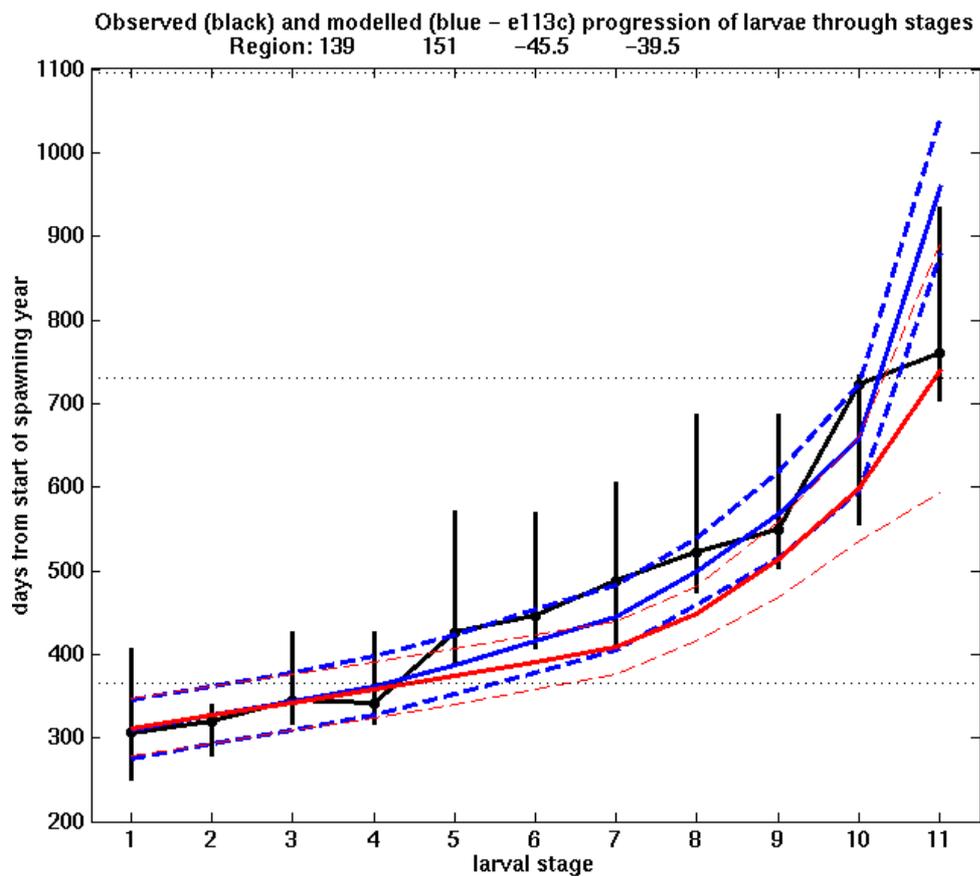


**Figure 12: Fast growth model – progression of modelled and observed phyllosoma stages over a calendar year. Black = normalised abundance of phyllosoma (observed) from Bruce *et al.* (2000). Blue = predicted.**

### *Standard growth run*

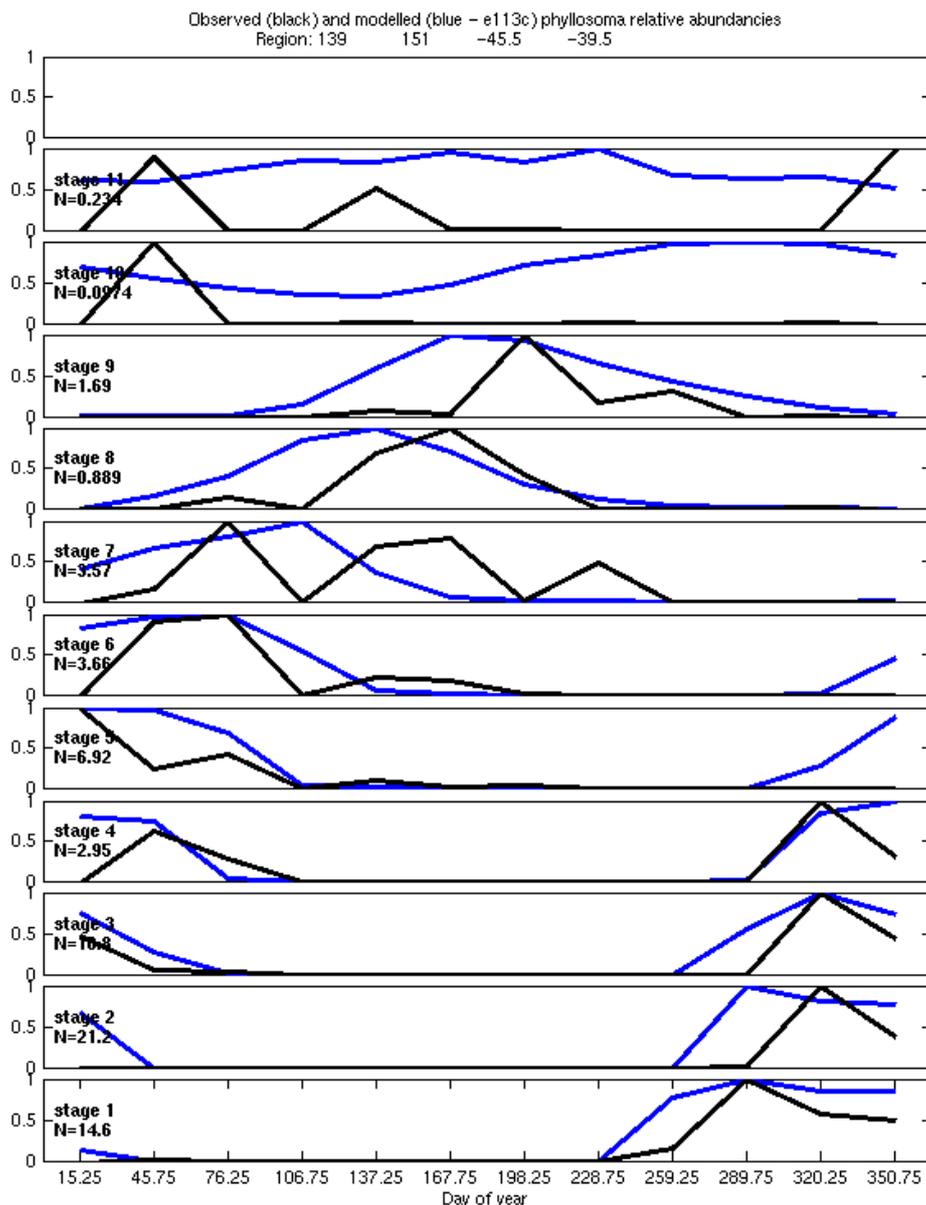
Model predictions from the standard growth run agree with observed data from most stages, particularly 1 to 4 (Figure 13). The model suggests a slightly faster growth for stages 5 and 6, but predictions remain largely within the range of observed data for stages 7 and 8. Model stages 9 to 10/11 fall within the range of field data, although the model may again slightly under-estimate growth rate by stage 11. Modelled stage 11 phyllosomata are present in the water column from May to November, covering the winter-spring settlement period in Tasmania.

Model predictions indicate that larvae grow at a more rapid rate in SA waters. Modelled stage 10/11 phyllosomata are present in the water column from August matching the commencement of the peak settlement period in that region. However, the model predicts that the supply of stage 10/11 larvae is centred in the summer which does not conform with settlement observations.



**Figure 13: Standard growth - modelled versus observed seasonal occurrence of phyllosoma stages. Black = observed field data from Bruce *et al.* (2000) – points are the average, vertical bars indicate range. Blue = model predictions (solid line = average and range boundaries marked by dashed lines) for the eastern Tasmanian region denoted by the blue box in Figure 10; red = model predictions (solid line = average and range boundaries marked by dashed lines) for the South Australia region denoted by the red box in Figure 10. Dotted horizontal lines denote the start of calendar years (i.e. 1 January).**

Examining stages over a calendar year (Figure 14) again suggests a similar pattern. The predicted temporal occurrence of stages matches the Tasmanian observations for most stages. The exception being stage 7 where larvae are observed in the water column at later dates than that predicted.

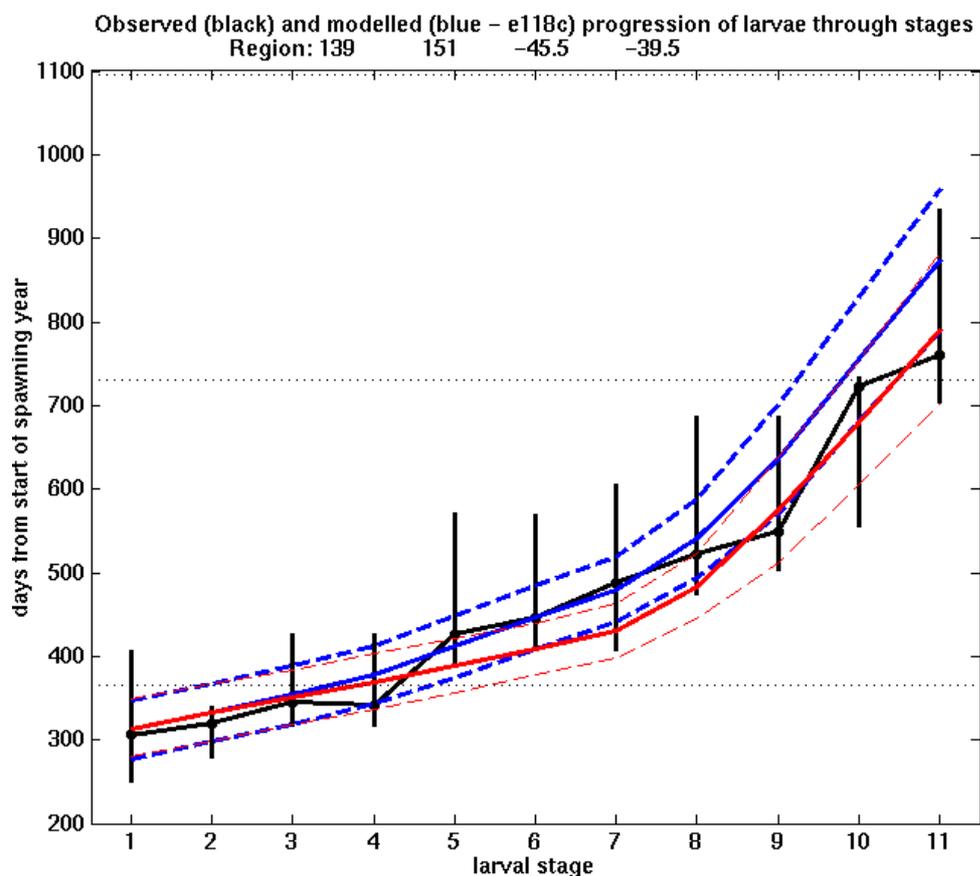


**Figure 14: Standard growth model – progression of modelled and observed phyllosoma stages over a calendar year. Black = normalised abundance of phyllosoma (observed) from Bruce *et al.* (2000). Blue = predicted.**

### *Slow growth run*

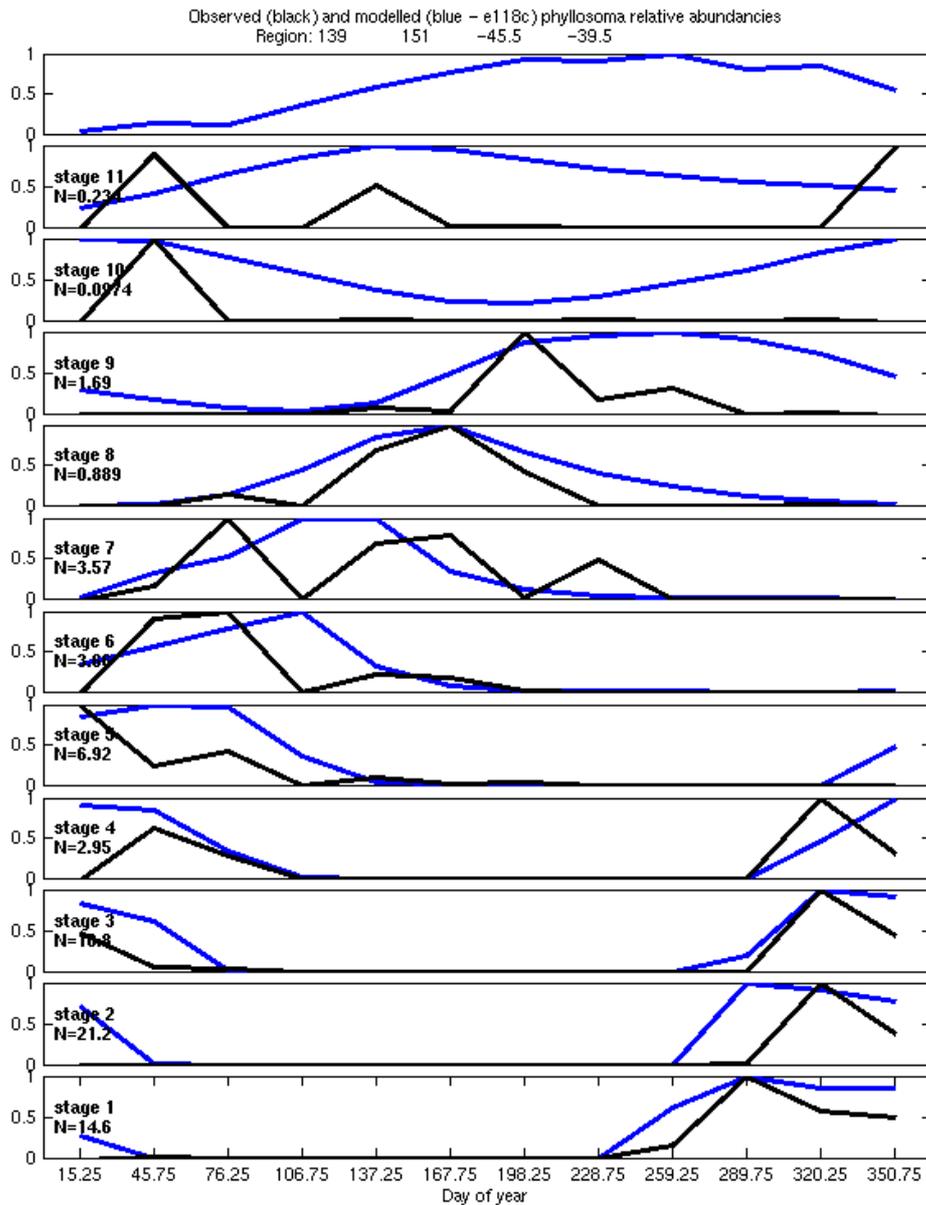
The slow growth run predictions agree with observed data for stages 5 to 8 (Figure 15). Model stages 1 to 4 are growing, on average, slower than observed but still fall largely within their range. The model deviates from the observed data for late stage larvae with model stages 10/11 in particular growing much slower than that observed. Modelled stage 11 phyllosomata are present in the water column from March to September, which coincides with the period of highest observed settlement period in Tasmania.

Model predictions indicate that larvae grow at a more rapid rate in SA waters. Modelled stage 11 phyllosomata are present in the water column from December to May which places them out of phase with the peak settlement period in that region.



**Figure 15: Slow growth - modelled verses observed seasonal occurrence of phyllosoma stages. Black = observed field data from Bruce *et al.* (2000) – points are the average, vertical bars indicate range. Blue = model predictions (solid line = average and range boundaries marked by dashed lines) for the eastern Tasmanian region denoted by the blue box in Figure 10; red = model predictions (solid line = average and range boundaries marked by dashed lines) for the South Australia region denoted by the red box in Figure 10. Dotted horizontal lines denote the start of calendar years (i.e. 1 January).**

The predicted temporal occurrence of stages matches the Tasmanian observations for most stages, although stage 3 larvae are predicted to be present in the water column at dates later than observed (Figure 16).



**Figure 16: Slow growth model – progression of modelled and observed phyllosoma stages over a calendar year. Black = normalised abundance of phyllosoma (observed) from Bruce *et al.* (2000). Blue = predicted.**

### **Model comparisons**

The three model runs show subtle differences in their abilities to match the observed data. The main areas of disparity are in the models' abilities to balance the match between the mid-stage larvae (stages 5 to 9) and other stages. The slow growth run achieves the best fit with these mid-stages, but the predicted availability of immediately presettlement stage phyllosoma and puerulus is out of phase with that required for the timing of settlement for modelled larvae in South Australia.

The differences observed between the model predictions and observed data for mid-stage larvae may reflect their change in habitat. Early stage larvae (1 to 4) are found in shelf waters, whereas mid-stage phyllosomata (5 to 9) are almost exclusively found seaward of the shelf break (Booth and Phillips 1994, Bruce *et al.* 2000). Thus the transition between stages 4 and 5 sees a change in habitat from more productive shelf conditions to oligotrophic offshore waters. This may see a concomittal reduction in growth rate of some individuals that cannot be explained by our temperature-based growth model alone. Late stage phyllosomata are found closer to the shelf and slope (Chiswell and Booth 1999) where they may be again exposed to more productive waters and hence show an increase

in growth rate. It is thus possible that our use of a simple growth model may not be applicable to all stages and different growth parameters may be required at different times during the larval phase.

The fast growth run has the latest stages of phyllosomata available for settlement closest to the correct time of year, thus providing the best fit to the observed data. The timing of settlement is much better known than the occurrence of healthy mid-stage larvae, so we place more weight in model results that satisfy settlement observations. This will be further examined in the next section.

The model predicts that regional temperatures have a significant influence on growth rate of phyllosomata with SA 'sampled' larvae moving through their stages at a far more rapid rate than in Tasmanian waters.

A robust result common to each model is the presence of two cohorts of larvae in the water column throughout the year. Observations from individual field studies commonly describe the capture of two size ranges of *J. edwardsii* phyllosoma in plankton sampling. Chiswell and Booth (1999) identified two distinct size classes of phyllosoma off the east coast of New Zealand's North Island. Mid-stage larvae were presumed to be from the 1997 spawning and late-stage larvae/puerulus from the 1996 spawning. Off southern Australian waters, Booth and Ovenden (2000) recorded a similar bimodal range of sizes in the GAB, again attributing these to two annual cohorts. The most extensive study of *J. edwardsii* phyllosomata in Australian waters has been by Bruce *et al.* 2000. They analysed plankton samples taken over multiple years and seasons across southeastern Australia but concentrating in Tasmanian waters. Their data similarly identified two cohorts of phyllosoma at all times of the year. These data have led researchers to conclude that two cohorts are present in the water column at any one time, and taken together with the timing of settlement, to the corresponding conclusion that the pelagic larval duration of *J. edwardsii* can last in excess of 12 months and perhaps as long as 22-24 months (Booth 1994, Bruce *et al.* 2000).

The implications of these results with respect to total larval duration and settlement patterns are also discussed in subsequent sections.

## **Timing of puerulus settlement over a 'standard' year**

The timing of puerulus settlement predicted by the three growth model runs was compared to the observed data from puerulus collectors maintained by State-based researchers at the locations identified in Figure 10. Multiple collectors are maintained at each site and sampled approximately monthly (see Frusher *et al.* 1997 for details). For our purposes, we averaged the number of pueruli caught by month for all the individual collectors across sites within the egg production assessment areas identified in Figure 1. The sites combined for each area are identified in Figure 17. Data are plotted as the bi-monthly (60 d) running-mean for each area. In doing so we note that the 'efficiencies' of puerulus collectors are not equal, due to local effects (e.g. the presence of competing habitat, local hydrological effects) so it is not clear what weighting is appropriate when forming averages over several stations and collectors. In the absence of data to the contrary, we have thus chosen to weight them evenly. Accordingly, the plots in Figure 17 are normalized to be dimensionless indices, for the exclusive purpose of correlating the observed and modelled histories of puerulus settlement.

Naturally, we are unable to simulate specific site-based puerulus collectors within the larval transport model. In order to compare model outputs to the observed data, we count the number of model puerulus reaching the coast every day. To be consistent with the observations, we show the total count per month, summed along the stretch of coastline falling within each egg production assessment area and use these values for comparisons.

### **Observed settlement data**

One of the salient features of the observations is that the annual cycle of puerulus settlement (Figure 17) is distinctly different between the SA-King Island area, where settlement is predominantly in winter, and the Recherche Bay to Bicheno area, where settlement can be equally strong in summer and winter but also occurs in spring. It is important to note that in some cases, the average is very much influenced by a large settlement event that happened in a single year, as shown.

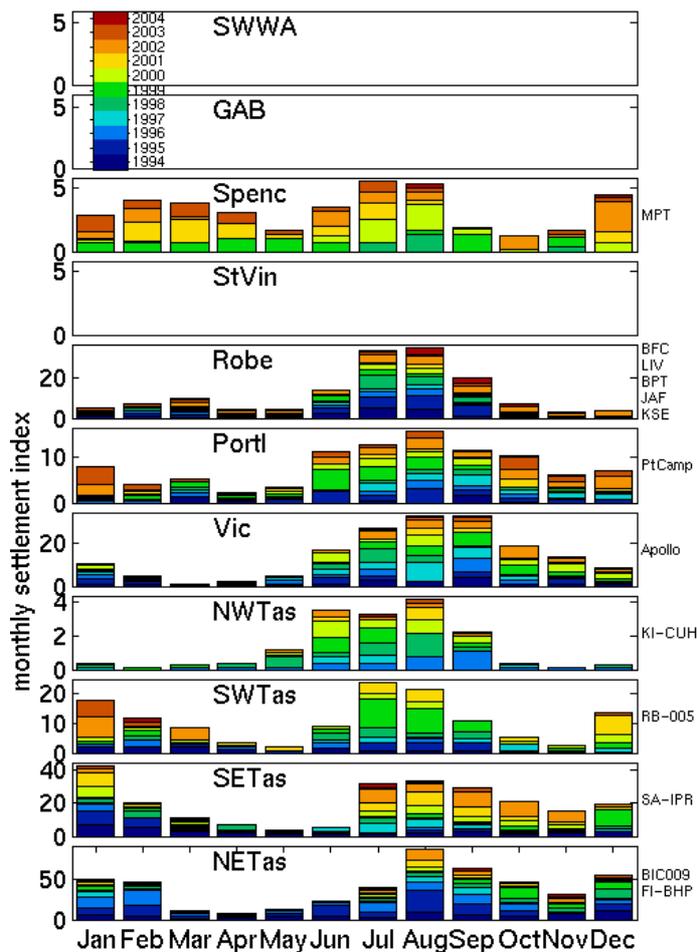


Figure 17. The combined annual cycle of observed rates of puerulus settlement aggregated by model zone (egg production assessment areas). State-maintained puerulus collector sites contributing data to each zone are identified on the right-hand side of the figure. South Australian collector sites: MPT – McLaren Point; BFC - Black Fellow’s Caves; LIV – Livingstons; BPT - Beachport; JAF - Cape Jaffa; KSE - Kingston SE. Victorian collector sites: Portl - Portland; Apollo - Apollo Bay. Tasmanian collector sites: Ki-CUH - King Island; RB-005 - Recherche Bay; SA-IPR - South Arm; BIC009 - Bichen; CFI-BHP – Flinders Island. Note that there are no collectors maintained in zones SWWA, GAB or StVin, hence, no data are shown. Contributions of individual years to the monthly averages are color-coded according to the key.

## Model outputs

### Fast growth run

The strong annual cycle of settlement predicted by the model agrees with field observations of a predominantly winter settlement for the South Australian to King Island (northwest Tasmanian) regions, shifting to summer and winter peaks or a pattern of more protracted settlement for the remainder of Tasmanian waters (Figure 18). However, the July to September peak in observed settlement is not as well predicted by the model for SE Tasmania. Puerulus settling in their first year after hatching dominate settlement during the winter peak in regions from Western Australia to northwest Tasmania. Year one puerulus contribute primarily to settlement in that latter half of the year in the remaining Tasmanian waters. Larvae in their second year after hatching contribute to summer or low level year-round settlement across all zones and are the source for mid and late-summer settlement peaks in Tasmanian waters.

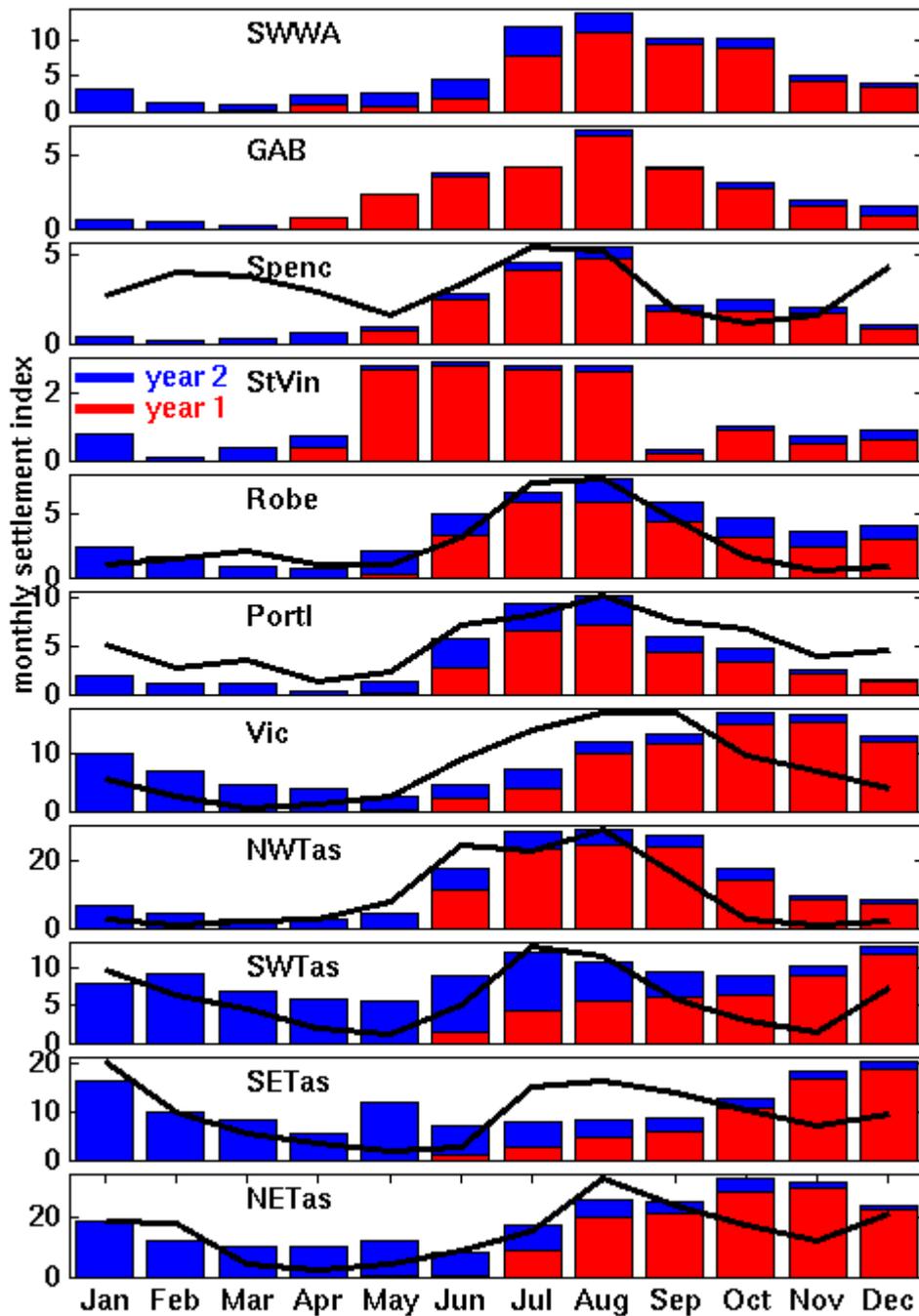


Figure 18: Fast growth – modelled verses observed annual pattern of combined puerulus settlement across egg production assessment zones. Note that there are no observed settlement data for SWWA, GAB and StVin. Model predictions include puerulus settling in their first (red) and second (blue) years post hatching. Observed data (black line) are a linear representation of Figure 17.

### Standard growth run

In contrast to the fast-growth model, the settlement pattern predicted by the standard growth model is poorly correlated with observed data for all zones with the exception of Portland (Figure 19). Predicted settlement peaks are too late for South Australian and northwest Tasmanian zones. The pattern predicted for remaining Tasmanian waters shifts to a more consistent year-round settlement. Puerulus settling in their first year after hatching dominate settlement during the latter months of the year across all zones. Puerulus settling in their second year after hatching dominate the first half of the year across all zones and to the majority of settlement in Tasmanian waters.

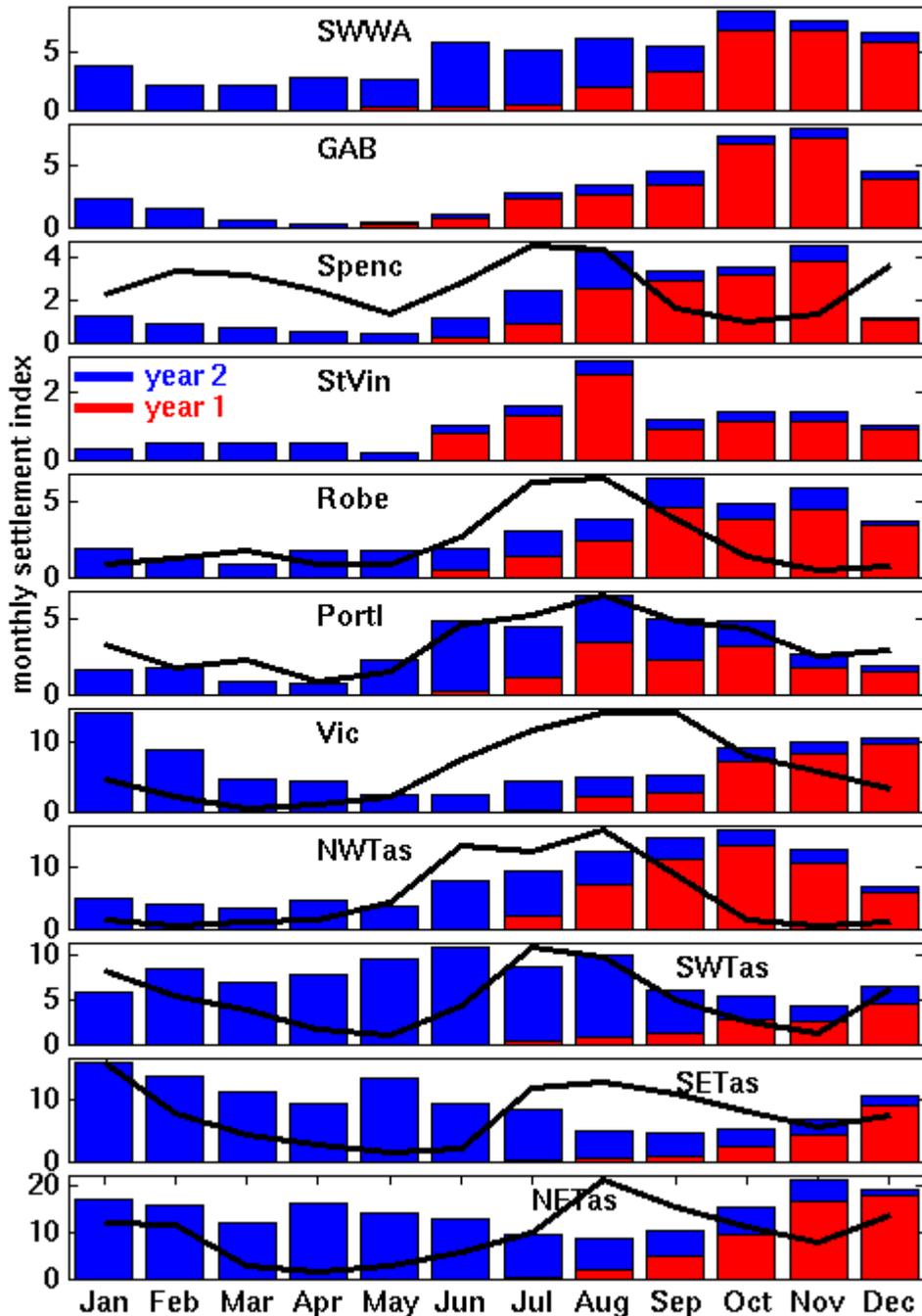


Figure 19: Standard growth – modelled verses observed annual pattern of combined puerulus settlement across egg production assessment zones. Note that there are no observed settlement data for SWWA, GAB and StVin. Model predictions include puerulus settling in their first (red) and second (blue) years post hatching. Observed data (black line) are a linear representation of Figure 17.

### Slow growth run

The settlement pattern predicted by the slow growth model is, like the standard growth model, poorly correlated with observed data for all zones, with the exception of perhaps Portland (Figure 20). Predicted settlement is more evenly distributed throughout the year in most zones with the loss of seasonal peaks. The pattern predicted for remaining Tasmanian waters shifts to a more consistent year-round settlement. There are very few model puerulus settling in their first year after hatching.

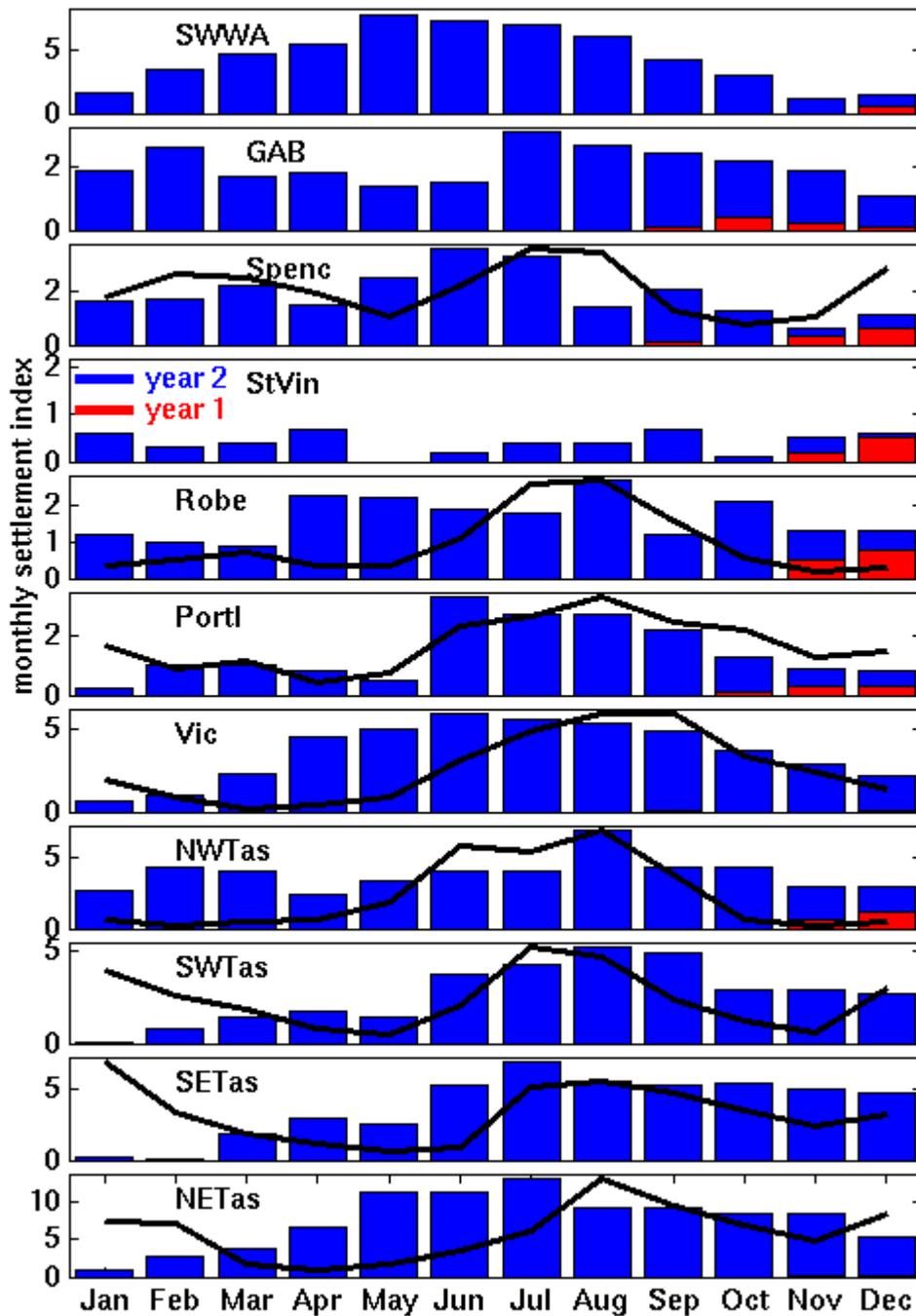


Figure 20: Slow growth – modelled verses observed annual pattern of combined puerulus settlement across egg production assessment zones. Note that there are no observed settlement data for SWWA, GAB and StVin. Model predictions include puerulus settling in their first (red) and second (blue) years post spawning. Observed data (black line) are a linear representation of Figure 17.

### Model comparisons

The three model runs provide very different predictions of puerulus settlement patterns across zones. Predicted settlement from the standard and slow growth model runs were poorly correlated with observed settlement patterns. Standard and slow growth runs tend to smear predicted settlement patterns throughout the year rather than providing concordance with the seasonal settlement cycle and its variation across regions. However, the fast growth run was largely consistent with observed patterns of settlement and captured the change in observed settlement patterns west and east of King Island.

Use of the different growth parameters, as expected, had a marked effect on the predicted contribution to settlement by puerulus in their first and second year after spawning. The fast growth model predicts that the winter settlement peak in South Australian waters largely comprises year one puerulus and that year two puerulus contribute to the more extended settlement periods in Tasmanian zones and the observed summer peaks in particular. Very few puerulus settle in their first year after spawning in the slow growth model.

We conclude from these comparisons that the fast growth model run provides the best overall fit to observed annual settlement patterns.

## **Seasonal and interannual rates of settlement over the period 1993-2004 and environmental correlates with settlement**

The skill of each model run was also tested by comparing the individual (as opposed to average) seasonal and interannual rates of predicted settlement to that observed within the same regions (South Australia and eastern Tasmania). The same puerulus collector data were used as in the above comparisons but plotted as a monthly time series for the period 1993-2004. The predicted data from each of the model runs are again the total count of settling puerulus per month, summed along the stretch of coastline falling within the two regions delineated in Figure 10.

We also explored correlations between settlement and environmental parameters that are generally considered relevant to larval transport and survival. Of these parameters, wind, depending on direction and strength, and the associated effects on circulation have been correlated or suggested as having significant influence on larval transport processes important to rock lobster settlement (Harris *et al.* 1988, Booth 1994, Caputi *et al.* 2001). Previous analyses by McGarvey and Mathews (2001) noted a correlation between August westerly winds and model-derived recruitment based on time series reconstructed from total annual catches of *J. edwardsii* in South Australia. So, we compared both observed settlement patterns and those predicted from the larval transport model to corresponding wind data in these analyses. Following the thesis of McGarvey and Mathews (2001), we compared settlement patterns to the relevant regional wind stress vector that would produce onshore transport of coastal waters (downwelling) and hence facilitate the onshore transport of pueruli. Ekman transport of surface waters is to the left of the wind direction in the Southern Hemisphere. Thus, for such downwelling to occur, wind direction must be alongshore (or close to it), with the coastline to the left of the dominant wind direction. We used data from the same two areas delineated in Figure 10 for these comparisons. Wind stress vectors (running-mean averaged over 25 days) were resolved relative to 120° (True) and 30° (True) respectively for South Australia and eastern Tasmania due to the different orientation of the two respective coastlines. Wind stress facilitating downwelling in these analyses is plotted as positive and that producing upwelling (transport away from the coast) is negative. Estimates of the daily-mean windstress were taken from the 'NCEP/NCAR 40-year reanalysis' (Kalnay *et al.* 1996) and averaged over the boxed regions delineated in Figure 10.

We compared other parameters to observed and predicted settlement patterns including sea surface temperature (SST), SST anomaly and Chlorophyll-a (the latter from SeaWiifs). However, to reduce the complexity of this report we have chosen only to present the wind comparisons here, as analyses of the other variables yielded no useful correlations. Details pertaining to these other variables are presented on the accompanying CD.

### **Observed settlement data**

Settlement of puerulus is highly seasonal in South Australia and occurs primarily in winter. However, smaller summer-autumn peaks sometimes occur and there can be a low level of settlement at most times of the year. Settlement in eastern Tasmania is highly variable and can occur at any time of the year. Winter-spring peaks are common but in some years, settlement can be equally strong during summer.

Significant differences in the magnitude of settlement occur between years. The most notable features of the interannual variability over the period are:

- 1) strong settlement in 1995 and 2002 in both eastern Tasmania and South Australia

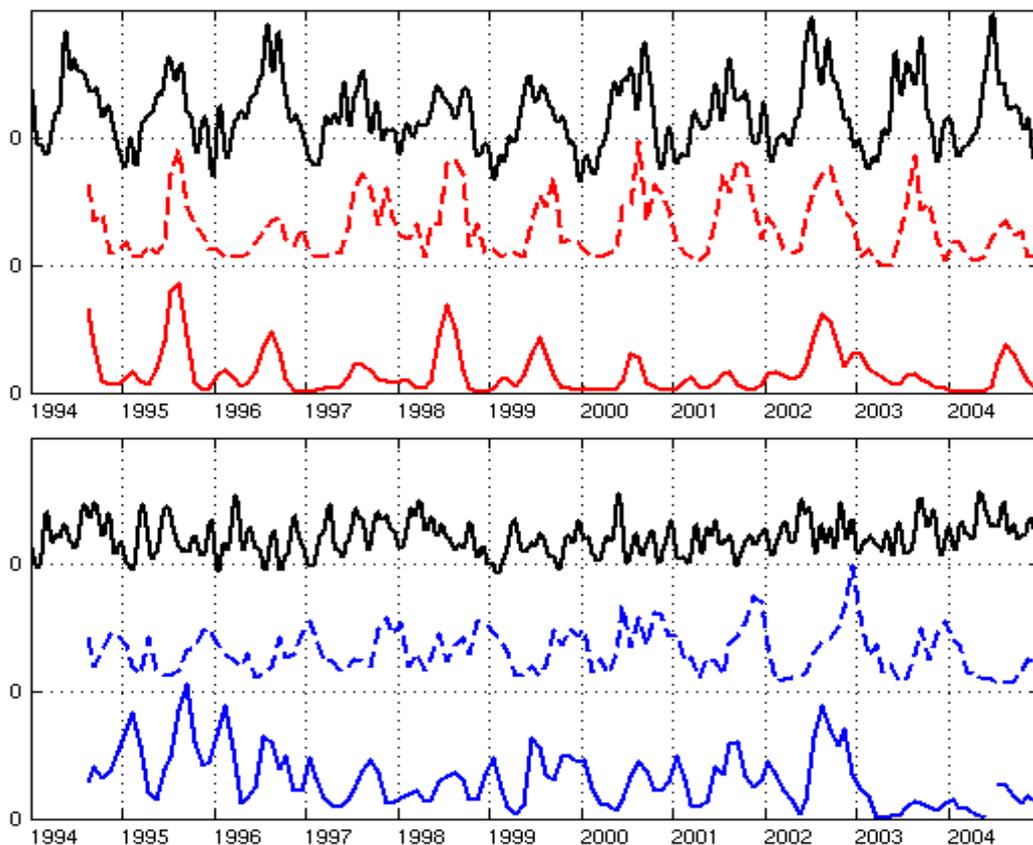
- 2) strong settlement in 1998 in South Australia only, and
- 3) weak settlement in 2003 and 2004 in both South Australia and eastern Tasmania.

## Model outputs

### Fast growth run

The strong annual cycle of predominantly winter settlement in South Australia is well captured over the time series (Figure 21). Interannual variability is less well captured by the model, although there are elements of similarity. The observed strong settlement in 1995 and lower settlement in 1996 are captured by the model but several subsequent years are also predicted with similar settlement levels to 1995, particularly for the years 1997 to 2003. These are not reflected in the observed data.

The strength and variability of the modelled annual cycle of settlement are similar to the observed patterns in eastern Tasmania. Settlement is less seasonal than in South Australia as observed. Modelled variance increases over the years, with settlement peaking in 2002 before dropping to a lower level in 2004, as do the observed data. The strong settlement events in 1995 and 1996 are not reproduced by the model.

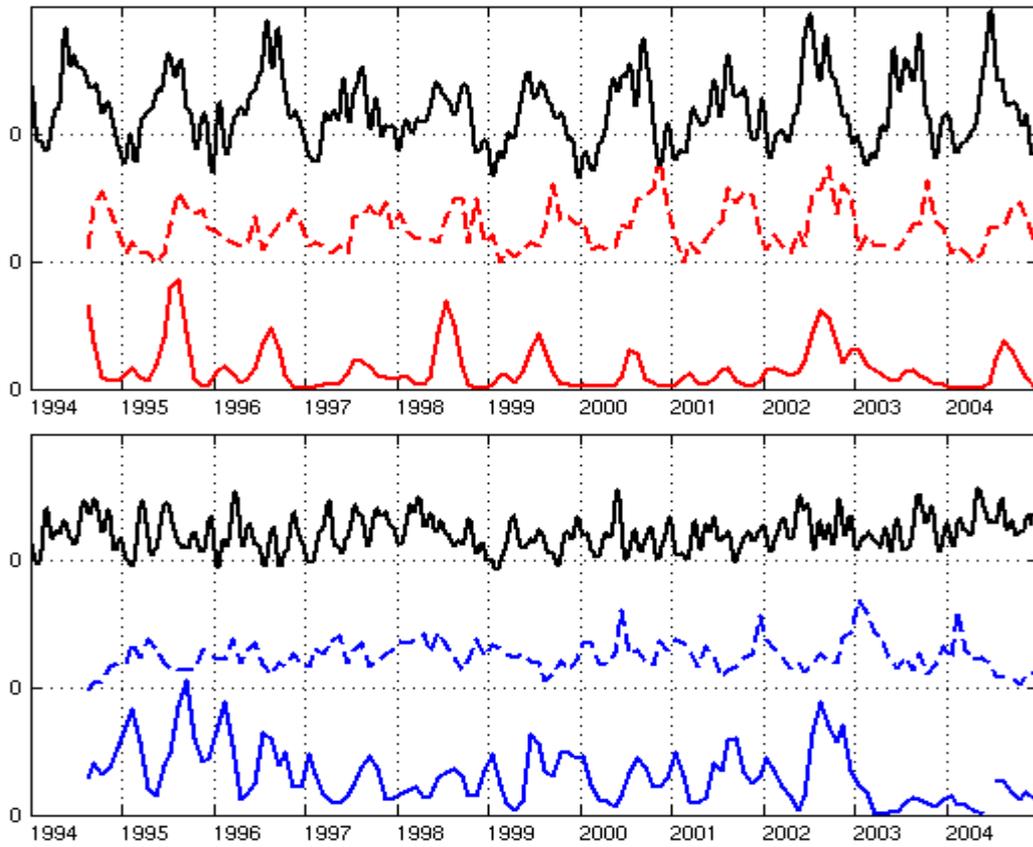


**Figure 21: Fast growth model run - comparison between observed (solid red/solid blue lines) and predicted (dotted red/dotted blue lines) puerulus settlement, and estimates of the corresponding regional mean windstress (black). Top panel: Red = data from South Australia; Bottom panel: Blue = data from eastern Tasmania – see Figure 10 for boundaries of areas compared. The daily-mean windstress values are taken from the 'NCEP/NCAR 40-year reanalysis' (Kalnay *et al.* 1996) – see text for details.**

### Standard growth run

Modelled and observed patterns of settlement over the period show little correlation (Figure 22). Seasonal peaks are present in the model's predictions for South Australia but shift more into spring and in some cases early summer and are thus starting to slip out of phase with observations. Predicted interannual differences in the strength of settlement are slight compared to observations.

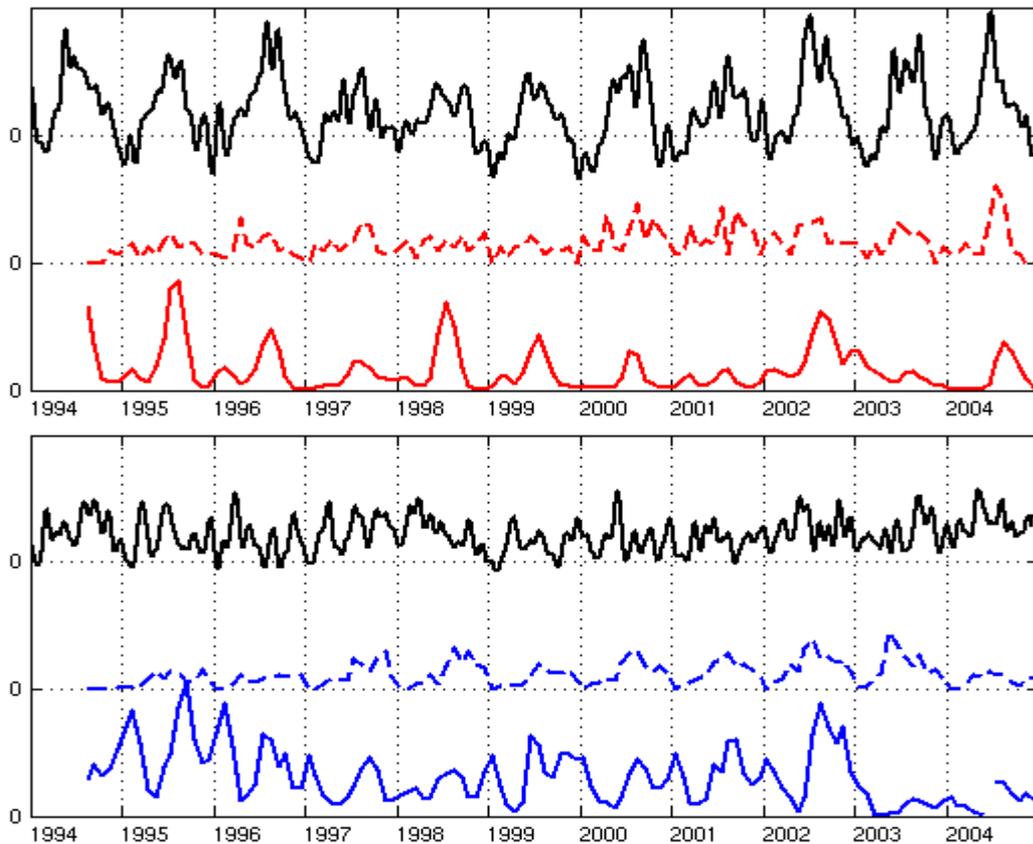
Similarly for eastern Tasmania, predicted settlement patterns show little correlation to observations in either timing or interannual variability.



**Figure 22: Standard growth model run - comparison between observed (solid red/solid blue lines) and predicted (dotted red/dotted blue lines) puerulus settlement, and estimates of the corresponding regional mean windstress (black). Top panel: Red = data from South Australia; Bottom panel: Blue = data from eastern Tasmania – see Figure 10 for boundaries of areas compared. The daily-mean windstress values are taken from the 'NCEP/NCAR 40-year reanalysis' (Kalnay *et al.* 1996) – see text for details.**

### *Slow growth run*

Modelled and observed patterns of settlement over the period show no resemblance to observed data for either South Australia or eastern Tasmania (Figure 23).



**Figure 23: Slow growth model run - comparison between observed (solid red/solid blue lines) and predicted (dotted red/dotted blue lines) puerulus settlement, and estimates of the corresponding regional mean windstress (black). Top panel: Red = data from South Australia; Bottom panel: Blue = data from eastern Tasmania – see Figure 10 for boundaries of areas compared. The daily-mean windstress values are taken from the 'NCEP/NCAR 40-year reanalysis' (Kalnay *et al.* 1996) – see text for details.**

### **Model comparisons**

The three model runs differ significantly in their skill at reproducing observed patterns of settlement. None of the models are able to reproduce all aspects of the observed interannual variability. The standard and slow growth model runs offer little overall skill. However, the fast growth run does considerably better with respect to the timing of settlement over the time series and the overall scale of variability over the time period, although it too fails to reproduce the magnitude of observed settlement in most years.

We conclude, from these comparisons that, although not a perfect fit, the fast growth model again provides the best fit to the observed data of the three model runs.

### **Wind data**

South Australia has a strong seasonal cycle of winds that favour downwelling in winter. This produces an onshore transport of surface waters that peaks in winter at the time of puerulus settlement. In summer, a weakening and occasional reversal of wind direction favours upwelling and offshore transport of surface waters. This seasonal pattern is consistent with the seasonal cycle of puerulus settlement. However, correlations between settlement magnitude and either observed or predicted settlement strength were poor. The 1998 peak settlement occurred in a year of relatively low windstress and the 2003 low in observed settlement occurred during a year of relatively high windstress. Thus it would appear that although the seasonal cycle in windstress may contribute to

winter settlement being more pronounced in SA, there is no simple relationship between this index of wind forcing, and either the modelled or observed interannual variability of puerulus settlement.

Eastern Tasmania has no strong annual cycle in downwelling favourable windstress. In fact, the windstress is favourable to onshore transport, albeit weaker than South Australia, at most times of the year. This may be the reason for a lower seasonal signal in settlement data compared to South Australia with settlement, recorded at all times of the year and a summer peak sometimes equal to or exceeding the level of winter settlement. However it also suggests that wind driven onshore transport alone is unlikely to be the primary cause of the observed significant seasonal and interannual settlement variability and that there are other contributory factors in this region.

Year-round settlement of puerulus recorded for Tasmanian, to a lesser extent in South Australian waters, and specifically summer-time settlement, can only occur if the larval stage of *J. edwardsii* is completed in  $\leq 3$  months or it can extend beyond 12 months duration. The former appears unlikely based on all available evidence from field sampling and rearing studies. This line of argument is thus supportive of the conclusion by Booth and Phillips (1999) and Bruce *et al.* (2000) that larval duration in *J. edwardsii* can exceed 12 months. This will be explored further below.

### **Overall conclusion regarding choice of model**

Comparisons of model runs using three different growth parameters suggest that outputs from the fast-growth model are the most consistent with available field data. The remaining sections of the report thus focus on using fast-growth model runs only. However, for completeness, outputs from the standard and slow-growth model runs are included on the accompanying CD.

## Spatial distribution of phyllosoma - southern Australia and the Tasman Sea

Modelled phyllosomata were largely restricted to within 600 to 1000 km of the coast over the period of their pelagic larval duration (Figure 24). This distribution is consistent with observations from field studies and various hypotheses regarding the distance offshore from which larvae may successfully return to coastal waters and settle. However, there have been insufficient, wide-ranging field surveys of larval abundance to adequately verify the model's large-scale picture of larval dispersal into the open ocean.

Bruce *et al.* (2000) recorded *J. edwardsii* phyllosoma up to 250 km east of Tasmania – the limit of their sampling, and reported on phyllosoma up to 500 km south of the GAB coast based on data from sampling by J. D. Booth, NIWA (see Booth and Ovenden 2000). Both zones fall within the model's prediction of larval distribution. Bruce *et al.* (2000) also reported phyllosomata to a distance of only 70 km south of Tasmania, despite sampling extending considerably further. The model predicts that significant numbers of phyllosoma should occur up to 500 km south of Tasmania (Figure 24). However, the sampling of Bruce *et al.* (2000) in this area was covered by a single cruise at these distances offshore and was largely restricted to surface tows with many taken during the day. It is thus unlikely that these field observations are indicative of the true extent of the distribution of *J. edwardsii* larvae in the area.

Booth and Ovenden (2000) reported finding *Jasus* larvae, and *J. edwardsii* in particular, within 1000 km of natal adult populations for different populations across much of the range of the genus in the Southern Hemisphere. Although they recognised that not all such larvae may successfully settle, they concluded that those eventually recruiting to benthic populations can still be transported 100s of km from shore during their larval duration. In studies off New Zealand's North Island, Booth *et al.* (1998) recorded *J. edwardsii* larvae up to 1300 km offshore.

This scale of offshore distribution for rock lobster phyllosoma is apparent for several other species and is generally considered to be a consistent aspect of this group's early life history (Dennis *et al.* 2001, Cobb 1997, Cobb *et al.* 1997, Phillips 1981).

Booth and Ovenden (2000) refer to *J. edwardsii* larvae occurring across the Tasman Sea which is also consistent with our model's predictions. The modelling work of Chiswell *et al.* (2003) also predicts that *J. edwardsii* larvae from Australian waters should be distributed across the Tasman Sea and concluded that there may be significant levels of settlement of these larvae along the west coast of New Zealand's South Island. Both studies corroborate the mitochondrial DNA data of Ovenden *et al.* (1992) which showed Australian and New Zealand populations of *J. edwardsii* to be genetically indistinguishable. Our model suggests that although such exchange is possible across the Tasman Sea, it is likely to occur at a much lower level than that predicted by Chiswell *et al.* (2003). Our modelled distributions of phyllosomata originating from Australia and New Zealand were often separated by a region of low overall abundance between 160° E and 165° E in the Tasman Sea (Figure 24). The results suggest that New Zealand larvae derived from spawning on the west coasts of the North and South Island are primarily confined to waters east of 160° - 165° E and within 500 kilometres of those coasts. The latter is the region where Booth and Ovenden (2000) recorded their *J. edwardsii* larvae during their Tasman Sea sampling.

These data thus suggest that the lack of a defined eddy field is not incompatible with *J. edwardsii* larvae being retained within a biologically reasonable distance from their source population for periods equal to or greater than their larval duration. It would appear that the mechanism may be the lack of advection in offshore waters west of the South Island facilitated by the low mean velocities in that area. This may provide an alternative mechanism facilitating the maintenance of *J. edwardsii* populations along the west coast of the South Island and is consistent with model predictions for much of southern Australia within the Great Australian Bight where, apart from shelf flows, currents and eddy fields are also weak.

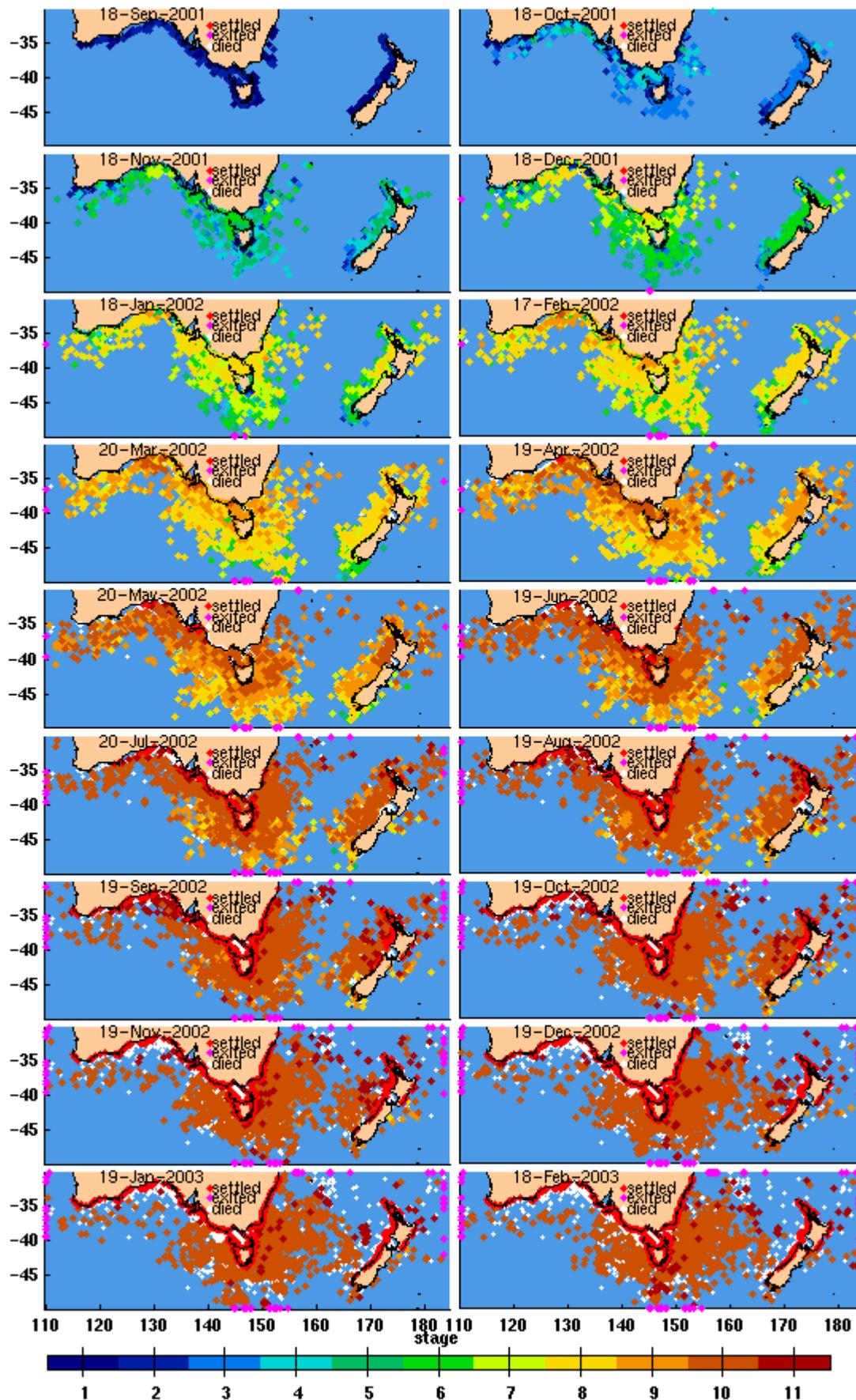


Figure 24. Distribution of phyllosoma stages from a single year-class (fast-growth model run) at 30-day intervals, starting 18 September 2001. Larvae are colour coded by developmental stage according to the above key.

## **Larval transport dynamics and regional connectivity of populations**

Model outputs allow us to examine the transport dynamics of phyllosomata and we do so in this section by first examining the overall transport of larvae originating from a single hatching period – in this case the 2001/02 season. The choice of this period was arbitrary as transport dynamics were largely similar between years. We then examine the trajectories of individual larvae for each egg production assessment area in turn. These outputs allow for an analysis of the regional connectivity of these areas and the population as a whole throughout southern Australia and across the Tasman Sea to New Zealand. Transport dynamics and the trajectories of larvae from all years are illustrated on the accompanying CD. The dependence of each assessment region on recruits derived from other regions is subsequently examined in an analysis of ‘source’ and ‘sink’ dynamics.

### ***Overall transport dynamics***

Larval distribution is initially restricted to shelf waters and, predictably, is restricted to areas adjacent to their origin of hatching (Figure 25). Larvae quickly disperse both alongshore and into offshore waters, particularly off southwest Western Australia, southeast South Australia and southeast Tasmania where shelf edge flows interact with cyclonic and anticyclonic eddies drawing water away from the shelf. Despite these dispersal patterns, there remains some regional integrity to the distribution of larvae. This is particularly prevalent in southwest Western Australia and the Great Australian Bight where the abundances of larvae natal to those areas dominate the adjacent offshore waters over the 18 month period featured. Mixing of larvae and loss of regional integrity in larval abundance is more prevalent between southeast South Australia, Tasmania and eastern Victoria.

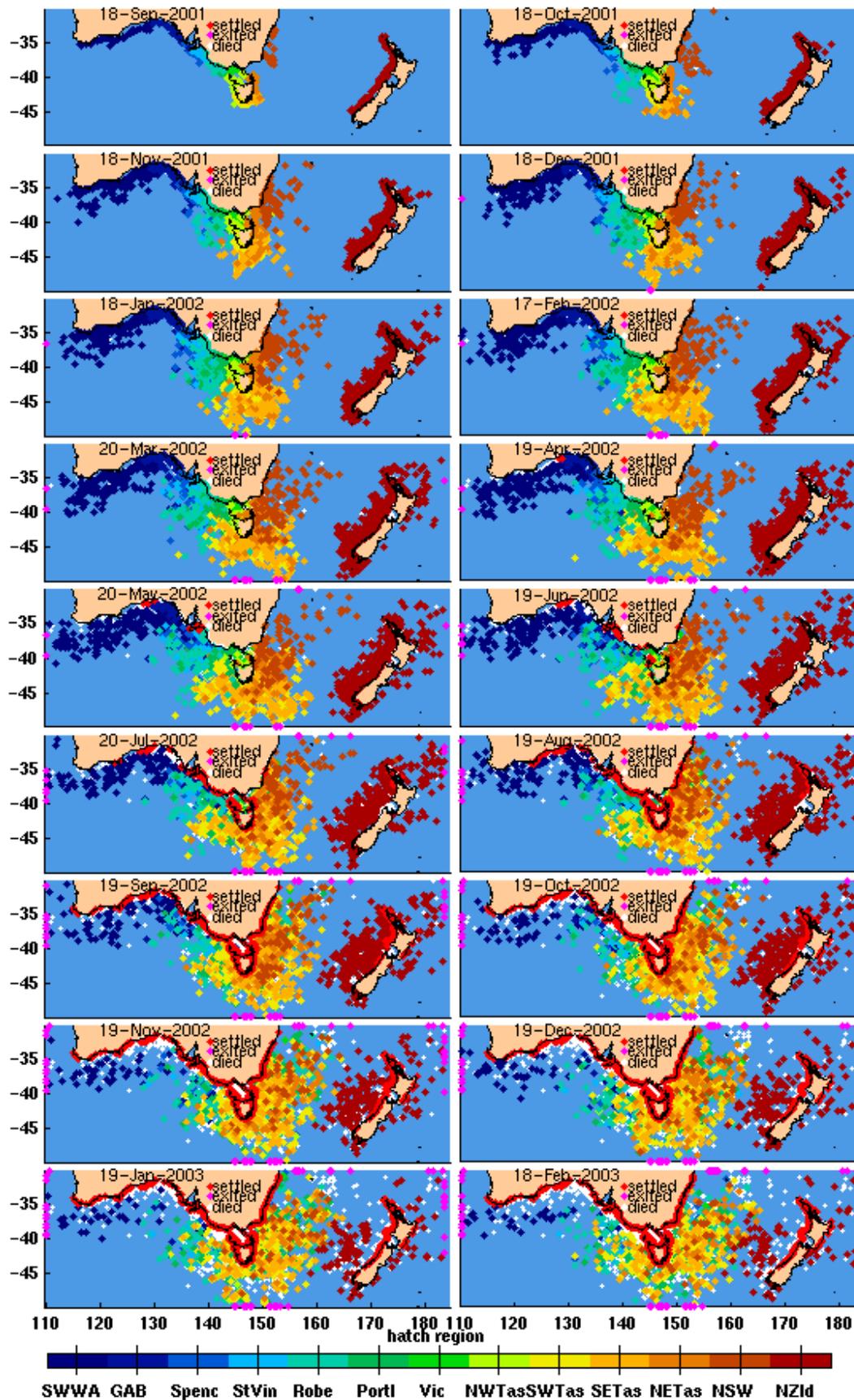


Figure 25. Distribution of phyllosoma stages from a single year-class (fast-growth model run) at 30-day intervals, starting 18 September 2001. Larvae are colour coded by origin of hatching according to the above key.

### **Trajectories of modelled larvae**

We describe the trajectories of modelled phyllosomata, below, for those hatched in late 2000, following this cohort until December 2002. Trajectories are described for both larvae recruiting to, and dispersing from, each of the egg production assessment regions in turn. Comments regarding trajectories from other years (see the accompanying CD) are included where relevant. Although the model domain includes NSW and New Zealand waters, we do not discuss these areas specifically in this section of the report. Larval trajectories for these two regions are, however, also included on the accompanying CD.

#### ***Southwest Western Australia (SWWA – Figure 26)***

Model larvae leaving or entering the SWWA region show the influences of both the Leeuwin Current, the South Australian Current (SAC) and the associated energetic mesoscale eddies that occur seaward of the shelf break in the vicinity of southern Western Australia and the western GAB (see Ridgway and Condie 2004 for definition of the SAC; Cresswell and Griffin 2004 provide a description of the regional oceanography, including these features). The trajectories of larvae recruiting to SWWA extend from approximately 112° E to 132° E and up to 700 km from the coast. Tracks are concentrated in the immediate offshore vicinity of the SWWA region and suggest a high degree of self recruitment. Recruitment of larvae sourced from farther east (eg as far as southeast SA) is predicted in some years, although such examples are dwarfed by the number of recruits sourced locally.

Larvae originating in SWWA are widely dispersed throughout most of the Australian range of *J. edwardsii*, with successful recruitment extending as far east as SE Tasmania in some years. Most successful recruitment occurs between SWWA and western Bass Strait. This illustrates the extent to which west to east transport dominates the overall pattern of flow across southern Australia. However, there is considerable complexity associated with the individual trajectories, particularly in waters south of the GAB where low energy eddies and counterflows limit easterly advection when larvae are offshore and away from the more zonal shelf edge flows. The model predicts that larvae may occur in a broad band from SWWA to western Tasmania and up to 1000 km south of the South Australian coast in the GAB.

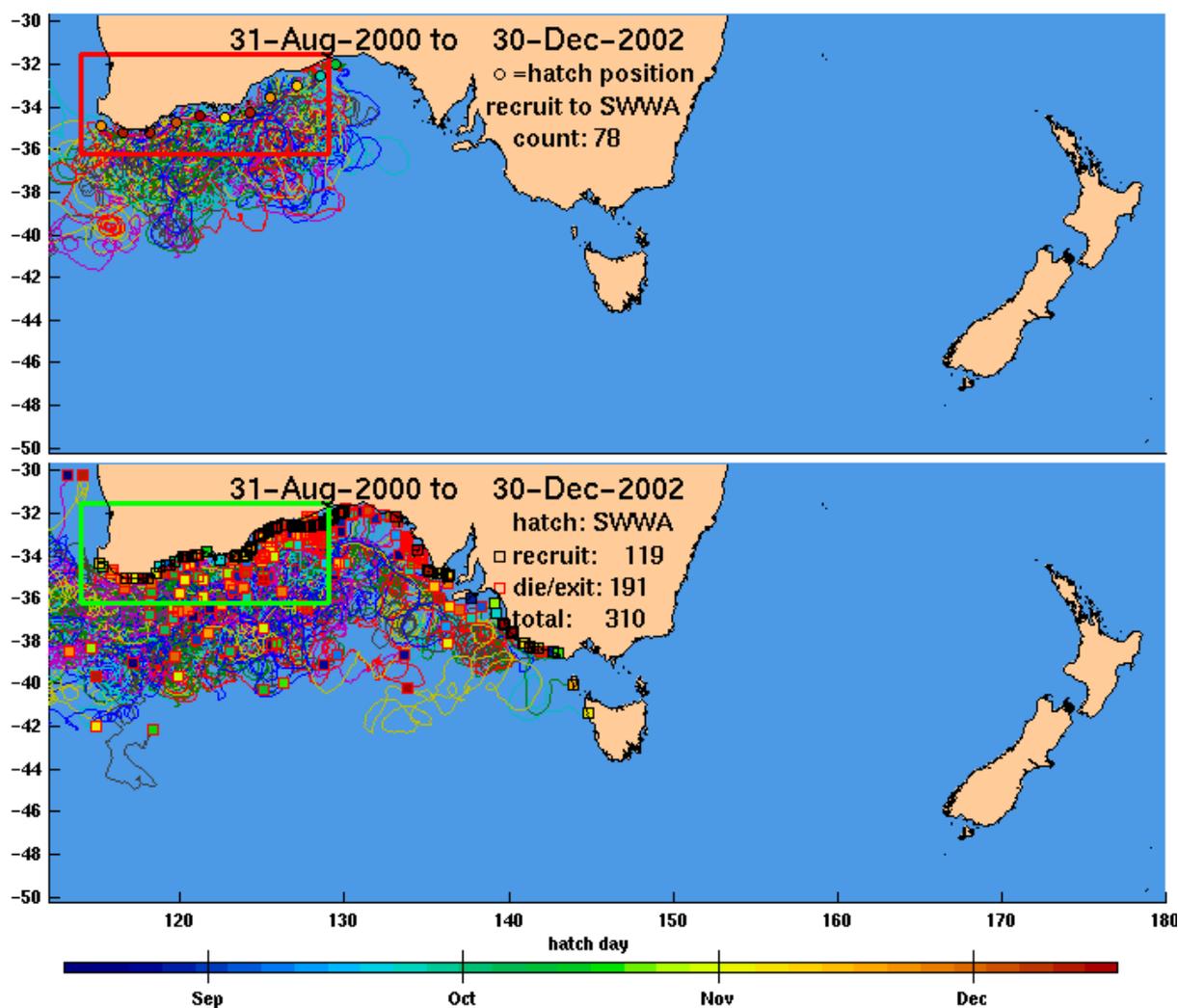


Figure 26: Tracks of individual larvae hatched in 2000/01. The upper panel shows the tracks and origins of larvae that settled in the SWWA region during 2001-2002. The lower panel shows tracks and end-points (black squares for those that settle, red squares for those that died) of larvae that hatched in the SWWA region. Fill colours of squares denote the hatching dates for each larva (see key below figure). Tracks are coloured simply to help distinguish individuals.

### *Northern Zone (South Australia)*

The Northern Zone of the South Australian fishery comprises three of the egg production regions, namely the Great Australian Bight - GAB, Spencer Gulf – Spenc and Gulf St Vincent - St Vin. These three regions are discussed in turn.

### *Great Australian Bight (GAB – Figure 27)*

Model larvae leaving or entering the GAB region similarly show the influences of the SAC and the associated eddy field offshore to the west and south. The trajectories of larvae recruiting to the GAB extend from approximately 115° E to 148° E and up to 600 km from the coast. Tracks suggest that recruitment is sourced primarily from SWWA and locally, although some recruitment may occur from as far east as SE Tasmania in some years.

Larvae originating in the GAB are widely dispersed throughout most of southern Australia with the exception of SWWA. Successful recruitment occurs across all regions from the GAB to NE Tasmania in most years although most occurs between the GAB and western Tasmania. Some larvae hatched in the GAB are transported via southern Tasmania into the Tasman Sea as far as 160° E, although none were recorded making it as far as New Zealand. Many modelled larvae hatched in the GAB are influenced by the high mortality which is assumed to occur in shelf waters and died before they were transported into offshore waters.

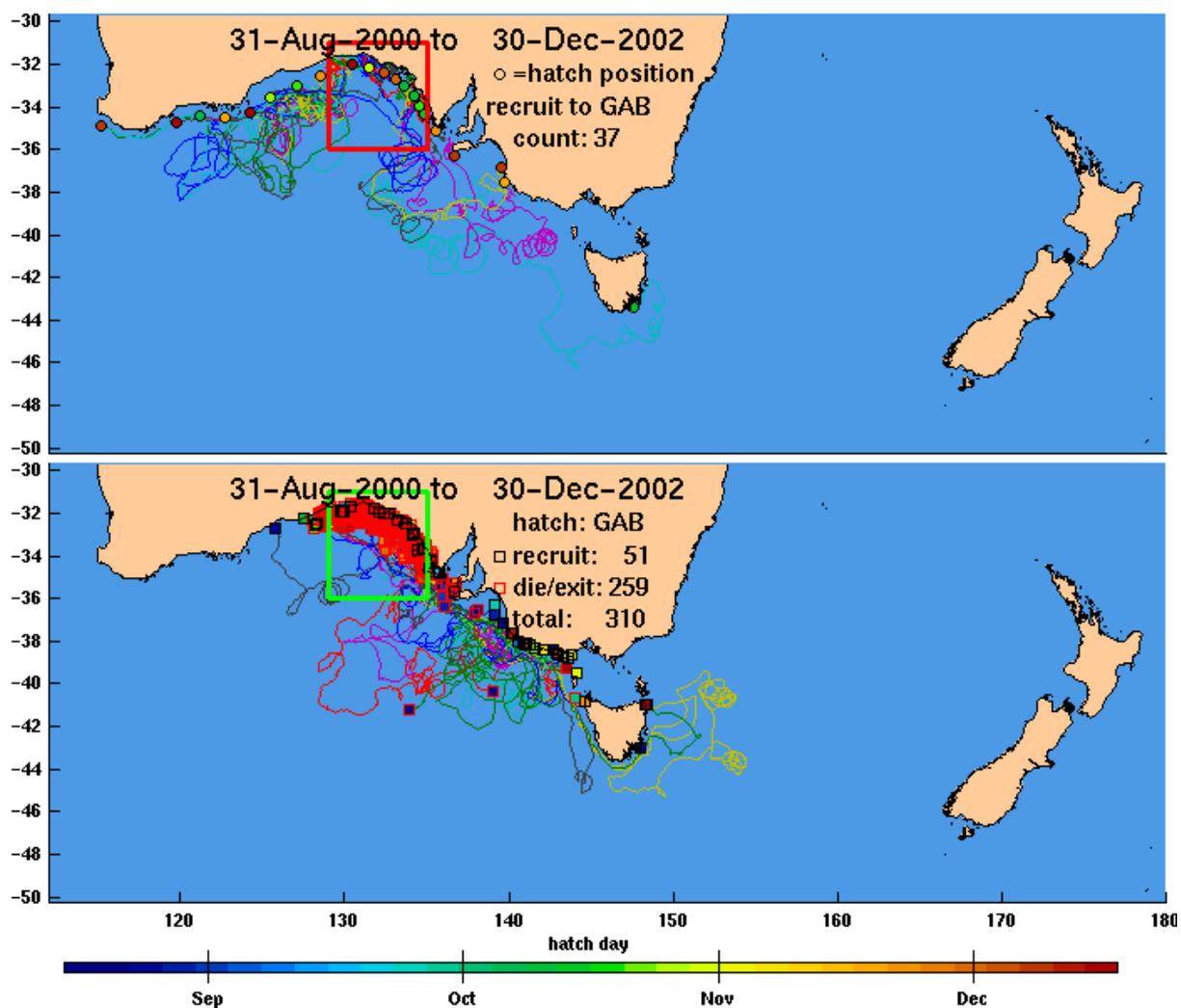


Figure 27: Tracks of individual larvae hatched in 2000/01. The upper panel shows the tracks and origins of larvae that settled in the GAB region during 2001-2002. The lower panel shows tracks and end-points (black squares for those that settle, red squares for those that died) of larvae that hatched in the GAB region. Fill colours of squares denote the hatching dates for each larva (see key below figure). Tracks are coloured simply to help distinguish individuals.

### Spencer (Figure 28)

The trajectories of larvae recruiting to the Spencer region are similar to that for the GAB. Recruitment is sourced primarily from SWWA and the GAB, combined with a small amount of self recruitment as well as low level recruitment from more easterly zones. Recruitment in some years may occur from as far as eastern Tasmania. Trajectories extend up to 750 km from the coast.

Larvae originating in the Spencer region suffer the similar effects of shelf-based mortality that is predicted for GAB-sourced larvae. Those that are successfully transported offshore are widely dispersed, particularly to the south and east. Successful recruitment ranges across all regions from the GAB to NE Tasmania in most years. Some larvae are transported via southern Tasmania into the Tasman Sea although, as with those originating from the GAB, none were recorded making it as far as New Zealand.

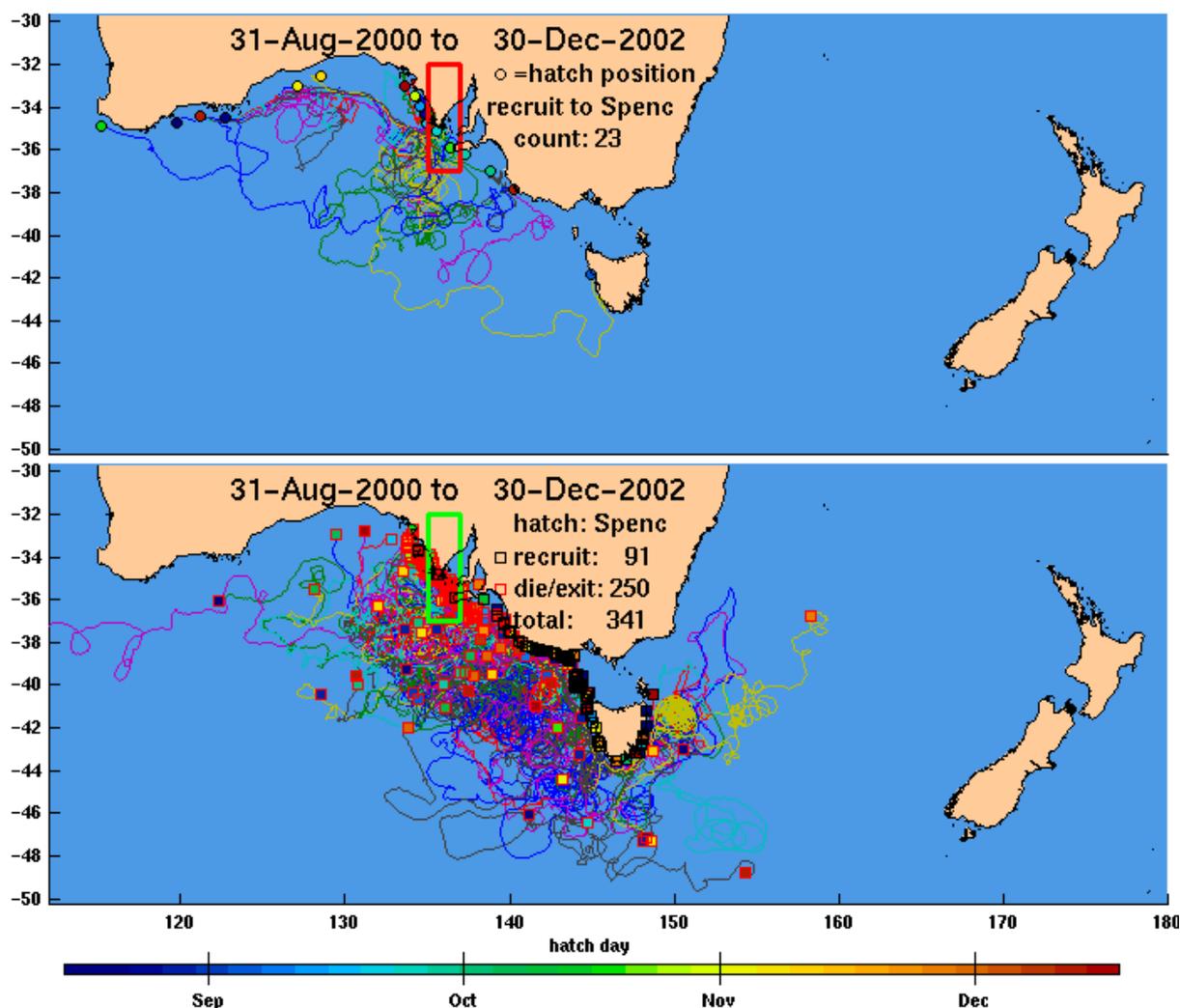
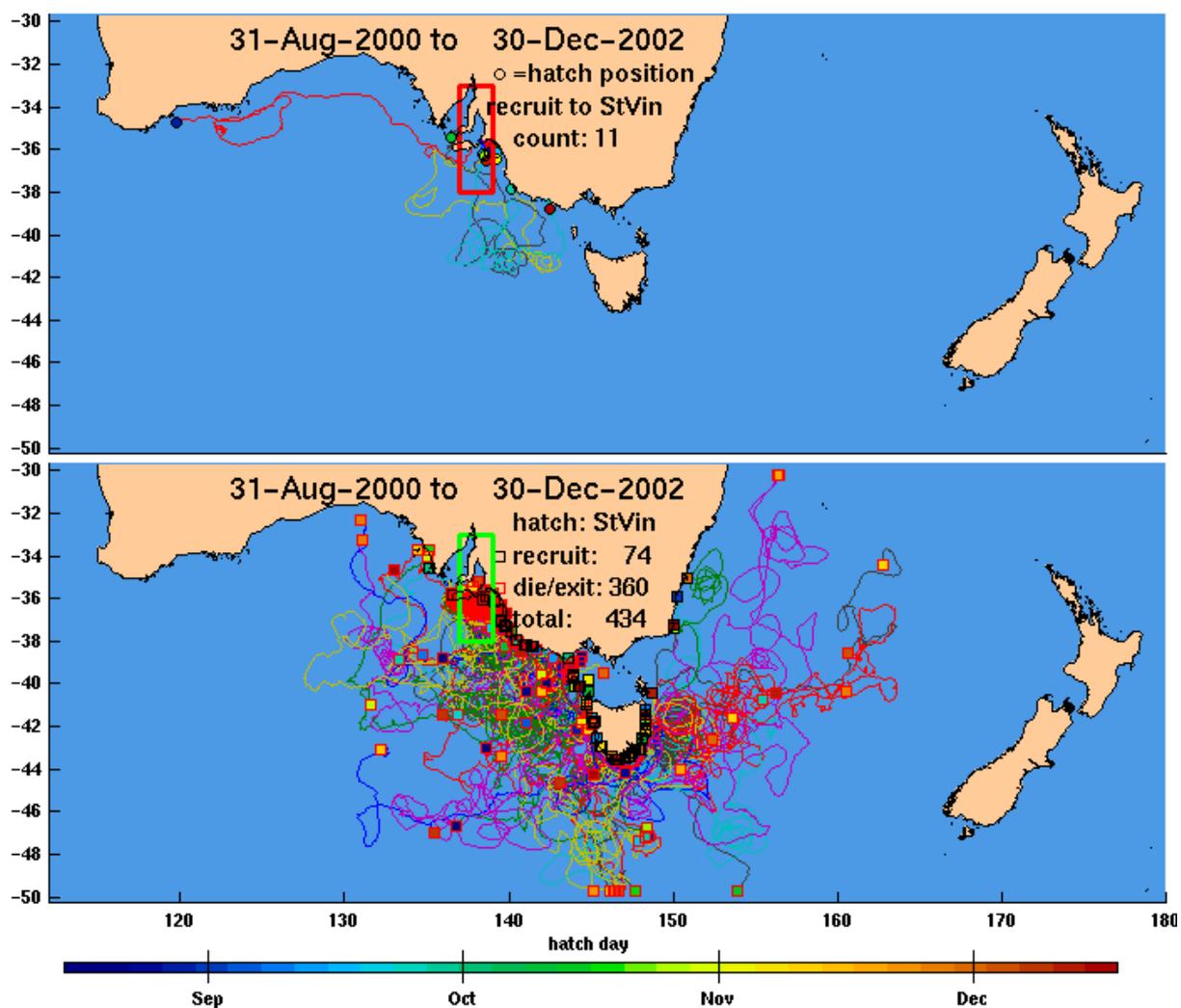


Figure 28: Tracks of individual larvae hatched in 2000/01. The upper panel shows the tracks and origins of larvae that settled in the Spencer region during 2001-2002. The lower panel shows tracks and end-points (black squares for those that settle, red squares for those that died) of larvae that hatched in the Spencer region. Fill colours of squares denote the hatching dates for each larva (see key below figure). Tracks are coloured simply to help distinguish individuals.

### St Vincent (Figure 29)

St Vincent is a relatively small region and hence the number of modelled larvae settling there is low. However, the trajectories of these larvae show similarities with the other regions within the Northern Zone. That is, a combination of recruitment primarily based on local and adjacent regions. There are again examples of low level recruitment from distant sources including the Cape Leeuwin region of SWWA and as far east as SW Tasmania in some years. Trajectories extend up to 600 km from the coast.

Mortality is again high over the wide shelf within and adjacent to the St Vincent region. Those larvae that are successfully transported offshore are widely dispersed primarily to the south and east. Successful recruitment ranges across all regions from SWWA to NE Tasmania, although the dominant areas for settlement in most years range from the St Vincent region to NE Tasmania. Larvae originating from the St Vincent region are also transported into the Tasman Sea although as with those originating from other areas of the Northern Zone, none were recorded making it as far as New Zealand.



**Figure 29: Tracks of individual larvae hatched in 2000/01. The upper panel shows the tracks and origins of larvae that settled in the St Vincent region during 2001-2002. The lower panel shows tracks and end-points (black squares for those that settle, red squares for those that died) of larvae that hatched in the St Vincent region. Fill colours of squares denote the hatching dates for each larva (see key below figure). Tracks are coloured simply to help distinguish individuals.**

### *Southern Zone (South Australia)*

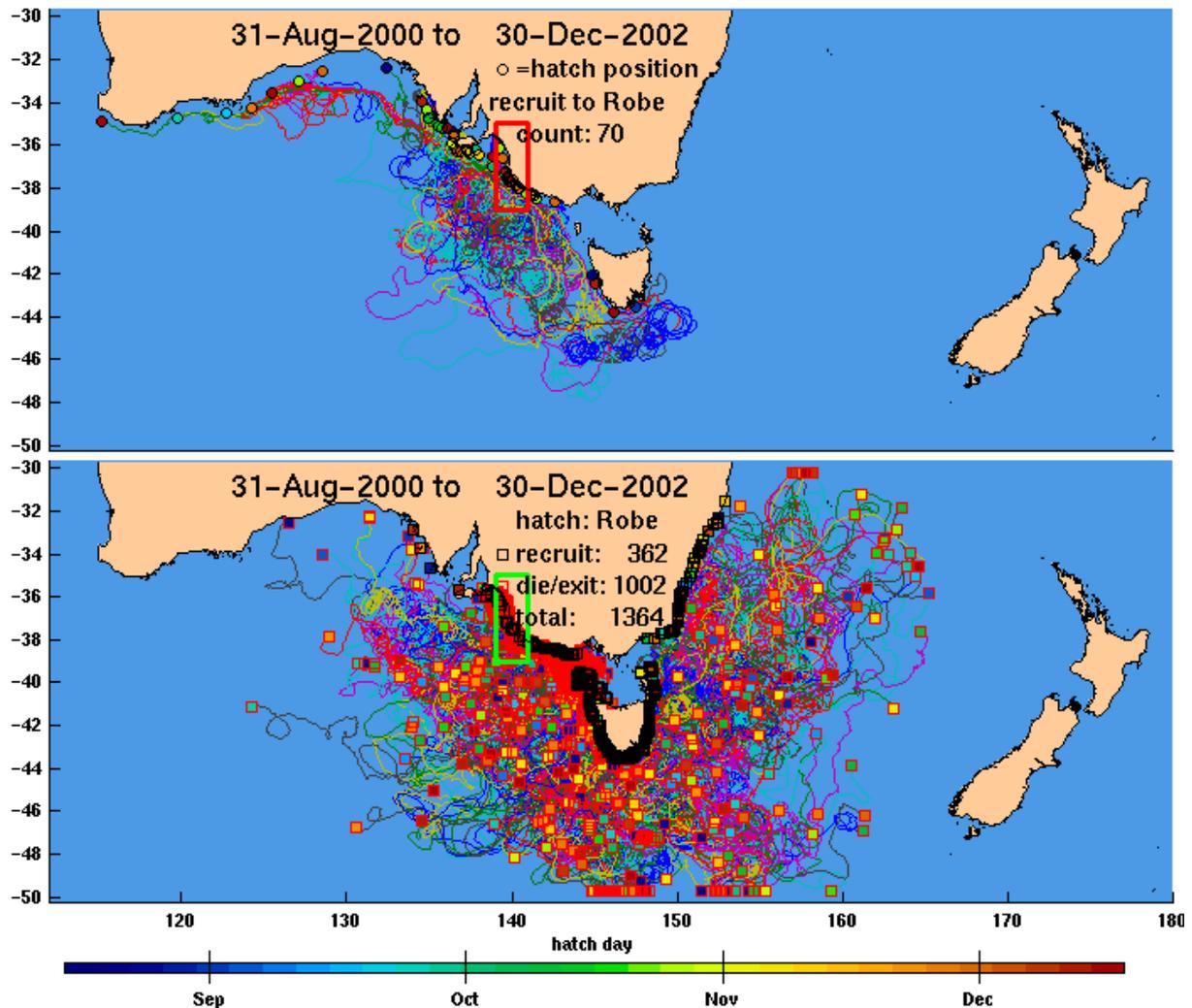
The Southern Zone of South Australia has the highest levels of egg production in southern Australia. The Management Zone is described by the single egg production assessment region of 'Robe' in the model.

### *Robe (Figure 30)*

Model larvae leaving or entering the Robe region have complex trajectories influenced by the SAC, Zeehan Current, low energy mesoscale eddies in offshore waters south of the region and to the west of Tasmania. The trajectories of larvae recruiting to Robe extend from approximately 115° E to 150° E and up to 750 km from the coast. Most tracks are concentrated in the offshore area immediately to the south of the Robe/Spencer/St Vincent/Portland regions. Some degree of self-recruitment is predicted in most years but the most significant levels of recruitment occur from regions to the west of Robe. Although at a lower level, recruitment from regions to the east (Portland, southwest Tasmania and eastern Tasmania) is predicted in several years.

Larvae originating in Robe are widely dispersed throughout the region bounded by 130° E and 165° E. Successful recruitment is concentrated in the region extending from Robe to NE Victoria, although considerable mortality is predicted for larvae entering Bass Strait and this no doubt limits settlement throughout much of Victorian waters. Some recruitment into eastern areas of South Australia's

Northern Zone is predicted in most years. Larvae were distributed in offshore waters west, south and east of Tasmania, the latter consistently to 165° E. Recruitment of low numbers of individuals to the North Island of New Zealand was predicted in two of the years over the modelled period.



**Figure 30: Tracks of individual larvae hatched in 2000/01. The upper panel shows the tracks and origins of larvae that settled in the Robe region during 2001-2002. The lower panel shows tracks and end-points (black squares for those that settle, red squares for those that died) of larvae that hatched in the Robe region. Fill colours of squares denote the hatching dates for each larva (see key below figure). Tracks are coloured simply to help distinguish individuals.**

### *Western Zone (Victoria)*

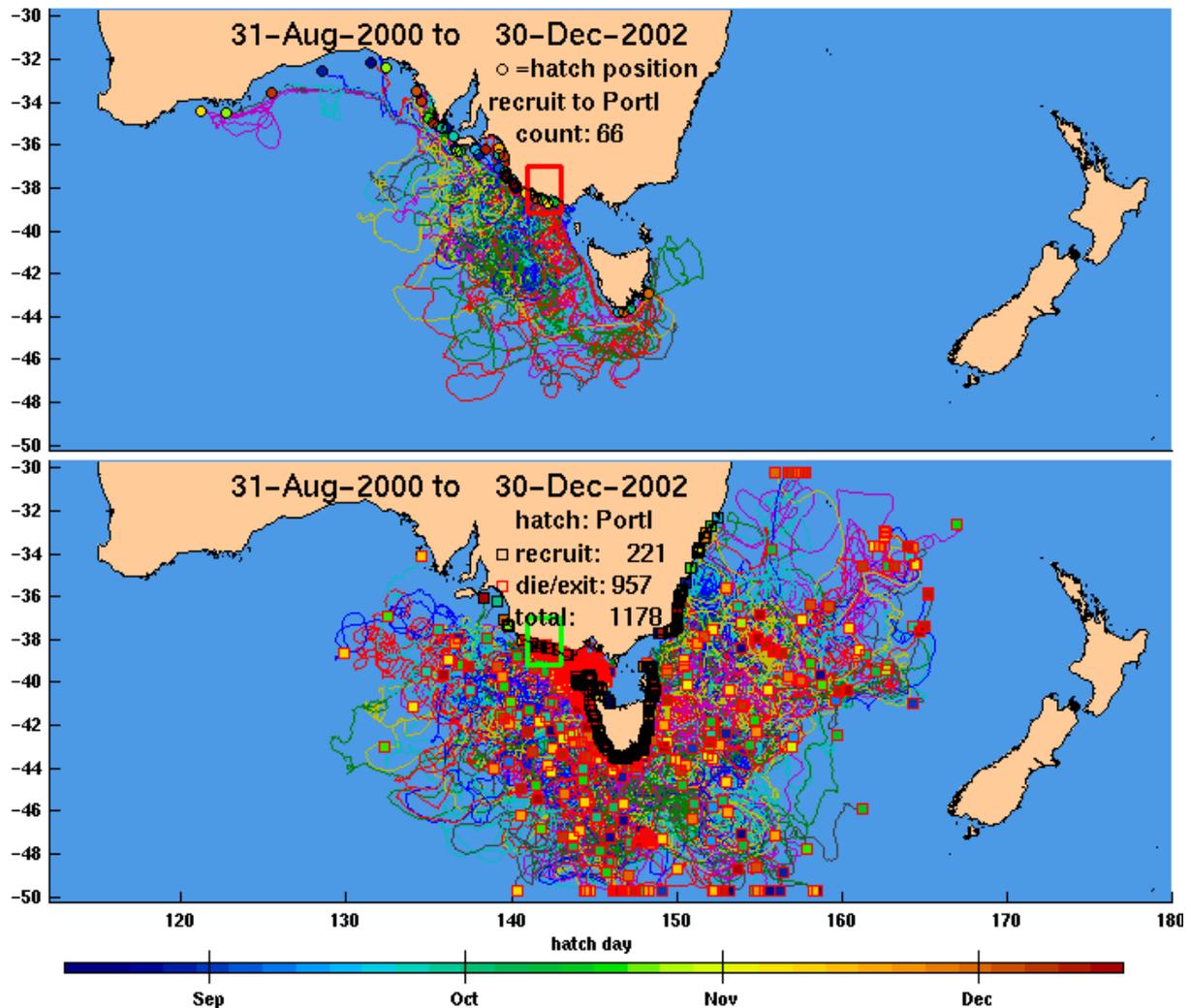
The Western Zone of Victoria also has significant levels of egg production. The Management Zone is described by the single egg production assessment region of 'Portland - Portl' in the model.

### *Portland (Figure 31)*

Model larvae leaving or entering the Portland region have similar trajectories, and are similarly influenced, to those of Robe. The trajectories of larvae recruiting to Portland extend from approximately 115° E to 155° E and up to 600 km from the coast. Most tracks are concentrated in the offshore area immediately south of the Robe/Spencer/St Vincent/Portland regions and to the west of Tasmania. Some degree of self-recruitment is predicted in most years but the most significant levels of recruitment occur from regions to the west of Portland. Lower level recruitment from regions to the east (western and eastern Tasmania) is predicted in several years.

Larvae originating in Portland are again widely dispersed throughout the region bounded by 130° E and 165° E. Successful recruitment is concentrated in the region extending from Portland around southern Tasmania to NE Victoria. Western Bass Strait remains a bottleneck for larvae due to high

levels of mortality and this limits settlement throughout much of Victorian waters. Some recruitment into eastern areas of South Australia's Northern Zone is again predicted in most years. Larvae are distributed in offshore waters west, south and east of Tasmania, the latter consistently to 165° E in the Tasman Sea. Recruitment to the South Island of New Zealand was predicted in one year and to the North Island in another during the modelled period.



**Figure 31: Tracks of individual larvae hatched in 2000/01. The upper panel shows the tracks and origins of larvae that settled in the Portland region during 2001-2002. The lower panel shows tracks and end-points (black squares for those that settle, red squares for those that died) of larvae that hatched in the Portland region. Fill colours of squares denote the hatching dates for each larva (see key below figure). Tracks are coloured simply to help distinguish individuals.**

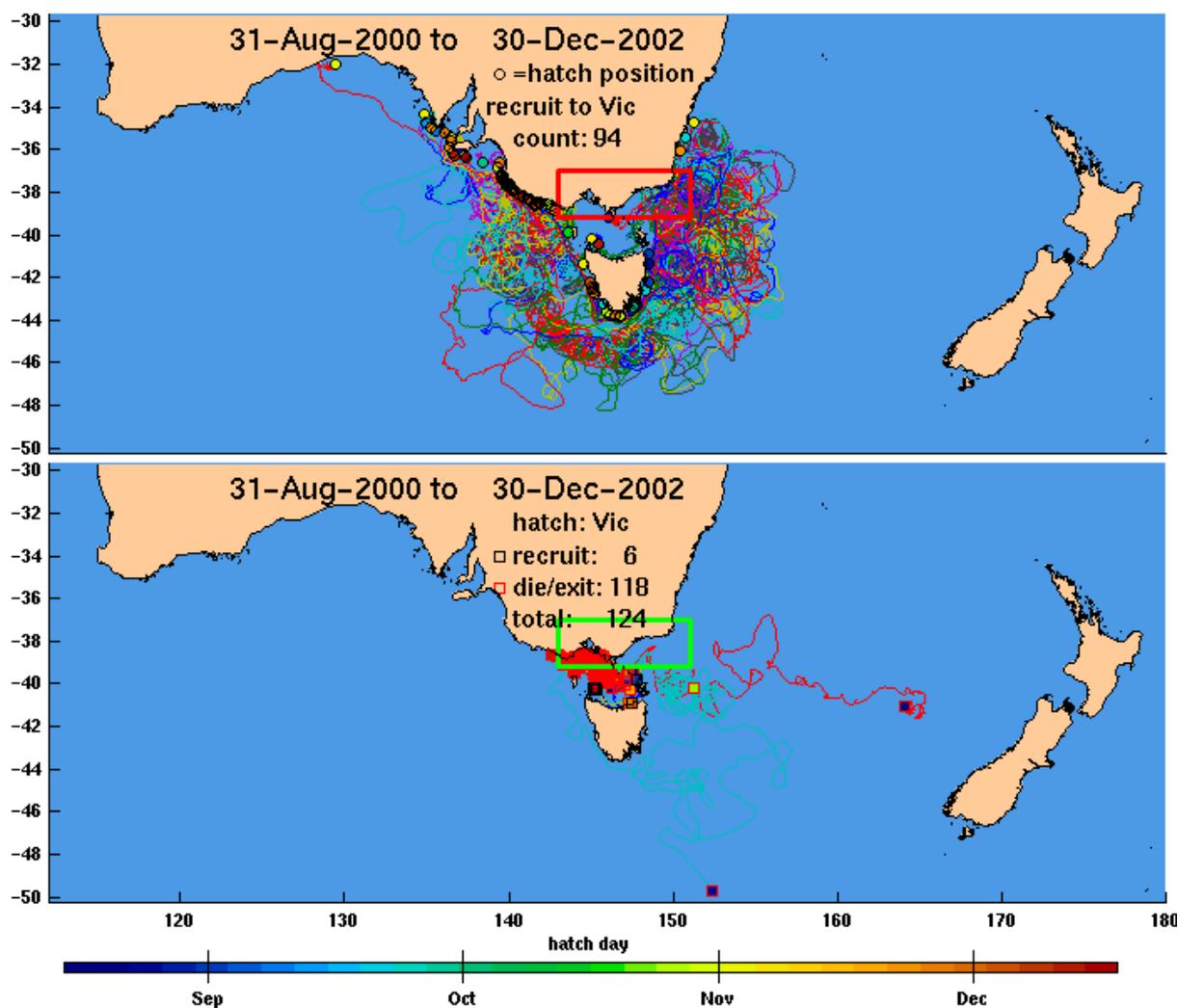
### *Eastern Zone (Victoria)*

The Eastern Management Zone of Victoria is described by the single egg production assessment region of 'Victoria - Vic' in the model.

### *Victoria (Figure 32)*

Recruitment to Victoria is sourced primarily from the Robe and Portland regions with some input from Tasmanian and Northern Zone (SA) regions. Larval trajectories of these recruits extend 135° E – 155° E and up to 600 km from shore in a band from SE South Australia to NE Victoria.

Only small numbers of larvae originating from Victorian waters are predicted to successfully recruit. This is due to the high level of mortality predicted during the residence times of larvae in Bass Strait waters.



**Figure 32: Tracks of individual larvae hatched in 2000/01. The upper panel shows the tracks and origins of larvae that settled in the Portland region during 2001-2002. The lower panel shows tracks and end-points (black squares for those that settle, red squares for those that died) of larvae that hatched in the Portland region. Fill colours of squares denote the hatching dates for each larva (see key below figure). Tracks are coloured simply to help distinguish individuals.**

### *Tasmania*

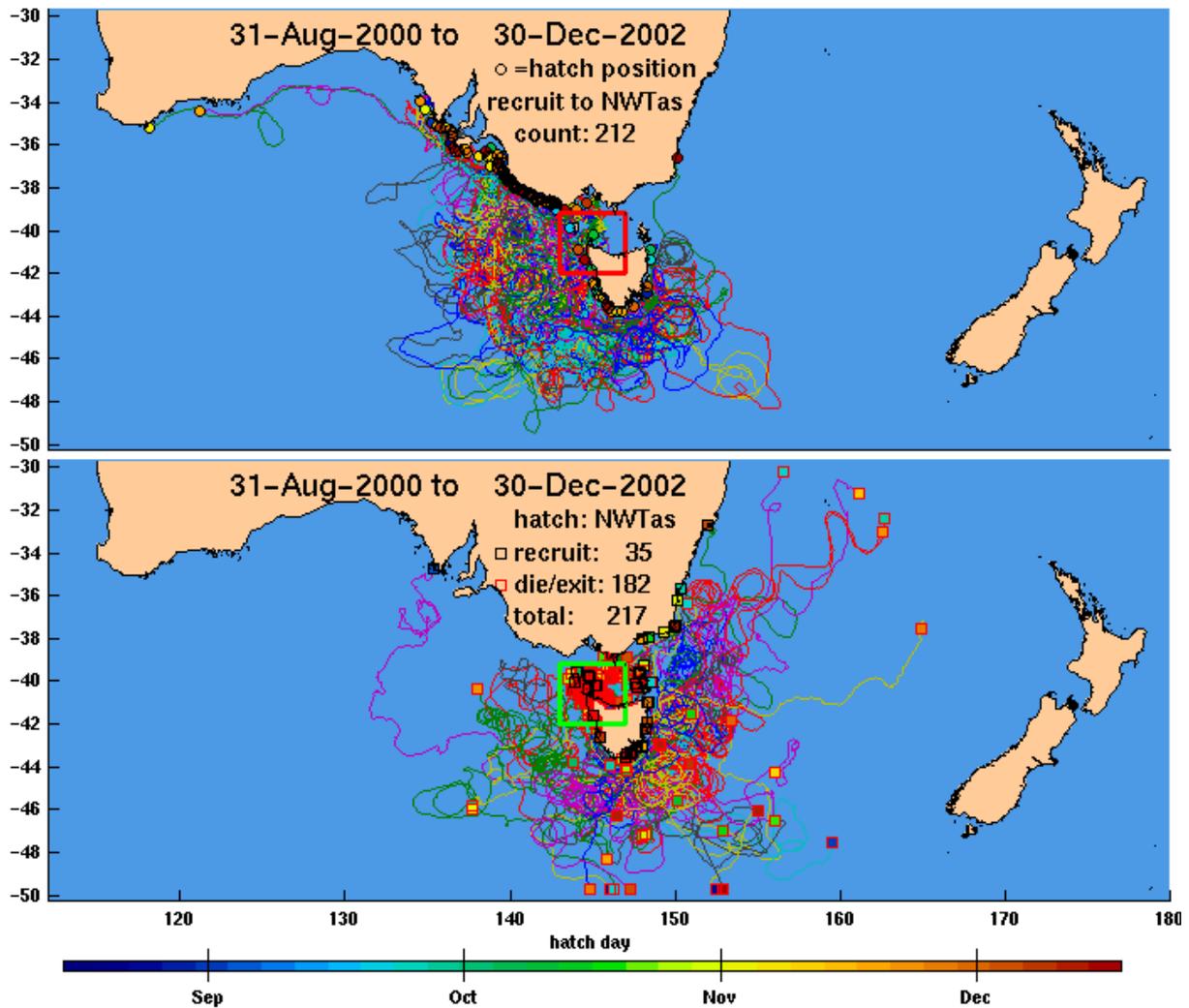
The Tasmanian rock lobster fishery is divided into eight stock assessment areas (see Gardner *et al.* 2005). For the purposes of the model, we have used four areas, each combining two of the stock assessment areas. We discuss each in turn starting in northwest Tasmania and continuing around Tasmania to the northeast.

#### *Tasmania stock assessment areas 5 + 6 (NW Tas - Figure 33)*

Model larvae leaving or entering the NW Tas region have similar trajectories and are similarly influenced to those of Portland and Robe. The trajectories of larvae recruiting to NW Tas extend from approximately 118° E to 155° E and up to 700 km from the coast. Most tracks are concentrated in offshore waters immediately south of the St Vincent/Robe/Portland regions and to the west of Tasmania. Although successfully recruiting larvae are sourced from as far west as the Esperance region of SWWA in most years, numbers are swamped by those recruiting from the area between Streaky Bay, in the southeastern section of the SA Northern Zone, and the SA/Victorian border. Significant levels of recruitment also come from larvae originating in southwest and southern Tasmania, with only occasional input from the east Tasmanian coast.

Many larvae originating in the NW Tas region are lost to Bass Strait. Those that are transported offshore follow trajectories that are bounded by approx 142° E – 165° E. The relatively few successful

settlers recruit primarily to Tasmanian waters. Occasional, low level recruitment west to the Robe and Portland regions is also predicted in some years.

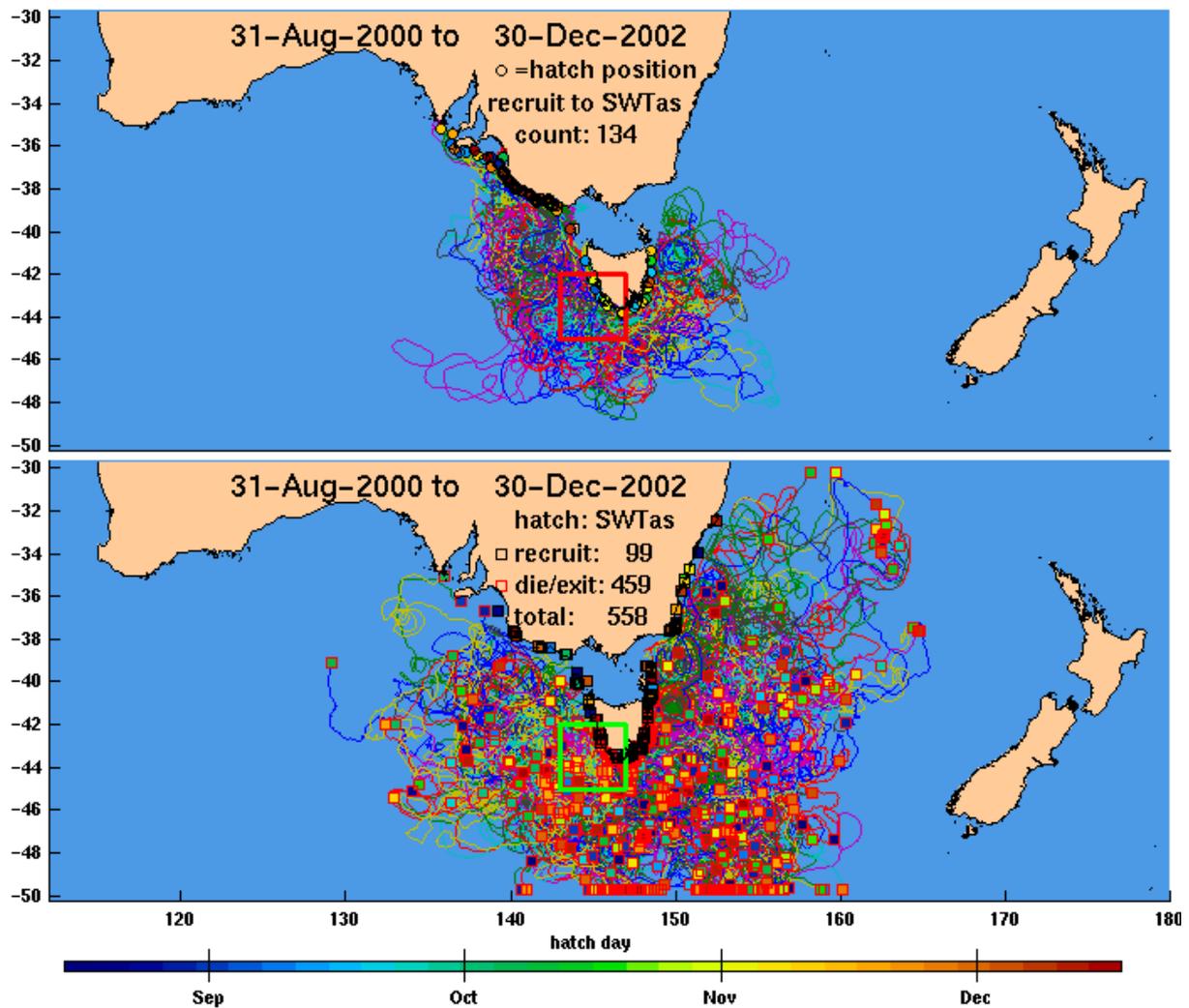


**Figure 33: Tracks of individual larvae hatched in 2000/01. The upper panel shows the tracks and origins of larvae that settled in the NW Tas region during 2001-2002. The lower panel shows tracks and end-points (black squares for those that settle, red squares for those that died) of larvae that hatched in the NW Tas region. Fill colours of squares denote the hatching dates for each larva (see key below figure). Tracks are coloured simply to help distinguish individuals.**

#### *Tasmania stock assessment areas 7 + 8 (SW Tas - Figure 34)*

Model larvae leaving or entering the SW Tas region have extensive trajectories that cover offshore waters to the west, south and east of Tasmania. The trajectories of larvae recruiting to SW Tas extend from approximately 123° E to 160° E with the majority following paths extending up to 600 km from the coast to the west of Tasmania and up to 900 km to the east. Successfully recruiting larvae are sourced from as far west as the Esperance region of SWWA in some years, but most recruitment is sourced from a combination of the Spencer/St Vincent/Robe/Portland regions and from all Tasmanian waters including a significant amount of self recruitment.

Many larvae originating in the SW Tas region recruit to Tasmanian waters, particularly to the SE and NE coasts. Recruitment west to the regions of Robe and Portland is predicted in several years and occasional recruitment may occur from SW Tasmania to as far west as the Streaky Bay area of the SA Northern Zone and east to both the North and South Islands of New Zealand. Larvae follow offshore trajectories that are bounded by approx 130° E – 175° E.

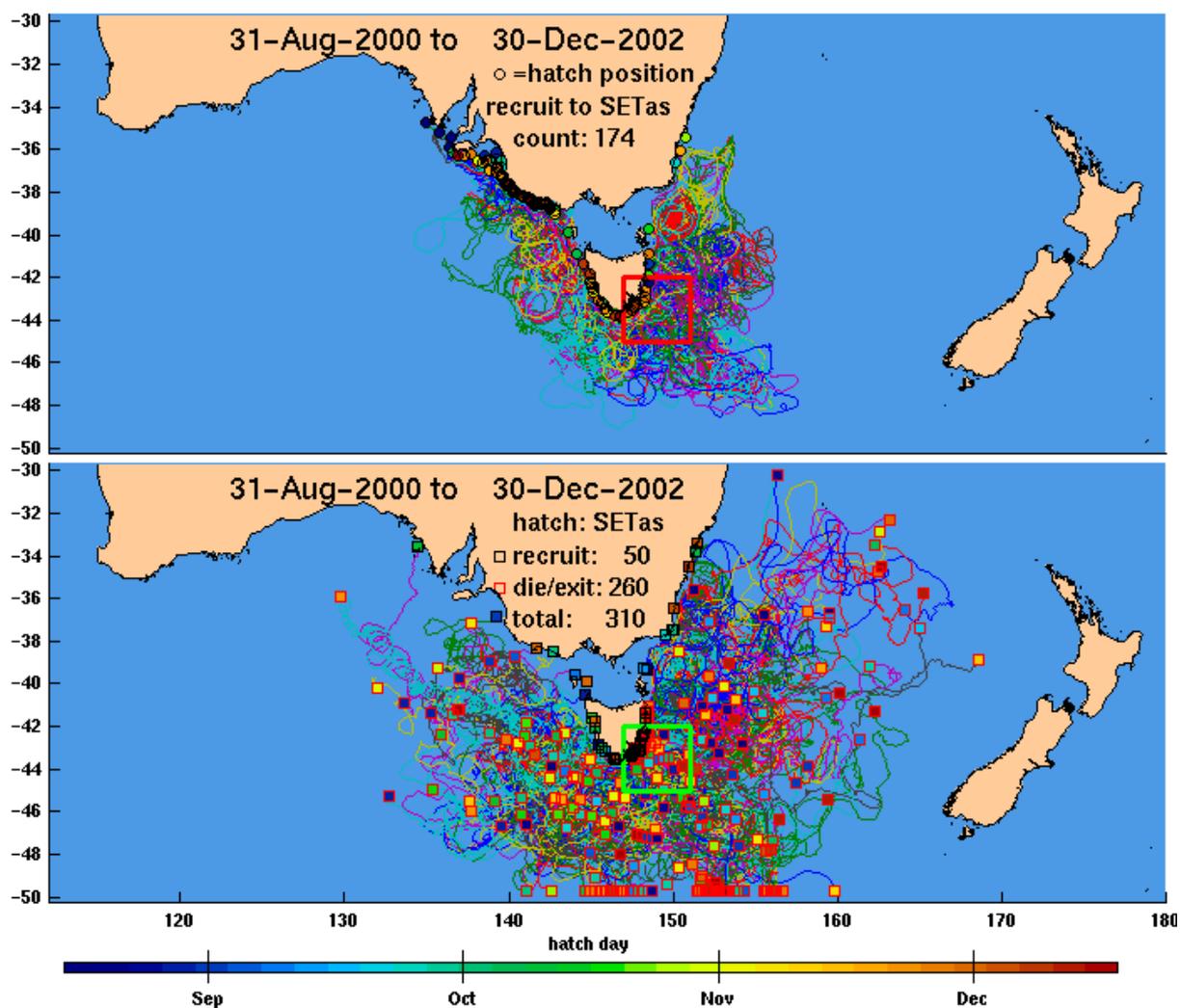


**Figure 34: Tracks of individual larvae hatched in 2000/01. The upper panel shows the tracks and origins of larvae that settled in the SW Tas region during 2001-2002. The lower panel shows tracks and end-points (black squares for those that settle, red squares for those that died) of larvae that hatched in the SW Tas region. Fill colours of squares denote the hatching dates for each larva (see key below figure). Tracks are coloured simply to help distinguish individuals.**

#### *Tasmania stock assessment areas 1 + 2 (SE Tas - Figure 35)*

Model larvae leaving or entering the SE Tas region have similar trajectories to those of SW Tasmania. The trajectories of larvae recruiting to SE Tas extend from approximately 125° E to 160° E and up to 500 km from the coast both west and south of Tasmania, and up to 700 km to the east. Successfully recruiting larvae are sourced from as far west as the Esperance region of SWWA in some years, but most originate from the Robe/Portland regions and all Tasmanian waters. A significant level of self-recruitment occurs in most years.

Many larvae originating in the SE Tas region settle in Tasmanian waters. Successful settlers also reach the Portland and Robe regions as well as the Streaky Bay area of SA's Northern Zone. Occasional settlement to New Zealand's North Island was also predicted. Larvae follow trajectories that are bounded by approx 135° E – 175° E, but the easterly extent of trajectories was mainly restricted to 165° E.



**Figure 35: Tracks of individual larvae hatched in 2000/01. The upper panel shows the tracks and origins of larvae that settled in the SE Tas region during 2001-2002. The lower panel shows tracks and end-points (black squares for those that settle, red squares for those that died) of larvae that hatched in the SE Tas region. Fill colours of squares denote the hatching dates for each larva (see key below figure). Tracks are coloured simply to help distinguish individuals.**

### *Tasmania stock assessment areas 3 + 4 (NE Tas) Figure 36*

Model larvae leaving or entering the NE Tas region show the influence of interactions with the complex oceanography off eastern and southern Tasmania. In particular, the trajectories of many larvae are influenced by eddies and features associated with the southerly extension of the East Australian Current. The trajectories of larvae recruiting to NE Tas extend from approximately 135° E in the GAB to 160° E in the Tasman Sea and up to 800 km from the coast. Most tracks are concentrated in offshore waters immediately to the northeast, southeast and south of Tasmania, with less extensive offshore trajectories occurring to the west and northwest of Tasmania. Significant numbers of recruits come from the Robe/Portland regions as well as Tasmanian waters including some degree of self recruitment.

Many larvae originating in the NE Tas region are lost to the Tasman Sea. Those that successfully settle primarily do so in Tasmanian waters with small numbers recruiting as far west as Streaky Bay in South Australia's Northern Zone and also to the Robe/Portland areas. No larvae from NE Tasmania successfully settled in New Zealand in any modelled year.

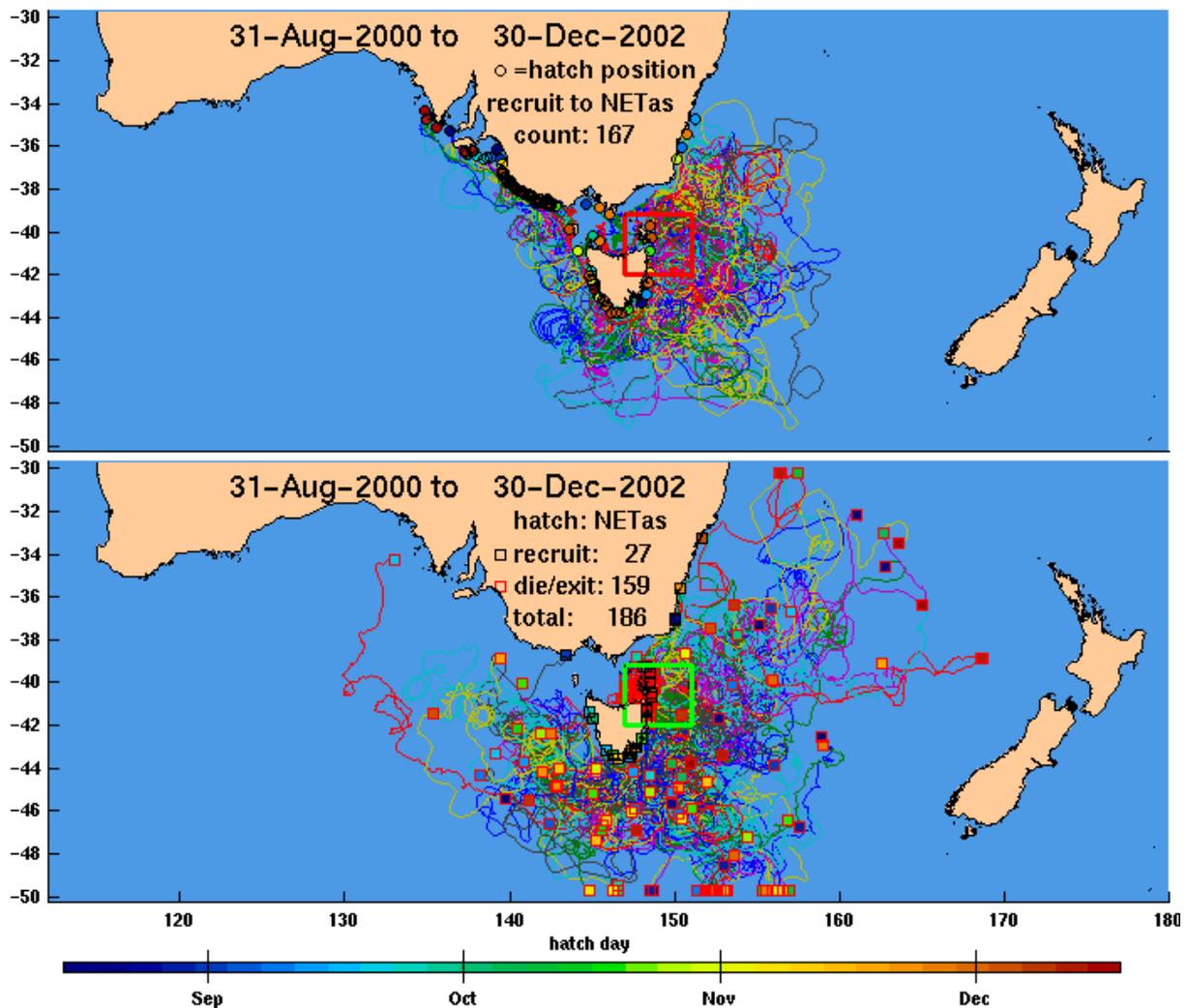


Figure 36: Tracks of individual larvae hatched in 2000/01. The upper panel shows the tracks and origins of larvae that settled in the NE Tas region during 2001-2002. The lower panel shows tracks and end-points (black squares for those that settle, red squares for those that died) of larvae that hatched in the NE Tas region. Fill colours of squares denote the hatching dates for each larva (see key below figure). Tracks are coloured simply to help distinguish individuals.

## Discussion

The paths taken by individual model larvae resemble the paths of satellite-tracked drifters across the domain of the model [see Cresswell (2000) for details of drifter tracks]. This gives us a fairly high degree of confidence that the ocean model is an adequate representation of the hydrodynamics and that if phyllosomata in the field do indeed behave as we have assumed, that their trajectories would resemble those of the model larvae. The trajectory plots show considerable opportunities for larvae to be maintained within a distance from the coast from where they can successfully settle. This predicted distance is within 1000 km and thus supports, at least in the Australian region, statements to this effect by Booth and Ovenden (2000). The extent to which some areas (eg SWWA) are predicted to be self-recruiting is a robust feature of all years, and indeed all model runs, regardless of the growth parameter used. In the case of SWWA, the extent of self-recruitment is linked to the presence of offshore energetic eddies associated with the Leeuwin Current extension into the western GAB. Offshore circulation in other areas around the southern coast of Australia assists both self-recruitment to regions and the transport of larvae against the dominant eastward flows. However, the most salient feature remains the west to east transport of considerable numbers of larvae. This eastward displacement will be discussed in the next section.

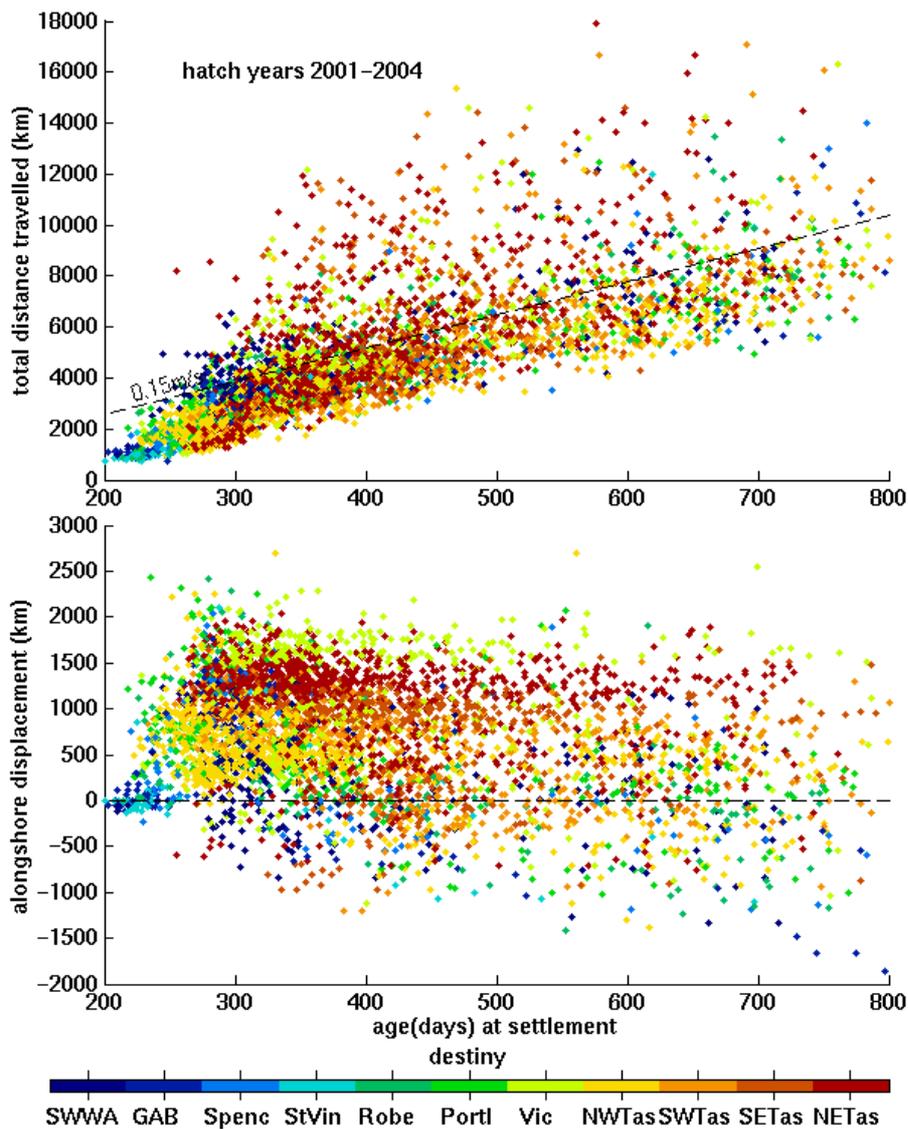
The overall geographical extent of the trajectory plots, and specifically, the geographical extent of predicted settlement locations matches the known distribution of *Jasus edwardsii* in Australian waters. This provides further confidence in the model and suggests that physical oceanographic processes (larval supply) play a role in establishing the distribution of the species in the Australian region.

### **Alongshore displacement of larvae and total distance travelled**

The transport of larvae can be thought of as the sum of advective and diffusive processes. One way to quantify the diffusive process is to measure the total distance travelled by the model larvae, which we define as the sum of the daily distances travelled. However, while total distance traveled is interesting and often requested, it is the net advection of larvae along the coast (or alongshore displacement) that is the more useful statistic for the purposes of understanding recruitment processes and regional connectivity. We define alongshore displacement of larvae as the distance, measured along a smooth line following the edge of the continental shelf from the point where a larva hatches, to the point where it settles as a puerulus. For these purposes, data are restricted to those larvae settling within the primary boundaries of the Australian fishery, SWWA to NETas (i.e. we have excluded model predictions from NSW and New Zealand from these analyses).

#### ***Model predictions***

Predictably, the total distance travelled is a function of larval duration (Figure 37). These distances are very much greater than the alongshore displacements, ranging from 1000 km for larvae that advance through the stages very quickly, to nearly 18,000 km for others. However, the salient feature is that larvae are much more likely to be displaced eastward than westward across southern Australia during their time at sea. The yearclass-mean alongshore displacements vary from ~590 km (1996, 2000) to ~890 km (1993-1995) eastwards. These results are similar between different growth-model runs. These same statistics for the standard growth model are ~580 km (1996, 2000) to ~900 km (1993-1995) and for the slow growth run - ~620 km (1996, 2000) to ~990 km (1993-1995). The extent of alongshore displacement plateaus after approximately 270 d at sea. Thereafter there is no relationship between time at sea and alongshore displacement. In all cases, the percentage of each year class displacing east correlates with the mean displacement distance, and ranges from 80% to 92%.



**Figure 37. Total distance travelled (upper panel) and net alongshore displacement (lower panel) of phyllosomata (fast growth model run).**

### Discussion

Predictably, the total distance travelled (being the summed distanced travelled by an individual larva over its pelagic phase) increases with larval duration. This increase with time is simply because larvae at sea are constantly being carried about by eddies and turbulent flows that take each individual in a variety of different directions. However, rapid mixing of larvae into offshore systems and, in particular, the circular paths described in the above trajectories, decouples total alongshore transport from larval duration after a period of approx 270 days. This suggests that on average *Jasus edwardsii* larvae reach their maximum capacity to disperse after a period of 270 days. Interestingly, this corresponds to the minimum larval duration recorded for *J. edwardsii* in rearing studies and may represent an evolutionary reason for this period being the minimum for competency to settle. The model predicts that most *J. edwardsii* pueruli, however, exceed this age at settlement in the wild. Predicted age at settlement and competency to metamorphose and settle will be discussed below.

Despite the eastward displacement of the majority of larvae, there is no evidence of a broadscale contranantant move by adults to spawning grounds upstream to the west [c.f. the annual spawning migrations of some rock lobster species eg *Jasus (Sagmariasus) verreauxi* [see Booth (1984) and Montgomery and Craig (2005) for details]. Similarly, there is no evidence of a gradual eastward displacement of the adult stock. This suggests that the numbers of larvae that are displaced alongshore

to the west against the dominant net-easterly flow, combined with those that self-recruit to various regions, are sufficient to maintain the population's present distribution. We return to the question of eastward net dispersal below.

## **Predicted age at settlement across southern Australia**

Previous estimates of the age of *J. edwardsii* puerulus at settlement range from approximately nine to 24 months (Lewis 1977, Lesser 1978, Kittaka *et al.* 1988, Booth 1994, Bruce *et al.* 2000, Olsen and Shepherd 2006). However, neither phyllosomata nor pueruli can be aged directly, so estimates are based on a variety of evidence and data. These include the minimum period between peak hatching and peak settlement, stage progression of larvae in the water column and monitoring larval development times in aquaculture. The rearing work of Kittaka *et al.* (1988) provides a baseline estimate of what is biologically possible for *J. edwardsii* in conditions of consistent temperature and food availability. However, with the exceptions of Lewis (1977) and Olsen and Shepherd (2006), estimates of the age at settlement based on field evidence are considerably older. This makes intuitive sense in that temperature conditions and food availability, two of the most important influences on larval growth, vary considerably in the wild and are not always conducive to maximising growth. These parameters vary regionally, seasonally and interannually across southern Australia.

The dates of hatching and settlement for each individual larva are tracked in our model and this provides predictions of the age at settlement for regions across southern Australia.

### ***Model predictions***

Figure 38 shows the model-based age at settlement of pueruli, by region, across southern Australia. The age at settlement varies from 220 to >800 days. Modes in settlement age range from approximately 250 to 300 days across the region from Western Australia to NW Tasmania, to approximately 360 to 400 days in southwestern and eastern Tasmania, and eastern Victoria. Much of the settlement into eastern Victoria is sourced from Tasmanian waters and thus explains this similarity in settlement ages. All regions, however, have larvae settling over the full range of settlement ages.

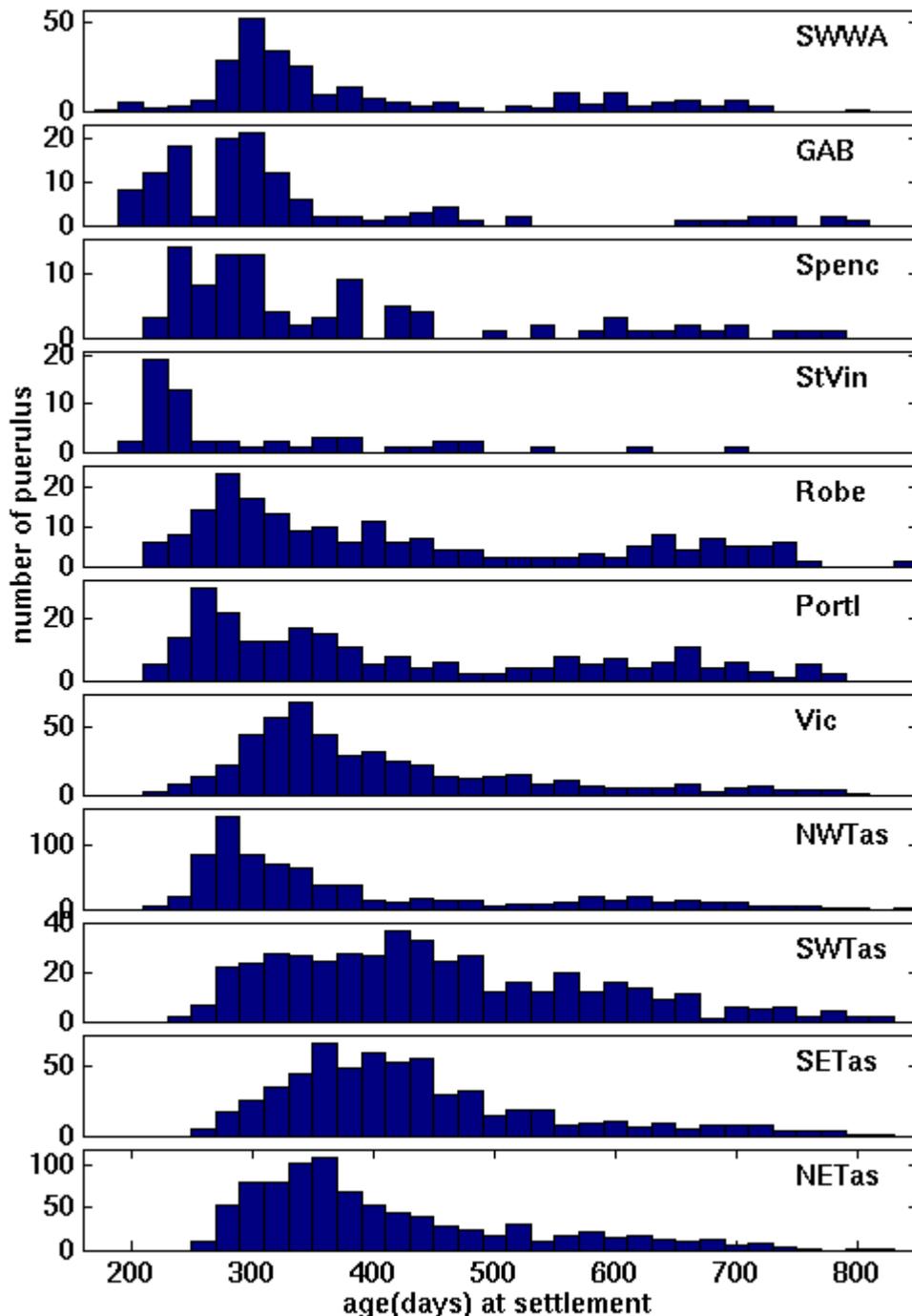


Figure 38. Model predictions of the age at settlement by region across southern Australia. Note that the vertical scale varies by region.

### Discussion

Age at settlement varies considerably among individual pueruli within any one region. However, most regions are dominated by pueruli settling within a more restricted age range. There is a general trend towards increasing age at settlement from west to southeast across southern Australia with longest larval durations predicted for Tasmanian waters. Most regions have a minor degree of bimodality in age at settlement, most notably Robe, where a second but relatively minor mode in settlement ages occurs ranging at 600 to 700 d. The latter is a response driven by winter-spring wind events in the second year after hatching which facilitate onshore transport of pueruli.

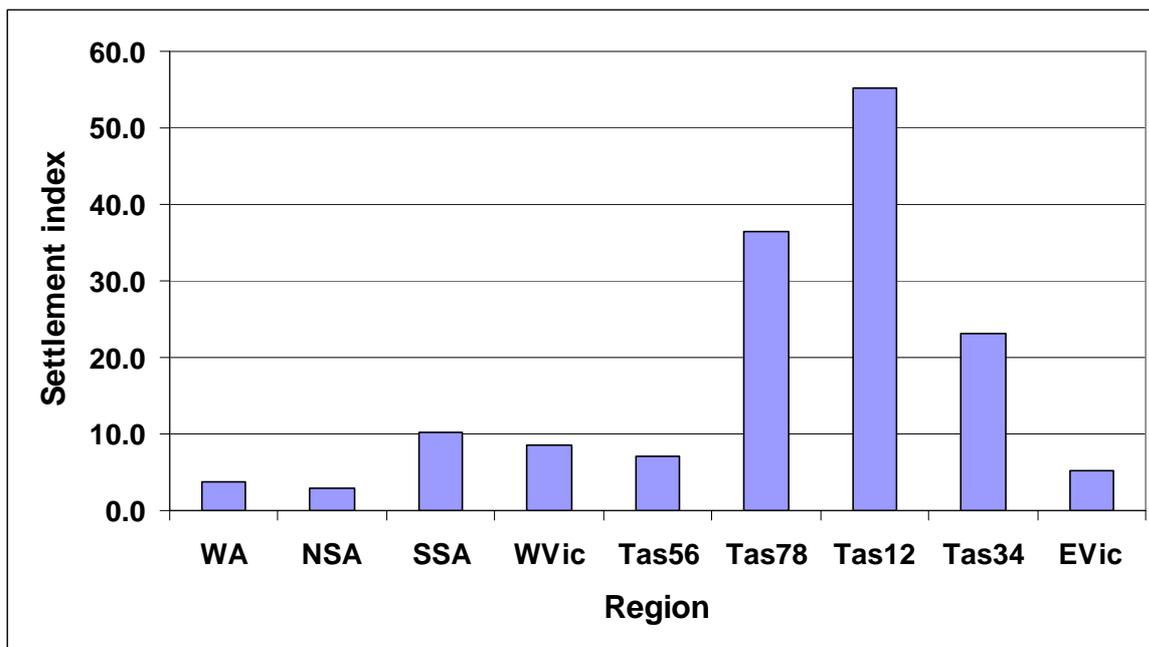
The predicted wide range of ages at settlement matches the range of estimates combined from field and aquaculture data of approximately 9 to 24 months. Some researchers have long held the belief that

an estimate of up to 24 months is excessive and nine months more appropriately aligns with spawning and recruitment periods in southern Australia (Lewis 1977, Olsen and Shepherd 2006). Bruce *et al.* (2000) provided evidence of an 18 to 24 month larval duration based on the consistent presence of two cohorts of larvae in southern Australian waters throughout the year. This corroborates well with estimates of Booth and Phillips (1999). However, both studies relied on data from phyllosoma caught in waters either south of, or within, the Subtropical Front (STF), a cooler water mass than where *J. edwardsii* larvae are found in Western Australian and South Australian waters. The temperature dependence of growth rates in larvae is well documented, thus it is reasonable to assume, all other parameters being equal (e.g. food availability) that larval growth rates in southern Australia would be regionally variable and in particular may be more rapid in areas such as Western Australia and South Australia which experience, on average, higher water temperatures than Tasmania. The variation in overall temperature history of any one larva may, at least in part, explain the wide ranging estimates for larval duration of 12 to 24 months and why 9 months provides a better fit in both the model and observed periods between spawning and settlement in South Australia while longer larval durations are better estimates for Tasmania and New Zealand. These model outputs thus explain this seeming discrepancy in empirically derived estimates of larval duration within and between regions and specifically, the general trend towards an increase in the modal age at settlement from west to east and south to Tasmania.

Larvae with long pelagic durations are well known to have wide windows of competency to settle (Victor 1986). This is believed to be an evolutionary response to the increased risk of being transported to regions distant from nursery areas, thus giving a substantial period to allow larvae to find suitable settlement habitat (Cowan 1991). The pelagic duration of *Jasus edwardsii* is indeed lengthy even at its likely minimum duration of 220 to 270 d. The range of estimates for age at settlement may thus also be indicative of *J. edwardsii* larvae having a correspondingly lengthy period of settlement competency provided the correct cues to metamorphose and settle to suitable habitat are encountered. This period of competency presumably allows for *J. edwardsii* larvae to metamorphose and settle at ages up to at least 18 to 24 months as predicted by some previous studies (Booth 1994, Bruce *et al.* 2000). Such lengthy larval durations presumably come at a cost because they increase the time of exposure to high predation rates inherent in planktonic habitats (Houde 1987). However, as noted by Cowan (1991), successful settlement also becomes as critical to the survival of individuals as does avoiding both planktonic predators and starvation in low productivity offshore waters. Thus a lengthy window of competency to metamorphose and settle in *Jasus edwardsii* may be worth the risk of loss to predation if it facilitates the successful transition to the juvenile stage in sufficient individuals.

## **Average predicted regional patterns of settlement**

The egg production assessment regions in the model differed in size, and hence comparing settlement directly between regions was difficult. In order to make settlement indices comparable between regions we calculated the average predicted settlement index per unit length of coastline (Figure 39). We used the same proxy of coastline length that we used to calculate alongshore displacement, that is, a smooth line following the edge of the continental shelf.



**Figure 39. Comparison of settlement indices between regions standardised per unit length of coastline.**

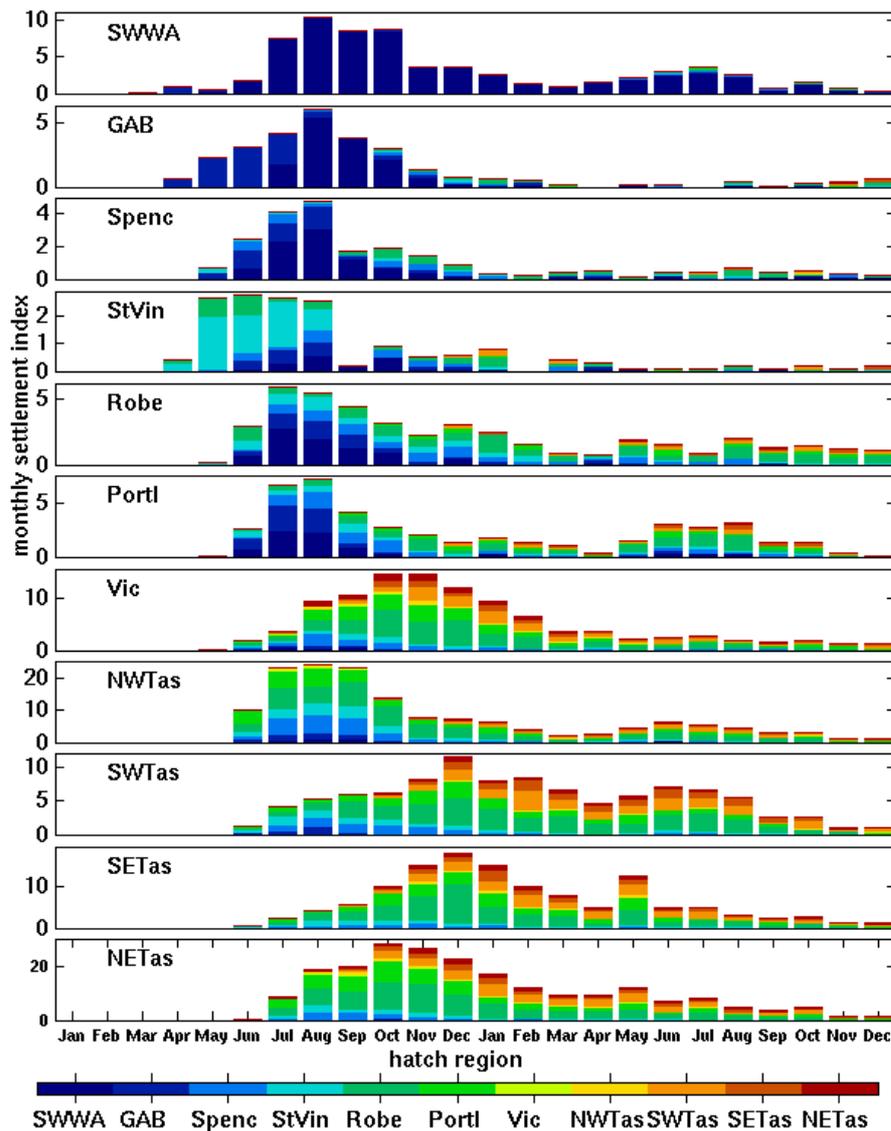
Settlement indices varied significantly, with Tasmanian regions (specifically southern and eastern regions) receiving considerably higher levels of settlement than other areas of the fishery. The highest rates of predicted settlement occurred in Tasmanian stock assessment areas 1+2. The highest rate of settlement for mainland regions was in the SA Southern Zone. Northern Zone, SA received the lowest settlement per unit coastline. A higher level of settlement in Tasmania compared to mainland regions of the fishery is consistent with observed data from puerulus collectors.

### **Sources of successfully settling puerulus**

One of the primary objectives of the present study was to identify where pueruli that successfully settle to regions of the fishery come from. The larval trajectory plots and along-shore displacement data above provide some indication of the linkages between regions which combine varying degrees of self recruitment and input from adjacent and distant areas. In this section we identify the model's predictions of where pueruli settling to each egg production assessment region come from, and examine these data with respect to the predicted total contribution that each region, on average, makes to settlement across the range of the Australian fishery.

Figure 40 captures the various patterns of monthly settlement for each region averaged over a 10 year period. Regions from SWWA to Portland are dominated by puerulus originating from SWWA and South Australia's Northern Zone. This is particularly the case in the first settlement season after hatching. Puerulus settling in their second year after hatching in these areas are sourced more broadly across the range of the fishery including from areas as far east as northeast Tasmania.

Puerulus settling in Tasmanian waters are sourced from a combination of Southern Zone SA and Tasmanian regions.



**Figure 40. Monthly settlement indices, averaged over 10 modelled yearclasses, from the first January after hatching to the second December. The origin of the settling larvae is colour-coded according to the key.**

Regions differed in their predicted contribution to successful settlement across the range of the fishery and can be described based on whether they were an overall source (i.e. regions that produced more successful settlers to the fishery as a whole than they received) or sink (i.e. regions that received more settling pueruli than they successfully produced to the fishery). These data provide details on what regions are most successful in supplying recruits to the fishery and are presented in Table 1.

Western regions (southwest Western Australia to western Victoria) were the most significant source regions on a fishery-wide basis, with the SA Northern and Southern Zones being the highest overall contributors. Eastern Victoria and NW Tasmania were consistently the lowest suppliers of pueruli to the fishery.

**Table 1: Average number of larvae (over 10 year-classes) settling in each zone (rows) and breakup into contribution from each zone (columns).**

| Zone                                                                                                                       | Total settlement | Settlement contribution by Zone |        |        |       |      |         |         |         |         |
|----------------------------------------------------------------------------------------------------------------------------|------------------|---------------------------------|--------|--------|-------|------|---------|---------|---------|---------|
|                                                                                                                            |                  | WA                              | NSA    | SSA    | WVic  | EVic | Tas 5/6 | Tas 7/8 | Tas 1/2 | Tas 3/4 |
| WA                                                                                                                         | 69.50            | 65.50                           | 3.30   | 0.60   | 0.10  | 0.00 | 0.00    | 0.00    | 0.00    | 0.00    |
| NSA                                                                                                                        | 30.10            | 15.80                           | 12.30  | 1.40   | 0.20  | 0.00 | 0.00    | 0.10    | 0.20    | 0.10    |
| SSA                                                                                                                        | 22.60            | 9.90                            | 8.90   | 3.40   | 0.00  | 0.00 | 0.10    | 0.20    | 0.10    | 0.00    |
| WVic                                                                                                                       | 16.20            | 2.30                            | 9.80   | 3.30   | 0.20  | 0.00 | 0.00    | 0.50    | 0.10    | 0.00    |
| EVic                                                                                                                       | 45.10            | 9.20                            | 18.90  | 11.50  | 2.80  | 0.00 | 0.10    | 1.60    | 0.80    | 0.20    |
| Tas56                                                                                                                      | 46.50            | 8.80                            | 19.00  | 11.10  | 3.30  | 0.00 | 0.10    | 2.30    | 1.80    | 0.10    |
| Tas78                                                                                                                      | 109.20           | 2.80                            | 17.70  | 33.40  | 21.70 | 1.00 | 3.40    | 15.50   | 7.90    | 5.80    |
| Tas12                                                                                                                      | 160.10           | 4.20                            | 52.30  | 52.30  | 31.90 | 1.20 | 2.20    | 9.90    | 4.00    | 2.10    |
| Tas34                                                                                                                      | 105.90           | 0.30                            | 19.80  | 34.60  | 16.50 | 0.10 | 1.40    | 18.40   | 11.60   | 3.20    |
| <b>Total contribution</b>                                                                                                  | 605.20           | 118.80                          | 162.00 | 151.60 | 76.70 | 2.30 | 7.30    | 48.50   | 26.50   | 11.50   |
| <b>Source strength: Total contribution/total settlement (<math>\geq 1.0</math> = source; <math>&lt; 1.0</math> = sink)</b> |                  |                                 |        |        |       |      |         |         |         |         |
|                                                                                                                            |                  | 1.71                            | 5.38   | 6.71   | 4.73  | 0.05 | 0.16    | 0.44    | 0.17    | 0.11    |

### **Source of puerulus settling in southwest Western Australia**

The model predicts that, on average, some 94% of pueruli that settle in SWWA waters originate from that zone. The remaining 6% comes primarily from SA's Northern and Southern Zones.

### **Source of puerulus settling in South Australian Northern and Southern Zones**

Pueruli settling to SA's Northern and Southern Zones are sourced primarily from their own waters and SWWA. In each case approximately 40-50% of settling puerulus originate from SWWA and 40% in both cases from Northern Zone waters.

### **Source of puerulus settling in Victoria**

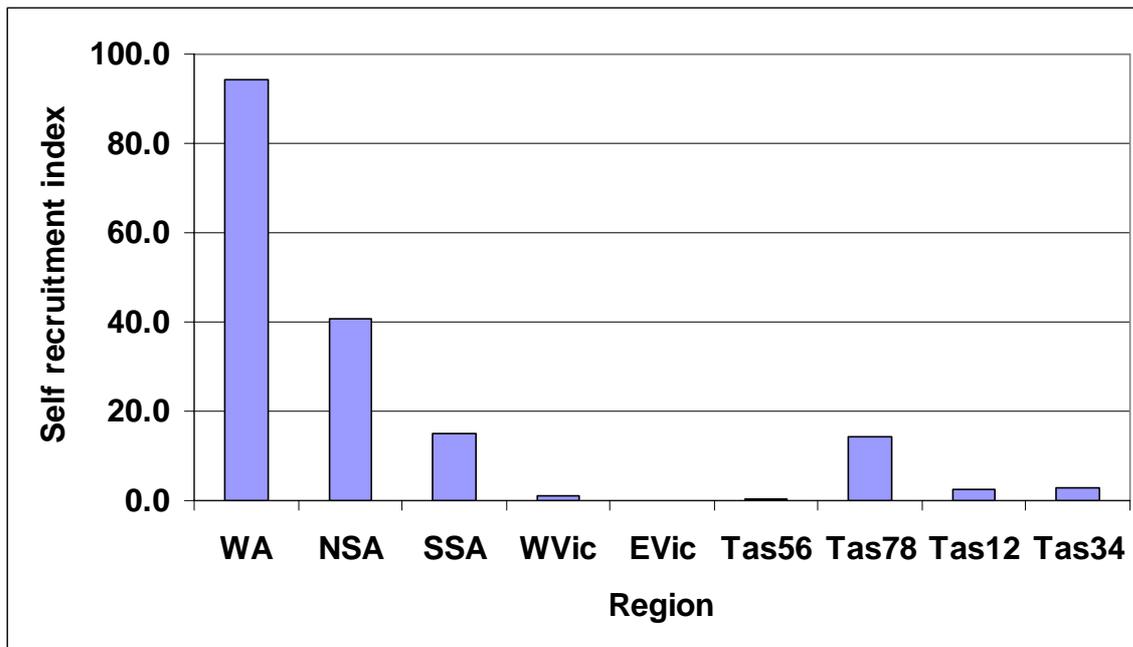
Pueruli settling in Victoria give the reverse situation to SWWA with some 95% originating from regions outside that State's waters. The main sources for Victorian settlement are from South Australian zones. Victoria, along with northwest Tasmania, has the lowest level of self recruitment across the range of the fishery.

### **Source of puerulus settling in Tasmanian waters**

Pueruli that successfully settle to Tasmanian waters are sourced from throughout the Australian range of the fishery. This contributes to the overall high level of settlement recorded in Tasmanian waters compared to the mainland components of the fishery (Figure 39). The majority of pueruli (79%) are sourced from outside Tasmanian waters – specifically the western regions of SWWA, South Australia and Western Victoria. Tasmanian derived puerulus account for 21% of those settling in that State's waters with nearly 17% derived from the southern Tasmanian regions. Northwest Tasmania provides the lowest supply of pueruli to Tasmanian waters.

## **Discussion**

One of the clearest and most robust of the model predictions is the dependence of the Western Australian component of the fishery on self recruitment. Reasonable levels of self recruitment are also predicted in some other zones, notably SA Northern and Southern Zones and to a lesser, but still significant extent, southwest Tasmania (Figure 41).



**Figure 41. Predicted levels of self-recruitment across regions**

The strength of self-recruitment to Western Australian waters has important ramifications for the management of that section of the fishery. The model predicts that for Western Australia to maintain a fishery for *J. edwardsii*, careful management of that resource is required as recruitment sourced from outside the WA region is low. The additional point regarding a sustainable WA component of the fishery is that recruits sourced from this region are also predicted to supply settlement into South Australian waters and in particular, the SA Northern Zone. The magnitude of supply from WA to the SA regions is dependent on the size of the spawning stock biomass in WA waters. However, this information is currently lacking. WA spawning stock biomass is considered to be relatively low compared to the Robe and Portland regions but maintaining a viable population in WA may be important to the South Australian fishery. Similarly, maintaining the SA Northern Zone may also contribute significantly to the sustainability of the adjacent SA Southern Zone and visa-versa.

We do however note that the supply of larvae from and settlement of puerulus to the Northern Zone is influenced in the model by the high larval mortality presumed to occur over the extremely wide continental shelf in this region. We are unable to confirm if this indeed occurs in the wild, but, it makes intuitive sense and we thus suspect this to be a real factor in establishing dynamics of the Northern Zone population.

The Tasmanian region marks a significant change in the pattern of supply for settling pueruli. Regions to the west of NW Tasmania are heavily dependent on recruits from SWWA and SA Northern Zone, as are Victorian waters. Tasmania, however receives recruits from a combination of SA Southern Zone, Western Victoria and its own regions – particularly the SW Tasmanian region.

The stock assessment regions within Tasmania varied significantly in their contributions with NW Tasmania offering, on average, the lowest contribution of successful settlers to Tasmanian waters. This suggests that the NW Tasmanian region, like eastern Victoria may be a less productive area for stock rebuilding in terms of overall benefits to the SRL fishery.

## CONCLUSIONS

The spatial and temporal scales over which rock lobster phyllosoma are found make it difficult to study larval transport by directly sampling phyllosoma at sea. Consequently, most published literature relies on speculative conclusions based on sampling over relatively small spatial scales. Biophysical models provide an important tool to explore hypotheses regarding regional connectivity and recruitment processes (e.g. Condie and Harris 2005, Chiswell and Booth 2003, Griffin *et al.* 2000) but only if the models adequately represent reality.

The preceding discussions and comparisons give us confidence that the larval transport model has indeed provided credible outputs. We now briefly scope the above outputs with respect to the initial project objectives in conclusion to this report.

This project commenced with four objectives and each has been met.

### **Objective 1: To examine the relationship between spawning region and settlement success across the range of the SRL fishery - identify where successfully settling puerulus come from**

Southern rock lobster (*Jasus edwardsii*) larvae spawn across their range in southern Australia. They have a protracted pelagic early life history and larvae are distributed into offshore waters to distances of up to approximately 1000 km from the coast. Transport of *J. edwardsii* larvae in southern Australia is dominated by an overall easterly displacement from natal spawning sites due primarily to currents that run parallel to the coast from southwest Western Australia to the east coast of Tasmania, particularly near to the shelf break. However, there is a complex field of eddies and currents in offshore waters over much of southern Australia that serves to isolate some larvae from the dominant easterly flow. This can result in a net westerly displacement of these larvae and, in some regions, promotes significant levels of self-recruitment despite the lengthy duration of the larval stage.

The main result of the dominant easterly flows are that the western regions of the fishery – specifically southwest Western Australia, Northern and Southern Zones of South Australia and the Victoria's Western Zone are significant sources of successfully settling pueruli for much of the overall fishery. The most important sources of successfully settling pueruli are the South Australian Zones and this suggests that careful management of these areas will offer significant benefits across the range of the fishery.

With the exception of southwest Western Australia, all regions receive more pueruli from outside their own boundaries than from self-recruitment. Southwest Western Australia, by virtue of being both the western-most region and being adjacent to the most energetic and consistently located eddy field in southern Australian waters, is predicted to receive nearly all of its settling pueruli from its own waters. Lower, but still significant, levels of self-recruitment are also predicted for both South Australian Zones and in southern Tasmania. Thus setting sustainable harvesting regimes and improving regional spawning stock biomass can have a local impact and does not just serve to benefit distant regions of the fishery.

Eastern Victoria and northwest Tasmania were the two regions predicted to be the poorest source regions for the fishery.

In terms of average overall contribution success, the nine regions examined (excluding NSW and New Zealand) were rated by the model in the following order from highest to lowest:

Northern Zone South Australia; Southern Zone South Australia; southwest Western Australia; Western Zone Victoria; Southwest Tasmania; Southeast Tasmania; Northeast Tasmania, Northwest Tasmania, Eastern Zone Victoria.

Two points are worth considering. First, the overall contribution of settling puerulus is dependent on the true levels of egg production in each region. For example, southwest Western Australia has the potential by virtue of its (western) location to be a significant source of pueruli for broad areas of the fishery – particularly the two South Australian Zones and western Victoria. However, this will not manifest in reality if spawning stock biomass in that area is either depleted or naturally low. Second it is worth pointing out that despite the significant differences between regions in their potential to

supply successfully settling pueruli, all regions contribute some level of supply and thus the lowest ranked regions should not be seen as unworthy of sustainable management practices.

**Objective 2: To model the effects on settlement, throughout the range of the fishery, of changing spawning output in various areas of the fishery – *provide information on whether increasing spawning stock biomass in some areas will help to increase recruitment and, hence, yield***

This objective has natural links to Objective 1 and assumes that increased levels of puerulus settlement will result in increased recruitment to the fishery and hence future yield. Evidence for such a link is provided by Gardner *et al.* (2001). The model predicts that regions differ significantly in their contribution to successful settlement across the fishery. Thus increasing spawning stock biomass in regions where contribution is highest, is more likely to have more overall benefit to the fishery than others. However, the same cautionary point applies. All regions contribute to settlement and thus none should be regarded as sacrificial in terms of managing spawning stock biomass. The areas of the fishery including, and to the west of, western Victoria have the greatest potential for contribution to settlement. Thus improving spawning stock biomass in these areas will provide the greatest overall benefits. Some regions have significant, but more localised, benefit relative to the full range of the fishery. Larvae produced in southern Tasmania (both the southwest and southeast regions) contribute significantly to settlement in Tasmanian waters and thus managing spawning stock biomass in these regions is equally important to the overall stability of the Tasmanian fishery. Eastern Victoria and northwest Tasmania are predicted to have the lowest input to settlement across the range of the fishery. Thus maintaining a stable level of spawning stock biomass may be more effective in terms of benefits accrued to the fishery than programs to greatly increase spawning stock biomass in these areas. However, the relatively minor contribution that NW Tasmania does have, is directed primarily back to Tasmanian waters. Northeast Tasmania contributes a higher proportion of recruits to the Tasmanian fishery than NW Tasmania and as both regions have depleted spawning stock biomass (Gardner *et al.* 2005) this suggests that, of these two, improving spawning stock biomass in NE Tasmania would have greater potential benefits to the Tasmanian fishery.

**Objective 3: To identify major physical processes contributing to differences in settlement between years and between regions – *help understand whether variations in puerulus settlement result from management changes or environmental effects***

The model produced significant levels of interannual variability in the levels of settlement across southern Australia. However, modelled settlement did not consistently match the observed data. We were unable to demonstrate significant correlations between any simple environmental index and the magnitude of either modelled or observed puerulus settlement across southern Australia. This is perhaps not surprising given that the domain of the fishery falls under the influence of several different circulation regimes bounded by the influences of the Leeuwin Current in the west and the East Australian Current in the east. These currents interact in complex ways with the zonal flows of southern Australia and the low energy eddy field south of the Great Australian Bight. McGarvey and Mathews (2001) correlated westerly winds with a reconstructed recruitment signal based on catch data for South Australian waters. We did find significant influences of winter winds in producing the timing of settlement in South Australia. However, there was no robust correlation between the strength of these winds and the magnitude of settlement that could be used for similar recruitment predictions to those seen for western rock lobster (*Panulirus cygnus*). Finding simple correlations between wind speed/direction and settlement is also complicated by the different orientation of coastlines across the domain of the fishery. For example, westerly winds that facilitate onshore winter flows across the GAB, promote largely offshore transport and hence reduce the opportunity for settlement in eastern Tasmania.

Despite the improvements in modelling growth and survival in this model, compared to the models for western rock lobster (Griffin *et al.* 2001) and tropical rock lobster (Pitcher *et al.* 2005), our representation of mortality and the understanding of the processes that influence it are still relatively crude. This currently limits our ability to progress a common understanding of processes contributing to the interannual variability in settlement.

**Objective 4: To identify mechanisms for incorporating findings of the project into on-going assessments of recruitment indices and stock status – *how best to develop the model outputs into a form that managers, researchers and industry can use on an on-going basis***

This project provides the first quantitative estimates of larval connectivity between management regions across the range of the southern rock lobster fishery. It explains the differences in seasonal settlement signals between South Australia and Tasmanian waters and provides an assessment of the relative contributions each egg production region provides by way of potential puerulus settlement back to the fishery. These findings alone provide benefits for managing spawning stock biomass and making decisions on which areas might best be targeted for accelerating stock rebuilding.

## **BENEFITS AND ADOPTION**

This project was designed to provide data on the connectivity provided by larval transport between management regions of the southern rock lobster fishery in Australian waters and an assessment of the source of successfully settling puerulus by region. The project has resulted in a more widespread appreciation of larval sources and will give managers and industry increased confidence in developing harvest strategies that will help sustain egg production.

A common appreciation among industry and managers of the connectivity by way of larval supply between and within regions is a fundamental prerequisite to adopting management strategies for spawning stock biomass that will benefit the SRL fishery across the board.

## **FURTHER DEVELOPMENT**

Further refinements to the model will require some field sampling to provide key trigger points on growth, the stages present at particular times of the year and offshore extent of larvae.

How pueruli know which direction to swim in order to reach shallow water is unknown as is how they choose where or when to settle once they reach shallow water. These are subject areas requiring further research.

Estimates of mortality and the true spatial and temporal variability in their effects remain some of the most limiting components of the biological model and require further research.

Despite its success in describing the distribution of larvae as well as the timing and overall pattern of settlement by region, the model failed to predict the observed interannual magnitude and variability of settlement throughout the region. Varying the temperature dependent growth rate made significant differences to the pattern of settlement. We suspect that our rather rigid and rudimentary estimates of growth and mortality are insufficient to recreate the interactions of these processes in the wild. Mortality used was only two phase (constant levels on and off the shelf). This is unlikely to be the case in the wild where prey and predator fields are not homogeneously distributed and no doubt vary both seasonally and interannually. The inclusion of spatially and temporally variable mortality fields (apart from using temperature) was beyond the level of this model in-lieu of there being no data to base estimates on. This is an area requiring further research.

A further limitation experienced by the project was the lack of available information on spawning stock biomass – particularly for the southwest Western Australian region. Given the model's predictions that this area is largely self recruiting but also has the potential to supply larvae to several other areas of the fishery, it would be highly beneficial to improve estimates of spawning stock biomass in this area.

## **PLANNED OUTCOMES**

The source of settling puerulus has held a long-term fascination with industry and researchers alike. This issue has also been a focus of interest from a management perspective in terms of understanding the connectivity between management zones, the influence of harvest strategies on regional spawning stock biomass and the implications of decisions taken at regional level for rebuilding of adult stocks. This project has provided the first quantitative assessment of these issues for industry managers and researchers.

A significant outcome has derived from the series of articles, briefings and seminars given to industry, researchers and management that have provided a far greater appreciation of the connectivity between zones provided by larval transport and a better understanding of the benefits of sustainably managing zones for both their own benefits and that of other areas of the fishery. Examples of these outputs are given in Appendix D and on the accompanying CD.

Information generated by the project has been referred to in several assessment reports across the range of the fishery.

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## **APPENDIX A: INTELLECTUAL PROPERTY**

No intellectual property arising from this project is envisaged to have commercial value

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## APPENDIX C: HYDRODYNAMIC MODEL - PERFORMANCE

We briefly examine some of the outputs of the hydrodynamic model below to demonstrate its ability to resolve known circulation features. The complete Bluelink system, comprising the OFAM model and the BODAS data-assimilation system are described by Oke *et al.* (2005), Oke *et al.* (2008) and Schiller *et al.* (2008).

### *Circulation features resolved by the hydrodynamic model*

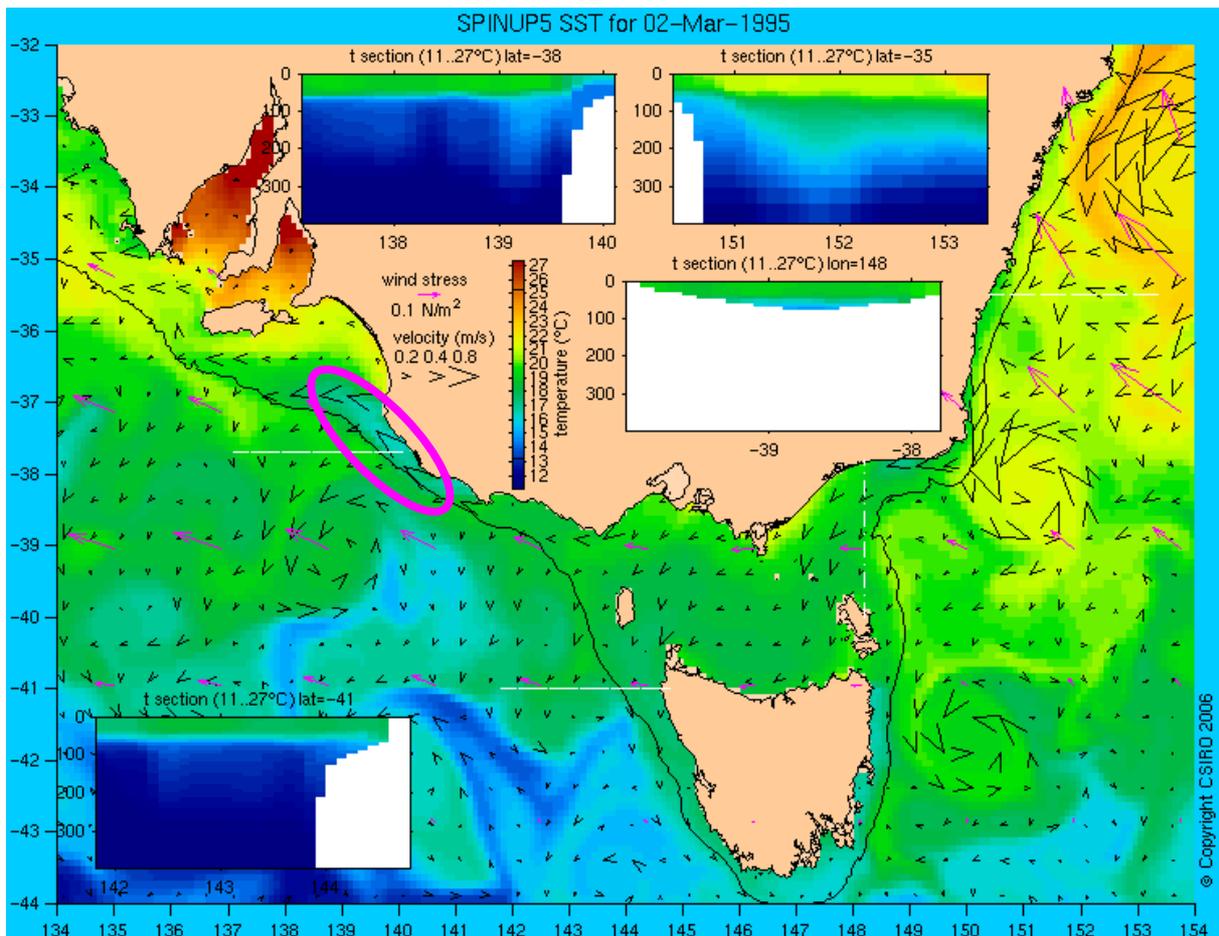
The simulation of ocean circulation by the physical model is best viewed as an animation. This animation is included in the accompanying CD. As in our previous work on southern rock lobster (Bruce *et al.* 2000), and CMAR's work on modelling transport processes in western and tropical rock lobster (Griffin *et al.* 2001, Pitcher *et al.* 2005), we have found these simulations enormously helpful in describing and illustrating the complex ocean dynamics in southern Australian waters to fishers, managers and fellow researchers.

The hydrodynamic model reproduces the known circulation fields within the domain including the Leeuwin and East Australian currents, and their associated energetic eddy fields. South of Western Australia, the Leeuwin Current turns eastwards and assumes a zonal flow extending along the shelf-break into the Great Australian Bight, GAB, (Ridgway and Condie 2004). The development of a series of offshore flows, eddies and westward meanders by the Leeuwin Current in this region, as described by Godfrey *et al.* (1986) and Cresswell and Griffin (2004), are well represented by the model.

One of the important circulation features across southern Australia is the seasonal variation of the flow along the continental shelf across the GAB and between Kangaroo Island and Tasmania. Infrared thermal imagery clearly shows plumes of cold upwelled water occasionally going northwestward in summer (Griffin *et al.* 1997) off southeast South Australia in response to southeasterly wind events, and a thin stream of warm water flowing southeastward relatively continuously across the entire region in winter (Anon. 2001). The winter current has been known variously as the Leeuwin Current Extension and the South Australian Current (SAC). We will follow Ridgway and Condie (2004) and refer to it as the SAC. The Zeehan Current refers to the eastern extension of the SAC that follows the shelf southwards along the western Tasmanian coast (Baines *et al.* 1983, Cresswell 2000).

The SAC and Zeehan Current are also well resolved by the model, and the modelled velocity estimates are consistent with observations that several satellite-tracked drifters have been carried distances of ~400 km/month (=0.15 m/s) by it (Godfrey *et al.* 1986, Cresswell, 2000). Daily-averaged surface temperature and current velocity fields resolved specific known events such as the March 1995 upwelling off the Bonney Coast as discussed by Griffin *et al.* (1997) (Figure 40).

Circulation dynamics south of the GAB and offshore from the SAC are dominated by a field of weak eddy systems. These anticyclonic and cyclonic features propagate slowly westwards from the Tasmanian and Victorian regions and are responsible for much of the circular motions of satellite tracked drifters deployed in the area (Cresswell 2000, Cresswell and Griffin 2004). They interact in complex ways with the Leeuwin Current, SAC and Zeehan Current, drawing shelf edge water offshore in the case of anticyclonic features; rejoining and accelerating shelf-edge flows in the case of cyclonic features (Ridgway and Condie 2004). These features too, are well represented in the model between latitudes 35° S – 43° S (see Figure 40).



**Figure 42. Daily-averaged model surface temperature and velocity field, and wind stress for 2 March 1995. Dashed white lines locate the vertical temperature sections – identified by either their latitude or longitude. Note that the model captures known features such as the Bonney coast upwelling (the cooler inshore waters southeast of Kangaroo Island – pink oval) and associated northwesterly shelf flows in the South Australian region, the EAC eddy-field off eastern Australia as well as offshore flows and weaker eddy fields extending westwards from Tasmania. Source: [www.cmar.csiro/bluelink/exproducts](http://www.cmar.csiro/bluelink/exproducts).**

## APPENDIX D: SCIENTIFIC OUTPUTS

### **The vertical distribution and diurnal migration patterns of *Jasus edwardsii* phyllosomas off the east coast of the North Island, New Zealand**

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### **Abstract**

The rock lobster *Jasus edwardsii* forms the basis of important fisheries in south-eastern Australia and New Zealand. Their long pelagic larval phyllosoma phase (12–24 months) raises many questions as to how the larvae are retained and/or recruited into local populations. Recent attempts to model the dispersal of *J. edwardsii* phyllosoma have had mixed success at reconstructing settlement patterns. However, these models have either ignored vertical distribution or have used that of the western rock lobster, *Panulirus cygnus*. We report on the vertical distribution and migration of *J. edwardsii* phyllosomas, collected in March/April 2003 from the Wairarapa Eddy off the east coast of the North Island, New Zealand, and provide a model to describe their vertical distribution. *J. edwardsii* phyllosoma were primarily recorded within the upper 100 m over similar depth ranges to those reported for other palinurid and scyllarid species. Well-defined changes in diel vertical distribution were restricted to late-stage larvae. Mid-stage phyllosomas were concentrated in the upper 20 m both

day and night. Late-stage phyllosomas were concentrated in the upper 20 m during the night, but they were absent from the upper 20 m during the day and distributed primarily between 20 and 100 m. Future modelling will benefit from using larval distribution and behaviour patterns specific to *J. edwardsii*.

**Keywords** *Jasus edwardsii*; rock lobster; *Antipodarctus aoteanus*; scyllarid; vertical distribution; diurnal vertical migration; Wairarapa Eddy; phyllosoma

## Introduction

The Palinuridae (spiny/rock lobsters) are found throughout the world's major oceans between c. 45°N and 45°S and form the basis of several important commercial fisheries (Lipcius & Eggleston 2000). *Jasus edwardsii* occurs from Dongara, Western Australia (29°15'S) around the south coast of Australia, including Tasmania, to Coffs Harbour, New South Wales (30°18'S) (Phillips *et al.* 2000), on seamounts and banks in the Tasman Sea, around mainland New Zealand, and at the Chatham Islands 800 km to the east of the South Island (Booth *et al.* 1990). In Australia, the commercial fishery for *J. edwardsii* is concentrated about the south-eastern region. In New Zealand, the main commercial fishery is along the east coast of the North Island south of East Cape, around Stewart Island, and in the south-west of the South Island.

Together with the Scyllaridae (slipper lobsters) and Synaxidae (coral lobsters), rock lobsters have a planktonic larval phase, the phyllosoma, remarkable in form and longevity (Phillips & Sastry 1980). The phyllosoma is dorso-ventrally flattened, leaf-like, and transparent. The phyllosoma of *J. edwardsii* passes through about 17 instars (Kittaka 2000), grouped into 11 stages (Lesser 1978), and takes c. 18 months (Bruce *et al.* 2000) to reach metamorphosis. Phyllosomas of stages V and above are almost exclusively distributed in waters seaward of the continental shelf and have been recorded up to 900 km from the shore (Booth *et al.* 1990). The post-larval puerulus is the transitional phase between the pelagic larval phase and benthic juvenile to adult phase.

During this extended offshore larval phase, there is the potential for widespread dispersal caused by currents and wind-driven flows. Since metamorphosis needs to take place within the swimming range of the puerulus to the coast (c. 200 km or less, Jeffs *et al.* 1999, 2001), there must be some means to prevent phyllosomas from dispersing too far from land. One such means may be to take advantage of different flow regimes between depths via diel vertical migration (DVM). For species that display DVM, the most common form is to rise to the surface layer at night and descend to deeper waters during the day. This pattern in DVM has been recorded for several lobster species (*Panulirus interruptus*, Johnson 1960; *P. cygnus*, Rimmer & Phillips 1979; *P. [argus]*, Yeung & McGowan 1991; *P. argus*, Hernandez *et al.* 2000; *P. longipes*, *Scyllarus cultrifer*, Minami *et al.* 2001). Diel vertical migration has also been reported for *Jasus lalandii* (Pollock 1986) and is believed to take place in *J. edwardsii* (Lesser 1978; Booth 1994; Bruce *et al.* 2000).

The extent of vertical migration can also differ between developmental stages. For example, early-stage *P. cygnus* phyllosomas perform relatively shallow DVMs as compared with late-stage phyllosomas (Rimmer & Phillips 1979). It is this behaviour that aids dispersal offshore of the early-stage phyllosomas, and return shoreward of the late-stage phyllosomas and pueruli (Rimmer & Phillips 1979; Griffin *et al.* 2001) because of differences in the direction of current regimes at different depths. Although DVM is thought to occur in *J. edwardsii*, the stage-specific details of this behaviour have not been reported.

The exact role that DVM, and changes in behaviour between stages, would play in *J. edwardsii* dispersal and recruitment is not clear. Deep DVM would effectively take larvae out of the wind-driven (Ekman) layer during the day, and/or bring them into the Ekman layer during the night. Deep migration to below the wind-driven layer may aid in retaining larvae within mesoscale eddies. Alternatively, surface wind-driven drift may occasionally facilitate recruitment via the transport of larvae towards the coast (Booth *et al.* 2000).

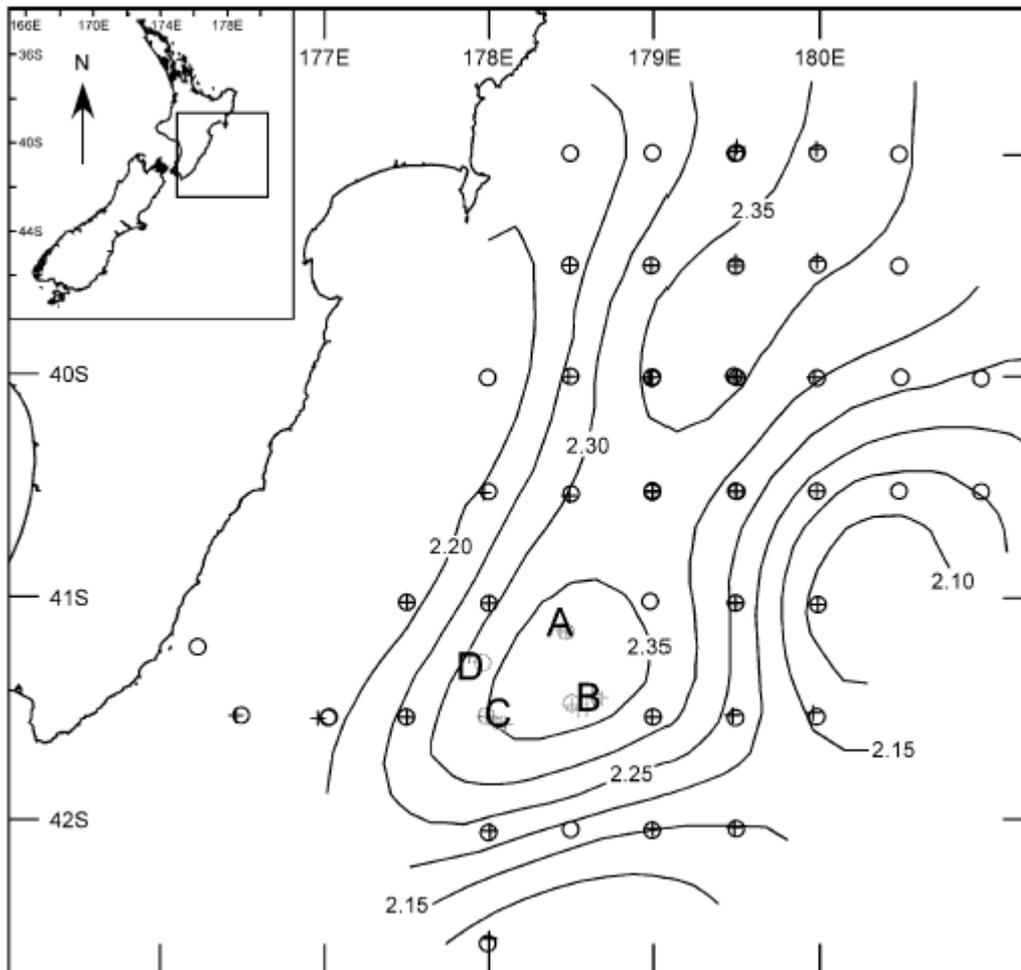
The Wairarapa Eddy, off the east coast of the North Island of New Zealand, is one of three large (100 km diam.) anticyclonic eddies appearing to be permanent features of the circulation in the region. In the mean, the eddy is centred near 41°S, 178°30'E, c. 180 km offshore. A detailed dynamical analysis of the eddy has not yet been made. However, it is probably formed by retroflexion of the East Cape Current as it hits the Chatham Rise.

The Wairarapa Eddy is believed to be important to the distribution of *J. edwardsii* phyllosomas in New Zealand as it is believed to entrain phyllosomas (Booth & Stewart 1992; Chiswell & Roemmich 1998; Chiswell & Booth 1999). Both historical larvae catches (Booth & Stewart 1992; Booth *et al.* 1998) and models of dispersal (Chiswell & Roemmich 1998; Chiswell & Booth 1999) show higher levels of larvae within the eddy than outside. Indeed, without the Wairarapa Eddy system it is possible that *J. edwardsii* would not be able to sustain a population off the south-east coast of the North Island.

Understanding the vertical pattern of distribution of phyllosomas is an important prerequisite for understanding and modelling transport processes, yet this remains unclear for *J. edwardsii* (Bruce *et al.* 2000). The aim of the present study was to examine the vertical distribution and DVM of *J. edwardsii* by analysing vertically stratified samples collected from the Wairarapa Eddy system off the east coast of New Zealand. New Zealand, and the Wairarapa Eddy in particular, were chosen for this study because of the availability of a suitable vessel, and because of the historic consistency of being able to locate high-density patches of phyllosoma. The results are compared with existing knowledge of *J. edwardsii* DVM both in New Zealand and in Australia.

## Methods

Sampling took place between 17 March and 2 April 2003 from the 70 m RV *Tangaroa* off the east coast of the North Island of New Zealand (Figure 1).



**Figure 1** Region of study off the east coast of the North Island, New Zealand in relation to the physical oceanography as derived from sea surface height anomalies derived from Conductivity-Temperature-Depth (CTD) data. (, CTD casts; +, surface net stations; A, B, C, and D denote the locations of the 24-h sampling stations).

The voyage was timed to coincide with the presence of two cohorts of *J. edwardsii* phyllosomas in the plankton within the region of the Wairarapa Eddy (Chiswell & Booth 1999), the oldest cohort from the spring 2001 (October–November) egg hatching and the more recent from the spring 2002 egg hatching. The oldest cohort would be expected to be at or close to final stage (Stages X–XI), whereas the younger cohort would consist of mid-stage (V–VIII) larvae.

#### *Physical oceanography*

A Seabird CTD (conductivity-temperature-depth) profiler, in a 12-place rosette with 1.2 litre Niskin bottles, was used to make continuous vertical profiles of temperature and salinity at each station. Water samples were collected to calibrate the conductivity sensor. CTD data collection and processing methods were the same as those detailed in Chiswell *et al.* (1993) and Walkington & Chiswell (1998). Temperature and salinity were processed to 2 dbar bins. Temperature was estimated to be accurate to 3

mK and salinity to  $5 \times 10^{-3}$ . CTD casts were made to within 20 m of the sea floor in a grid with nominal spacing of  $0.5^\circ$  in latitude and longitude.

#### *Net collections*

Two net systems were used to sample the zooplankton. Surface macrozooplankton (animals at least 2 mm; Omori & Ikeda 1984) were sampled with a square surface net (mouth area  $1 \text{ m}^2$ ; mesh size  $1000 \mu\text{m}$ ) fitted with a General Oceanics mechanical flowmeter. The surface net was typically deployed following each CTD cast, and concurrently with the start of a midwater trawl from the midship A-frame.

Macrozooplankton, including phyllosomas, greater than c. 1 cm in the water column were sampled with an Engel fine-meshed (12 mm stretch) midwater trawl (FMMWT) fitted with an opening/closing codend (MIDOC; Pearcy *et al.* 1977). The FMMWT was 60 m long with a nominal mouth area of  $70 \text{ m}^2$ . The MIDOC contained six codends with a mesh size of  $500 \mu\text{m}$ . An electronic timer triggered codends at pre-defined time intervals to give a 20 min sampling period per depth stratum. Probes concurrently collected data on depth, temperature, and light (relative) levels. FMMWT depth, headline height, and wing spread were monitored acoustically.

Prospecting tows (c. 30 min at a headline depth of 30 m) with the FMMWT were used to locate the first high-density patch of phyllosomas and thereby initiate the first 24-h sampling series. The trigger was  $\geq 60$  phyllosomas in a tow. A drogue, with the parachute set at a depth of 5 m, was deployed at the start of each series to mark the start position for each subsequent tow. Tows were made into the wind.

Three night tows and three day tows were taken during each 24-h sampling series (except for Series D, see Figure 1). Tows were not made within 1 h either side of dawn or dusk. A standard tow consisted of a 30 min oblique tow to 300 m followed by oblique tows for 20 min each through strata of 200–300, 100–200, 50–100, 20–50, and 20 m to the surface. Despite the discrete depth sampling provided by the opening/closing MIDOC system, phyllosomas from one sampling strata may become temporarily entangled in the net ahead of the codend and provide a source of contamination for subsequent strata (Dennis *et al.* 2001). To reduce the amount of contamination between strata, the final 5 min of each stratum's tow was held at the upper boundary of that stratum. On two separate occasions the sampling pattern was altered to allow us to explore to a greater depth (500 m).

Samples were sorted immediately after each tow. Phyllosomas were removed and at the same time catches rough sorted into the major groups—fish, euphausiids, cephalopods, prawns, gelatinous material, and amphipods/pteropods/isopods. Phyllosomas were further sorted into species. *J. edwardsii* phyllosomas were then staged according to Lesser (1978) as modified by Booth (1994). Phyllosomas were subsequently either frozen at  $-30^\circ\text{C}$ , preserved in 100% ethanol, or preserved in 10% buffered formalin in sea water.

### *Data analyses*

Larval counts were standardised to larval density (number per 1000 m<sup>3</sup>) by dividing the number of larvae caught by the volume of water filtered by each net. Volume filtered was calculated from the equation  $V = D \times A$ ; where  $D$  is distance travelled (derived from the flowmeter reading for the surface net, or from ship's speed (m s<sup>-1</sup>) x tow duration (s) for the FMMWT) and  $A$  = net mouth area (1 m<sup>2</sup> for the surface net, headline height x wing spread for the FMMWT). Because of the MIDOC codend design we were unable to close net 6 while the FMMWT was being brought back onto the deck of the ship. Tow duration for this net was estimated from the depth reading of the MIDOC timer. A stabilised depth reading indicated that the codend was on the surface and was taken to be the end of fishing for net 6.

A Poisson generalised linear model (GLM) (McCullagh & Nelder 1989) was used to model larval counts in terms of depth and time of day while controlling for both volume filtered per tow and regional variability in abundance. The typically patchy nature of zooplankton was accounted for by allowing for overdispersion of the Poisson model.

Data analyses were complicated by the failure of the closing device for net 5 on four of the 22 midwater tows. For these four tows, net 6 failed to open and the net 5 data represents the combined net 5 and 6 counts for the upper 50 m of the water column. Three separate approaches were taken to account for the failures: (1) the net 5 and 6 data from the failed tows were excluded from the analysis; (2) the net 5 and 6 data were amalgamated for all tows, reducing the depth resolution to the upper 50 m of the water column; and (3) the missing individual net 5 and 6 counts were imputed via the EM algorithm (Tanner 1996).

The Poisson distribution is an exponential family (McCullagh & Nelder 1989), and so the EM algorithm for imputing the missing counts takes a particularly simple form (Tanner 1996). Given the totals of the missing net 5 and 6 counts from the failed tows: (1) initial estimates of the missing values are constructed by dividing the known totals equally between nets 5 and 6, and the Poisson GLM fitted to this augmented data set; and (2) improved estimates of the missing values are constructed by dividing the known totals in the proportion predicted by the model, and the model refitted.

Step 2 was repeated until there were no more changes in the fit. Except for where the degree of significance differed such that it provided an alternative conclusion, we report only the results of the imputation approach.

## **Results**

### *Physical oceanography*

An analysis of the dynamic height, derived from hydrographic observations, identified two lobes in dynamic height (Figure 1). The northern lobe was centred near 39°40'S, 179°30'E, while the southern

lobe was centred near 41°40'S, 178°30'E. The southern lobe was centred near the mean of the Wairarapa Eddy as defined by Roemmich & Sutton (1998), but was somewhat smaller than suggested by the mean analysis.

Wind speeds were relatively consistent over the first three of the four 24-h sampling series. Over all 24-h sampling series, wind speeds averaged  $15.1 \pm 1.3$  (SE) knots. However, during the final 24-h sampling series wind speeds during the night tows were relatively high, resulting in a deeper mixed layer during the following day tows (Table 1).

**Table 1** Depth of mixed layer by day and night for each of the 24-h sampling series estimated from the depth at which the maximum change in temperature occurred, recorded by the electronics unit of the MIDOC codend on the FMMWT (fine-meshed midwater trawl).

| 24-h vertical series  | Depth of mixed layer (m) |       |
|-----------------------|--------------------------|-------|
|                       | Day                      | Night |
| A (25–26 Mar 2003)    | 43–61                    | 39–71 |
| B (27–28 Mar 2003)    | 41–56                    | 55–60 |
| C (29–30 Mar 2003)    | 36–50                    | 32–50 |
| D (31 Mar–1 Apr 2003) | 34–78                    | 27–37 |

### Net collections

Sampling was conducted within the lower lobe of the dynamic height field identified from the hydrographic observations (Figure 1). A total of 51 surface net tows and four vertical FMMWT series, comprising 22 (10 day, 12 night) tows, were taken. Total phyllosoma captures were dominated by *J. edwardsii* (930) with lower numbers of *Antipodarctus aoteanus* (193) and *Ibacus alticrenatus* (3) also recorded. No phyllosoma of the second commercially fished palinurid, *Sagmariasus verreauxi*, were recorded. The standardised number of *J. edwardsii* phyllosomas per FMMWT sample ranged from 0 to 1.65 per 1000 m<sup>3</sup> ( $\bar{X} \pm \text{SE} = 0.05 \pm 0.015$ ). The majority (90%) were mid-stage (V–VIII) phyllosomas, with the remainder being late-stage (VIII A–XI) phyllosomas. A total of 161 ( $\bar{X} = 0.11$  per 1000 m<sup>3</sup>) *J. edwardsii* phyllosomas were collected during the day, whereas 769 ( $\bar{X} = 0.55$  per 1000 m<sup>3</sup>) were collected at night.

### Data analyses

The three methods used to analyse the data, given the missing values, gave similar results with only minor differences in the degree of significance. Where confidence intervals and estimates of relative abundance are given, these are derived from the imputation model. Typically the EM algorithm used to derive imputed net 5 and 6 counts converged within eight iterations. For all models fitted, the

residual deviance exceeded the residual degrees of freedom by at least a factor of three, justifying the choice of an overdispersed Poisson model.

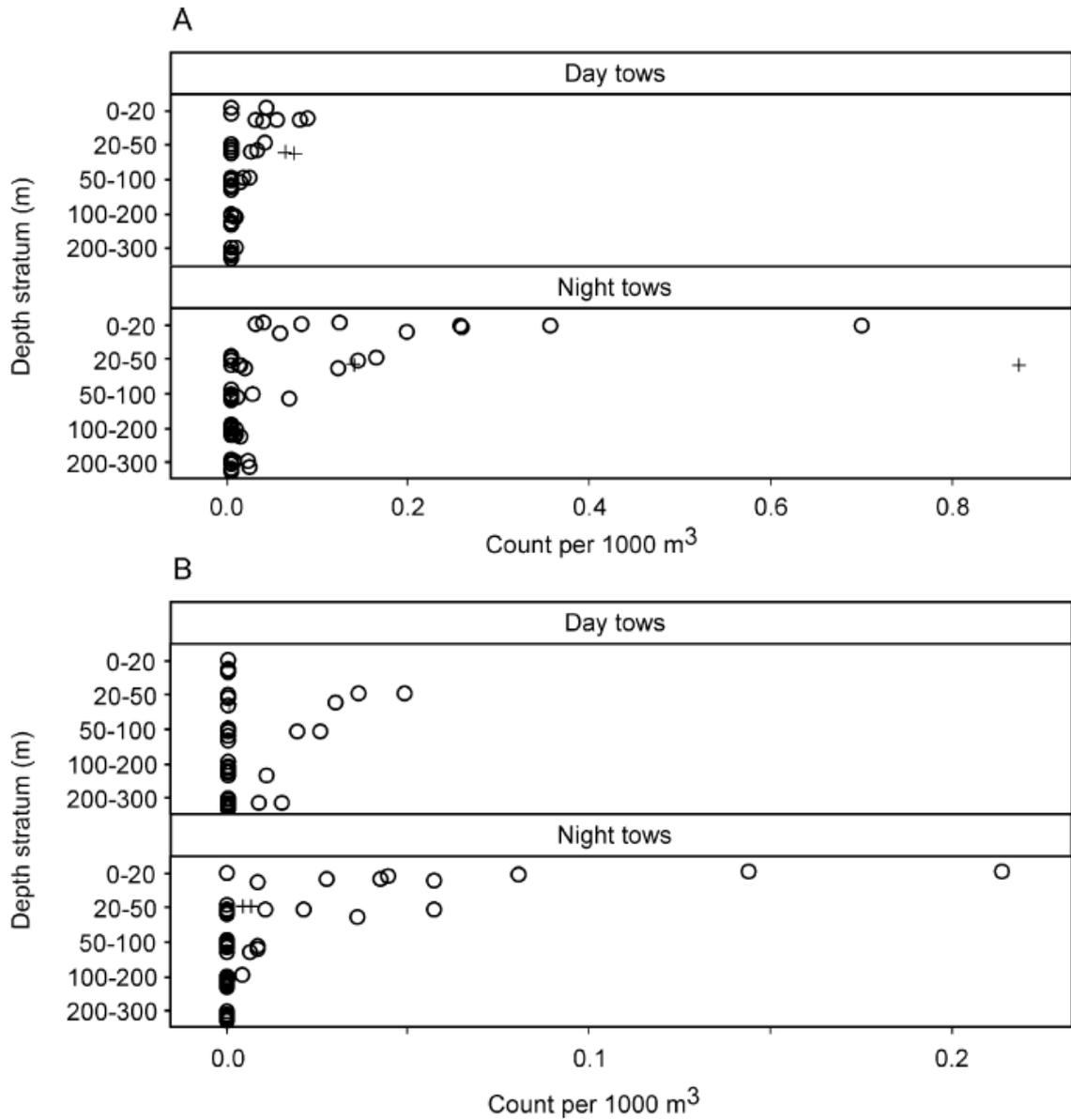
Total catches of *J. edwardsii* phyllosomas were significantly ( $F_{1, 17} = 14.1$ ,  $P < 0.002$ ) higher at night for all strata combined than during the day (Figure 2A: mid-stage phyllosomas; Figure 2B: late-stage phyllosomas). Based on the model, the 95% confidence interval for the ratio of day to night counts was 1.8–12.2. It was noted that one tow in particular had an extremely high catch. Even with this tow excluded from the analyses, the day–night difference remained significant ( $F_{1, 16} = 20.6$ ,  $P < 0.001$ ) although the 95% confidence interval was reduced to 1.8–5.8.

There was, however, no significant ( $F_{4, 97} = 1.6$ ,  $P = 0.17$ ) difference in the pattern of vertical distribution of phyllosomas (all stages combined) between day and night, after controlling for the observed day–night difference in total abundance. Phyllosomas were most abundant in the upper 50 m of the water column (and particularly the upper 20 m) regardless of time of day.

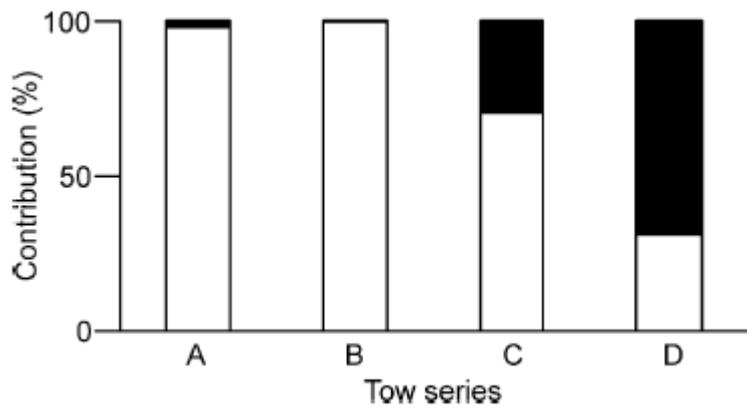
Although there was no difference in the pattern of vertical distribution of all phyllosoma stages combined, several lines of reason lead us to analyse the data separately for mid stage (V–VIII) and late stage (VIII A–XI) phyllosomas. First, on a series-by-series basis there was a difference in the spatial distribution of mid- and late-stages. Late-stage phyllosomas were almost exclusively found in tows from series C and D, located towards the inshore side of the eddy (Figure 3). Second, differences in the pattern of vertical distribution between stage groups have been reported within the Palinuridae for what is perhaps the best documented species, *Panulirus cygnus* (Chittleborough & Thomas 1969; Rimmer & Phillips 1979).

There was no significant ( $F_{4, 93} = 0.3$ ,  $P = 0.8$ ) difference in the vertical distribution of mid-stage phyllosomas between day and night. Nor was there any evidence of a difference in the vertical distribution of mid-stage phyllosomas between the “inshore side” (series C and D) and “central” (series A and B) regions of the eddy ( $F_{4, 93} = 0.17$ ,  $P = 0.9$ ). Mid-stage larvae occurred primarily (96% of the total recorded) within the upper 50 m both day and night (Figure 4), with 75% of larvae occurring in the upper 20 m of the water column.

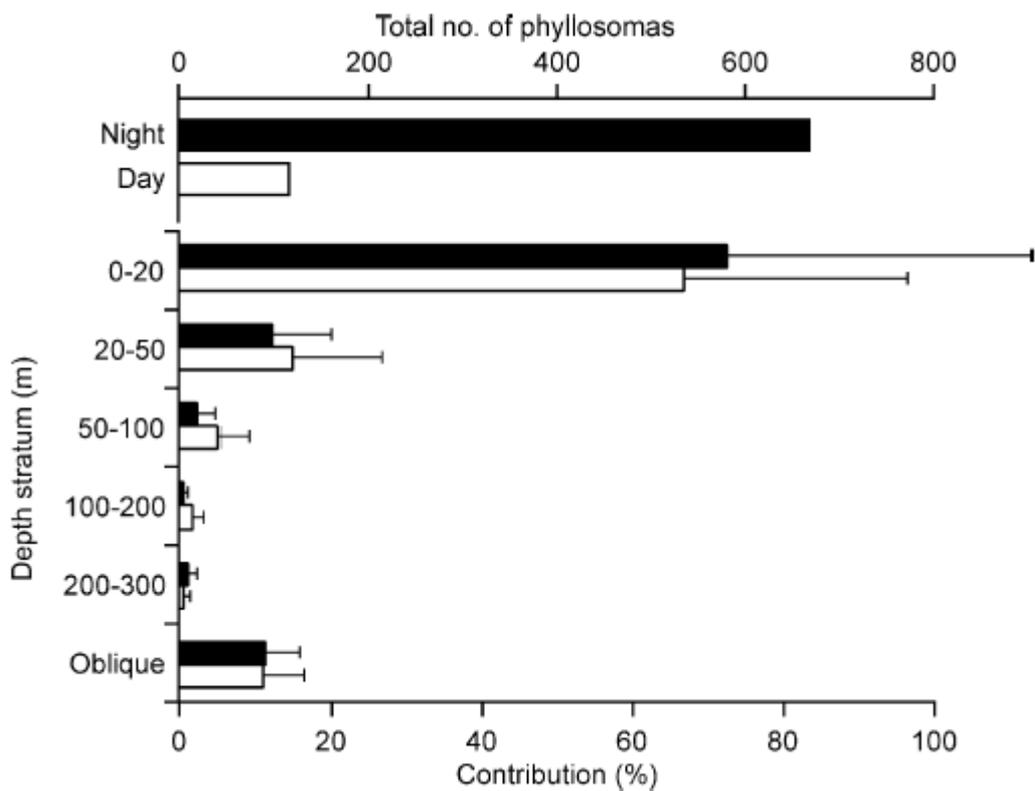
Too few late-stage phyllosomas were present in series A and B to permit analyses. However, there was a significant ( $F_{4, 34} = 10.5$ ,  $P < 0.001$ ) difference in the vertical distribution of late-stage phyllosomas for series C and D between day and night. During the night, late-stage phyllosomas were concentrated in the upper 50 m (95%) with the majority (68%) recorded in the upper 20 m (Figure 5). During the day, late-stage phyllosomas were absent from the upper 20 m; 58% of the total collected were recorded in the 20–50 m stratum, 23% in the 50–100 m stratum, and the remaining 19% of phyllosomas were recorded below 100 m.



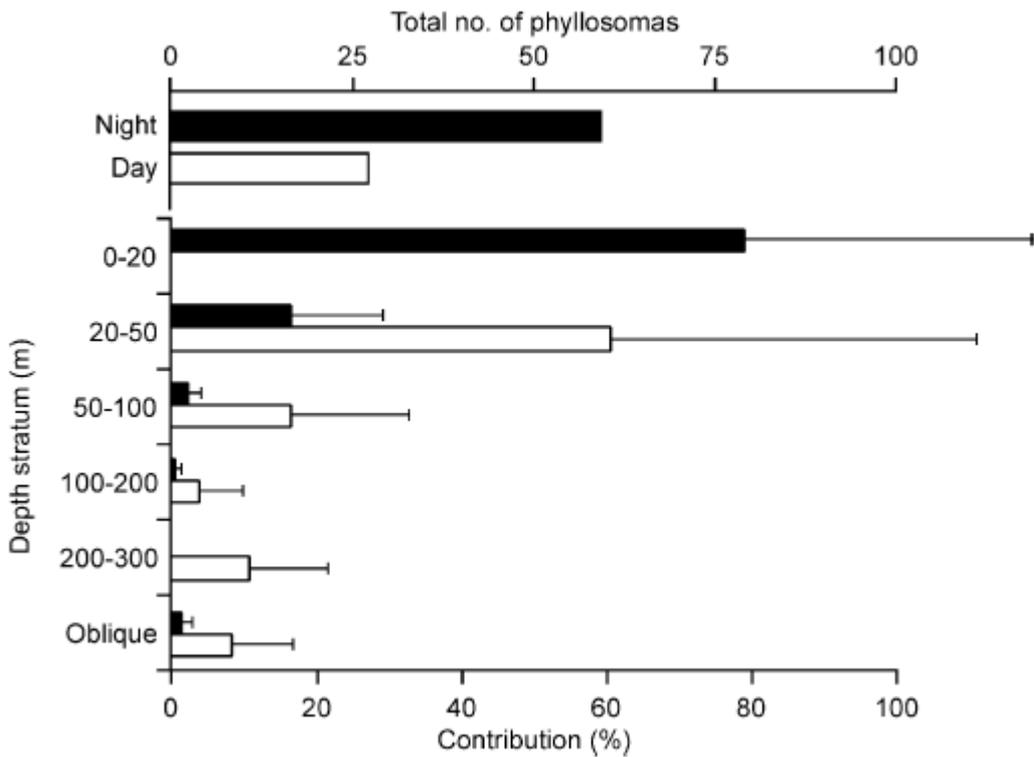
**Figure 2** Distribution of catch between day and night fine-mesh midwater trawl tows, as measured by abundance (count per 1000m<sup>3</sup>) for A, mid-stage and B, late-stage *Jasus edwardsii* phyllosomas, off the east coast of the North Island, New Zealand. Crosses (+) indicate failure of net 5 to close and therefore represent combined counts for nets 5 and 6.



**Figure 3** Contribution of mid-stage (open bars) and late-stage (closed bars) *Jasus edwardsii* phyllosomas to each of the four 24-h sampling series off the east coast of the North Island, New Zealand.

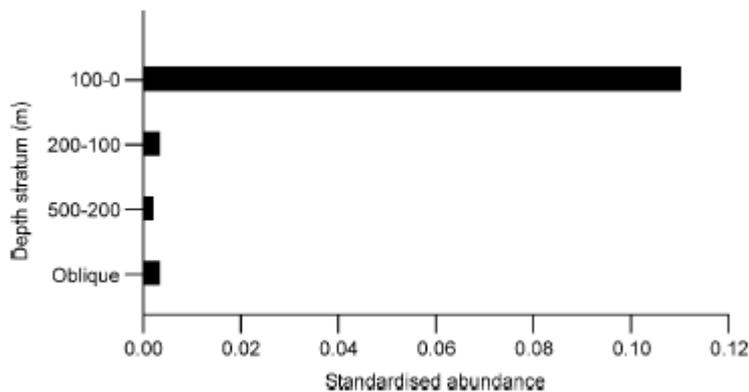


**Figure 4** Day/night comparison of mid-stage *Jasus edwardsii* phyllosomas caught by the fine-mesh midwater trawl net off the east coast of the North Island, New Zealand. Top axis provides total numbers (unstandardised). Lower axis indicates the percentage of phyllosomas contributing to either day (open bars) or night (closed bars) tows for each depth stratum, based on standardised abundance (per 1000 m<sup>3</sup> ± 1 SE).



**Figure 5** Day/night comparison of late-stage *Jasus edwardsii* phyllosomas caught by the fine-mesh midwater trawl net off the east coast of the North Island, New Zealand. Top axis provides total numbers (unstandardised). Lower axis indicates the percentage of phyllosomas contributing to either day (open bars) or night (closed bars) tows for each depth stratum, based on standardised abundance (per 1000 m<sup>3</sup> ± 1 SE).

Two deep FMMWT tows to 500 m were made during the day to determine if phyllosoma were descending to depths outside the 300 m range of our standard 24-h series. In both tows, *J. edwardsii* phyllosomas were again concentrated in the upper 100 m, with virtually none below 200 m (Figure 6).



**Figure 6** Vertical distribution of all *Jasus edwardsii* phyllosomas collected from two tows between the surface and 500 m during daylight hours off the east coast of the North Island, New Zealand.

## Discussion

*Jasus edwardsii* phyllosomas were primarily recorded within the upper 100 m and over similar depth ranges to those reported for other palinurid and scyllarid species. Diel differences in vertical

distribution were recorded for late stage phyllosomas only. However, a confounding result of the present study was the large difference in total phyllosoma abundance between day and night across all strata combined. In an ideal sampling scenario, we would expect the combined abundance of phyllosomas to be similar both day and night, with differences occurring between strata resulting from changes in vertical distribution. In addition, the patchy distribution of phyllosomas and the relatively low counts observed reduced the overall statistical power of our analyses. The extent of this is difficult to quantify, given both the over-dispersion of the data and the failure of net 5 to close on four occasions.

Several possible explanations for the difference in abundance between day and night tows were considered and each of these are discussed in turn.

(1) Phyllosomas may have migrated out of the depth range sampled, leaving day catches comprised mainly of stragglers. This would suggest that the primary day habitat for *J. edwardsii* phyllosoma was below 300 m (the limit of most of our sampling) and that they were able to ascend/descend to and from that depth during the 2-h period around dawn and dusk where no sampling occurred. The diel vertical movements of phyllosoma of all species for which data are available have been primarily restricted to within the upper 100 m of the water column. Although *Jasus* phyllosoma have been recorded to at least 300 m (Pollock 1986; Booth 1994; Bruce *et al.* 2000) and thus perhaps the deepest so far for phyllosoma, the number of larvae recorded below 150 m is extremely low. No *J. edwardsii* larvae were recorded below 300 m during our daytime sampling. This suggests that the deep distribution of *J. edwardsii* larvae may be the result of either low frequency events rather than a regular diel pattern or represent net contamination from upper strata. Furthermore, a vertical swimming rate in excess of  $4 \text{ cm s}^{-1}$  would be required for larvae to move between the surface and 300 m within the time period between our day and night tows. This is nearly 8 times the rate calculated for *P. cygnus* larvae (c.  $0.45\text{--}0.56 \text{ cm s}^{-1}$ ) by Rimmer & Phillips (1979) and 4 times that suggested for *J. edwardsii* by Chiswell & Booth (1999). Therefore it is unlikely that *J. edwardsii* phyllosomas were descending below our 0–300 m sampling range such that only stragglers were collected during the day.

(2) Phyllosomas may be avoiding the net during the day. Visual net avoidance has been demonstrated in a variety of planktonic taxa and mesopelagic species (e.g., Pearcy & Laurs 1966). However, this response is generally restricted to the more mobile species. Phyllosomas are relatively poor swimmers (Chiswell & Booth 1999; Yeung & Lee 2002 ( $<1 \text{ cm s}^{-1}$ )) and, given its  $70 \text{ m}^2$  mouth opening, it would seem unlikely that they would be able to avoid the FMMWT.

(3) Horizontal aggregation of phyllosomas at night may result in a tendency towards higher night catches. Phyllosomas of *P. cygnus* have been found to actively aggregate at night in areas of increased micronekton biomass (Ritz 1972). It is also possible that phyllosomas moving closer to the surface at night may aggregate because of physical forces such as Ekman surface slicks. Indeed, high variability in night catches of *P. cygnus*, even when replicate hauls were taken at a single station, were observed

by Ritz (1972). Furthermore, higher overall night versus day catches of *P. cygnus* appear to have taken place in two separate studies (Rimmer & Phillips 1979; Phillips & Pearce 1997). These studies suggested that night-time horizontal aggregation may result in a bias towards higher night catches.

(4) The sampling strategy utilised may have increased the bias towards higher night-time catches if larvae were migrating to the upper strata during that period. If vertical migration were occurring, we would expect there to be a difference in the number of phyllosoma caught between day and night because of the strata sampling design. Deeper strata covered a wider depth range than the more shallow strata sampled, and thus sampling effort was greater in these shallow strata. Any migration towards the surface at night would thus result in an increase in the overall number of phyllosoma caught at night. Nevertheless, it seems unlikely that this alone would account for differences as large as those observed. Nor can this difference be attributed to the extremely high catch in one trawl, as the ratio between day and night remained large even with this trawl excluded from the analyses.

(5) The net design may have resulted in a bias towards collecting more phyllosomas within the upper 20 m if phyllosomas were concentrated in this stratum at night as a result of vertical migration. The overall fishing efficiency of the FMMWT is affected by both the length of time the net fishes and by the area of the mouth. Because the codend of net 6 cannot be closed, it continues to fish while the net is brought onboard, thus increasing the length of time the net fishes in the 0–20 m stratum. However, counteracting this increase in fishing time, the effective mouth area of the net decreases as it begins to collapse on approach to the surface. A slight increase in overall fishing efficiency may bias the data towards greater night-time catches if phyllosomas were more concentrated in the upper 20 m at night as compared to day.

The significant difference between day and night catches prompted us to examine the vertical distribution of *Antipodarctus aoteanus* phyllosomas to see if similar confounding patterns in total abundance were repeated. *A. aoteanus* phyllosomas showed a similar tendency to concentrate in the 0–20 m stratum during the night. However, there was no evidence for a bias towards higher overall night-time catches, with roughly equal numbers being caught during the day and night. It is, thus, unlikely that net design or sampling strategy contributed to the difference observed between day and night catches in *J. edwardsii* and the most plausible reason for the observed differences was perhaps the influence of horizontal aggregations at night as suggested by Rimmer & Phillips (1979) and Phillips & Pearce (1997).

Although we were unable to fully account for the significant difference in overall abundance of *J. edwardsii* phyllosomas between day and night tows, we found no evidence to reject our conclusions regarding the diel vertical behaviour of mid and late stages.

### *Comparisons with other patterns of vertical distribution*

The vertical distribution and diel migration of phyllosomas are, in general, poorly understood despite the significance of such data for the modelling of transport processes. Published data exists for only a small number of species (Table 2). Generally, phyllosomas are reported to concentrate in the upper 30–50 m during the night and below 30–50 m during the day. Furthermore, the diel pattern did not appear to change between developmental stage for any of the species except *P. cygnus* (Rimmer & Phillips 1979).

The vertical distribution of *J. edwardsii* phyllosomas has been less well studied. Lesser (1978), Booth (1994), and Bruce *et al.* (2000) reported that *J. edwardsii* phyllosomas may undergo vertical migrations at least as extensive as those of the other species. However, these studies did not use nets capable of discrete depth sampling and this precluded a more detailed examination of vertical distribution.

Lesser (1978) reported on the night vertical distribution of *J. edwardsii* phyllosoma from samples taken off the east coast of the North Island, New Zealand. He indicated that at around stage V, *J. edwardsii* phyllosomas shift from a predominantly near-surface habit to one in deeper waters. Lesser (1978) found that later stages of *J. edwardsii* phyllosomas remained deeper in the water column, with stage VI phyllosomas largely in the 5–40 m depth stratum and Stage XI phyllosomas in the 40–60 m depth stratum.

Booth (1994) reported on the vertical distribution of *J. edwardsii* phyllosomas from the east coast of the North Island, New Zealand. He indicated that during the day phyllosomas vacated the upper 30 m of the water column, and could be found to depths of at least 310 m. During the night the highest concentrations of mid- and late-stage phyllosomas were within the upper 30 m.

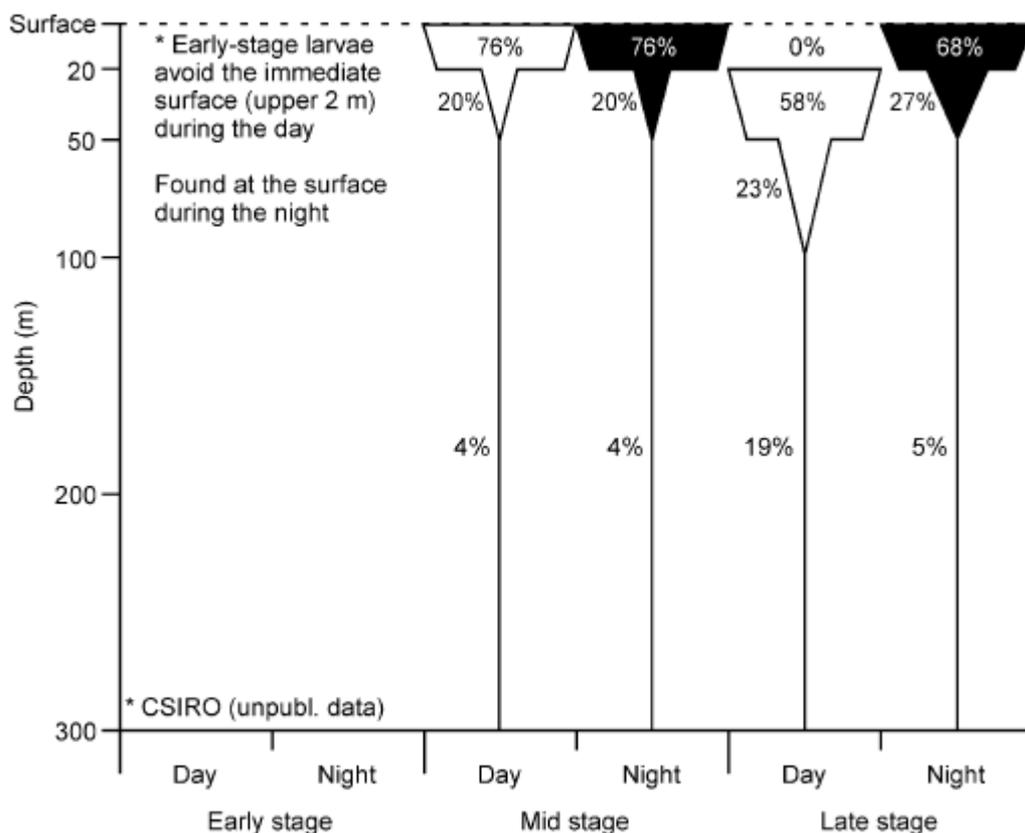
Bruce *et al.* (2000) reported on the vertical distribution of *J. edwardsii* phyllosomas off south-eastern Australia. They indicated that phyllosomas showed a tendency to move away from the surface (0–5 m) during the day. Although Bruce *et al.* (2000) had vertically stratified samples using a similar configuration to that of the present study, the width of depth strata was too large and phyllosoma numbers too low to permit rigorous statistical analyses.

The present study has built upon these previous studies to refine our understanding of DVM for *J. edwardsii* phyllosomas and a model summarising this behaviour is proposed in Figure 7. We are able to confirm that *J. edwardsii* phyllosomas undergo vertical distributions at least as extensive as other lobster species. Phyllosomas were primarily located within the upper 100 m of the water column with low level abundances recorded to 300 m. Diel vertical migration was restricted to late-stage phyllosomas which avoided the 0–20 m surface layer during the day.

**Table 2** Summary of vertical distribution for phyllosomas indicating the depth of the main concentration of phyllosomas. S, south of Matanzas, Cuba; N, north of Matanzas, Cuba.

| Species                    | <u>Depth (m)</u>     |           | <u>Depth (m)</u>         |             | Reference                      |
|----------------------------|----------------------|-----------|--------------------------|-------------|--------------------------------|
|                            | Day                  | Stage(s)  | Night                    | Stage(s)    |                                |
| <i>Panulirus argus</i>     | 50                   | all       | surface                  | all         | Buesa Mas (1970)               |
|                            | 10–20                | all       | surface                  | all         | Austin (1972)                  |
|                            | 25–50                | all       | 0–100                    | all         | Baisre (1976)                  |
|                            | 40–90(S)<br>30–70(N) | all       | 10–50(S)<br>dispersed(N) | all         | Hernandez <i>et al.</i> (2000) |
| <i>P. cygnus</i>           | 30–60                | early     | 0–30                     | early, late | Rimmer & Phillips (1979)       |
|                            | 50–120               | mid, late | 0–20                     | mid         | Phillips (1979)                |
| <i>P. longipes</i>         | 50–80                |           | 10–50                    |             | Minami <i>et al.</i> (2001)    |
| <i>Scyllarus cultrifer</i> | 50–80                |           | 10–50                    |             | Minami <i>et al.</i> (2001)    |
| <i>Jasus lalandii</i>      | 0–100                |           | 0–300                    |             | Pollock (1986)                 |
| <i>J. edwardsii</i>        |                      |           | 0–5                      | early       | Lesser (1978)                  |
|                            |                      |           | 5–40                     | mid (VI)    | (1978)                         |
|                            |                      |           | 40–60                    | late (XI)   |                                |
|                            | 30–310               |           | 0–30                     |             | Booth (1994)                   |
|                            | 0-20                 | mid       | 0-20                     | mid         | Present study                  |
|                            | 20-50                | late      | 0-20                     | late        |                                |

Vertical migration has either been ignored in previous attempts to model the transport and recruitment processes of *J. edwardsii* phyllosomas, or has been based upon that of *P. cygnus*. The current study highlights the need to use species-specific information on vertical distribution when modelling larval transport pathways.



**Figure 7** Vertical distribution model for early-, mid-, and late-stage *Jasus edwardsii* phyllosomas collected in vertically-stratified tows to 300 m off the east coast of the North Island, New Zealand. Numbers refer to percentage of phyllosoma within the depth stratum whereas the vertical lines indicate the remaining percentage (each column sums to 100%). Data for early-stage phyllosomas is from CSIRO unpubl. data for the south-east region of Australia.

### Acknowledgments

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## APPENDIX E: COMMUNICATION & EXTENSION

This section illustrates some of the articles and activities used for extension of results to industry managers and researchers during the course of the project.

### (i) South Australian Rock Lobster Industry Fact Sheet



## RESEARCH AND DEVELOPMENT

THE AUSTRALIAN SOUTHERN ROCKLOBSTER industry in South Australia takes an active role in assessing and determining research programs to not only ensure sustainable fishing, but also to increase the value of the fishery.

The most important research program is run jointly by the industry and South Australian Research & Development Institute (SARDI)\* each year to monitor and assess the state of lobster stocks, population dynamics, growth rates and fishing impacts.

The program, which began in 1993, has built up one of the world's most extensive lobster databases, allowing the fishery managers to make sound judgments.

Each year the Fishery Management Committees for the Southern and Northern Zones decide on specific research priorities for their region.

However, over the past year the industry has moved to streamline research projects of common interest across the two zones and also all Australian Southern Rocklobster-producing States.

A joint Northern and Southern Zone subcommittee was formed in 2003 to identify generic research issues, set priorities, source funding, seek independent input and manage projects.

On a national level, the recently formed Southern Rocklobster Council will determine research and industry development projects relevant to the species.



## RESEARCH AND DEVELOPMENT



New national programs include a 2½-year study into the fate of larvae in their oceanic phase, which involves researchers from South Australia, Victoria, Tasmania and New Zealand.

Led by the CSIRO Division of Marine Research in Hobart and funded by the Fisheries Research and Development Corporation (FRDC), the study aims to forge greater understanding of larval transport, which is the key to interpreting patterns of recruitment, connections between regions and the ramifications of changing harvesting strategies.

Recent State-based research programs include a study to assess the levels of stress suffered by lobsters during fishing and processing, and trialling new pot designs.

Flinders University is working with South Australian fishers to determine which handling practices or holding systems create the least stress on lobsters, and it is hoped future studies will look at the impact on animal survival and meat quality.

A three-year research program to reduce octopus predation has resulted in a radical new approach to pot design – square pots with a pyramid-shaped inner chamber, which have been tested at sea in the South-East region.

*\* SARDI is a division of the South Australian Government's Primary Industries & Resources SA (PIRSA).*

The program, funded by industry and the FRDC, aims to reduce octopus predation, which costs the State's lobster industry about \$3 million each year.

The FRDC also is funding the development of a complex computer model of the State's lobster population dynamics to improve long-term management.

The result of the three-year project run by SARDI will be one of the most advanced models in Australia for analysing the status of lobster stocks.

In the 2002/03 season, Southern Zone fishers tested the use of automated electronic scales to streamline the recording of catch sizes.

The trial suggested the digital scales would prove more efficient and accurate compared to the traditional, manual weighing system.

Fishers are issued with smart eye buttons that are used to identify them at the scales through a PIN number. Their catch is weighed in bins tagged with radio frequency identification, and the information is automatically emailed to the lobster quota officer.

The industry is now investigating full electronic data recording, from on board vessels to shore to the processing factory.

*Pictures: Rosey Boehm*

**(ii) Article submitted to South Australian Rock lobster Industry News  
(September 2003)**

**Where do rock lobster larvae come from?**

A new FRDC funded project is attempting shed light on the long debated question of where southern rock lobster recruits come from and how some areas of the fishery maintain their populations. The project, lead by CSIRO Marine Research, is collaborative with SARDI Aquatic Sciences, TAFI, MAFRI and NIWA (New Zealand). It combines sophisticated oceanographic models with knowledge of larval biology to simulate the transport of southern rock lobster larvae by ocean currents across southern Australia.

“Southern rock lobster have an offshore larval phase lasting up to two years, one of the longest of any of the world’s lobster species,” says CSIRO’s Barry Bruce who leads the project. “This provides ample opportunities for larvae to be transported from one management zone to another.”

Although it is generally accepted that recruits to each zone may come from other zones, there is currently no information available to assess this and thus provide a more targeted approach to managing spawning stock biomass. Industry, managers and researchers alike, have long been interested in where larvae come from and whether some areas of the fishery are more important in supplying recruits than others.

“What happens in the larval phase holds many of the answers” says Bruce. “Recent developments in modelling techniques now give us the tools to look at this in a detailed way”.

The two and a half year project is now entering its second year and is producing its first results. “From what we have seen so far, says Bruce, “the picture is far more complex that the standard thoughts that larvae from western areas just get transported to the east. We see evidence of some larvae moving between zones, both to the east and west and of others recruiting back to their spawning locations, the latter even in areas like the Northern Zone of South Australia”.

The work still has a long way to go before the team will be confident that the model is capturing what really happens. But, if successful, the project will give industry and managers a much better understanding of recruitment patterns, the connections between regions and the likely benefits and risks of increasing spawning biomass or changing harvesting strategies in these regions.

**(iii) TRLFA response to presentation of project results**



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BARRY BRUCE  
C / CSIRO  
HOBART.

YOUR RECENT PRESENTATION AT CFAC // TAROONA 31<sup>ST</sup> MARCH 2006.

Dear Barry

Further to our conversation at Taroona after your presentation on the 31<sup>st</sup> March I would like to formally invite you to do the same at our May 26<sup>th</sup> 2006 meeting at the Earlington Hotel Earl St. Launceston.

I will speak to you closer to the date but at this point in time have scheduled you for pre/lunch if this is okay.

May I take the opportunity to congratulate you on the work you have put into your presentation and the ease with which it can be followed by both academics and fishers and I can assure you that there will be much discussion afterwards.

We look forward to seeing you in Launceston in May.

*RODNEY*

RODNEY TRELOGGEN  
CHIEF EXECUTIVE OFFICER TRLFA

# Lobster larvae benefit all

NEW light has been shed on the mysterious early life of southern rocklobster in a FRDC-funded modelling project (2002/007) undertaken by CSIRO in collaboration with the research agencies of four Australian states and New Zealand.

It reveals a massive gene pool swirling off southern Australia with a high degree of mixing and identifies the spawning locations that are the major contributors to successful

recruitment of *Jasus edwardsii*, the species common to five Australian jurisdictions: Western Australia, South Australia, Tasmania, Victoria and New South Wales.

The model shows that spawning stocks in each of Australia's seven management zones contribute to a larval pool that can be transported hundreds of kilometres offshore.

The vast majority of the larvae are either transported east, where they may contribute to recruitment in

other zones, or they find their way back to their zone of origin.

A minority travels in the opposite direction, to recruit west of its zone of origin.

Principal Investigator Barry Bruce said the model showed some zones consistently contributed more recruits than others, but all Australian management zones shared in this mutually-beneficial transfer.

He said the model showed a trans-Tasman exchange also was possible, but likely to be minor.

Key to the reciprocity is a long, free-travelling larval stage.

"Females spawn every 12 months, but the larvae spend up to 24 months riding the ocean currents before settling," said CSIRO modeller Russ Bradford.

"This means there are two sets of larvae in the water at all times, one about 12 months older than the other. The larvae develop through 11 different stages, called phyllosoma, that depend on currents to reach an ultimate destination. These stages have different behaviours and this alters the way each travels," he said.

## Vertical movers

Larval sampling by CSIRO and NZ's National Institute of Water and Atmospheric Research confirmed that larvae move up and down in the water column. Sampling east of New Zealand found larvae to a depth of 600m, though most were in the upper 100m.

Among the bigger specimens, larvae in their middle stages were concentrated in the upper 20m day and night.

Later-stage larvae were concentrated in the upper 20m at night, but

## Bluelink's power did it

THE massive grunt of one of the world's most powerful computers was the factor that allowed the dispersion of Australasia's southern rocklobster larvae to be accurately modelled at last. Even so, crunching the data took the Melbourne-based super-computer three months – its longest run ever.

The project combined a model of regional egg production, larval behaviour, growth and survival with Bluelink, the best oceanographic circulation model yet produced for Australian waters, to simulate the transport and survival of rocklobster larvae over a 10 year period.

Bluelink is a \$15m partnership of CSIRO, the Bureau of Meteorology and the Royal Australian Navy, formed to deliver ocean forecasts for the Australian region that provide information on ocean currents, temperatures and salinity - and eddies, surface and subsurface ocean behaviour - for military use, commercial shipping, safety at sea, ecological sustainability and for regional and global climate forecasting.

"In practical terms we folded Australasia's accumulated rocklobster biological data into Bluelink's oceanographic data," said Principal Investigator Barry Bruce.



**Barry Bruce – all zones give and receive.**

"The results represent a leap in knowledge from the previous CSIRO-led study (FRDC 96/107)."

Practical checks appear to have validated them.

"We were able to spot-check their accuracy by asking the model to provide retrospective results we could compare to historical field data," contributing scientist Caleb Gardner of the Tasmanian Aquaculture and Fisheries Institute told the Tasmanian Rock Lobster Fishermen's Association (TRLFA).

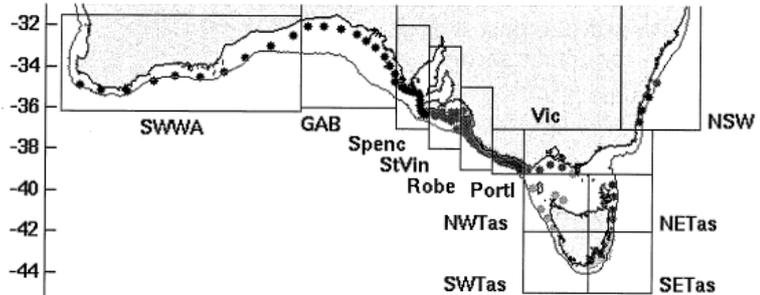
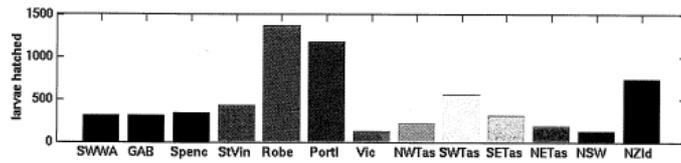
"The matching was good," he told TRLFA members fascinated by a project video showing pulses of larval production streaming across thousands of square kilometres of ocean.

**MORE: Barry Bruce, email Barry.Bruce@csiro.au**

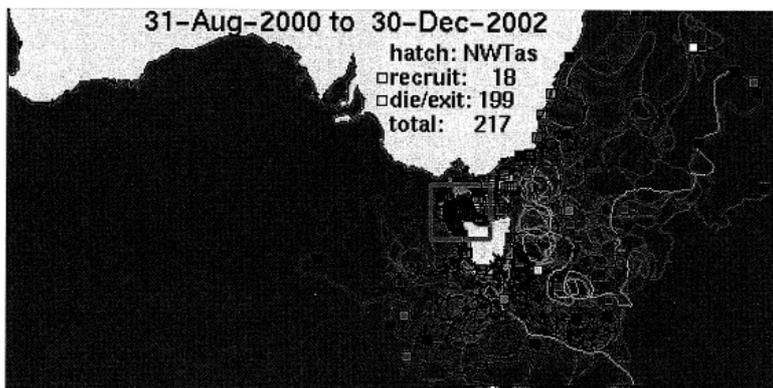
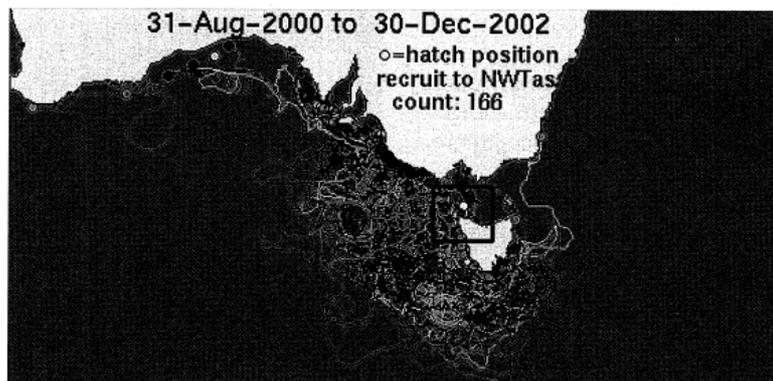
during the day were found deeper, mostly between 20m and 100m.

Although the final report on the modelling project is still being written, potential benefits for fishery management are apparent already:

- Australian jurisdictions may use the results to predict where recruitment benefits are likely to accrue if they increase the spawning biomass in any part of their fisheries
- The model confirms that Western Australia's breeding stock should continue to be carefully conserved, given that state's high degree of self-recruitment. In fact, despite a general west to east transport of larvae across southern Australia, WA's self-recruitment percentage is the highest of any southern Australian region
- The WA region also contributes recruits to South Australia's Northern Zone
- The model confirms that South Australia's Southern Zone and Victoria's Western Zone are the spawning heart of the species. These areas contribute recruits locally, as well as to the east, south and, to a more limited extent, to the west. Transport west is particularly likely to benefit the southeast region of SA's Northern Zone
- Some larvae produced off Tasmania's east and south coasts also contribute to recruitment in SA's Northern Zone
- For Tasmania, the model predicts that although its fishery receives recruits from South Australia and western Victoria, much of its



The area covered by the model spans the total distribution of southern rocklobster. Estimates of regional egg production - larvae hatched - represented in the bar graph were provided by State-based researchers.



The model's view of source and supply for north-west Tasmania.

recruitment comes from its own waters. Tasmania's south-west stock – including the southern females that start spawning before they reach legal size – is predicted to contribute the majority of recruits

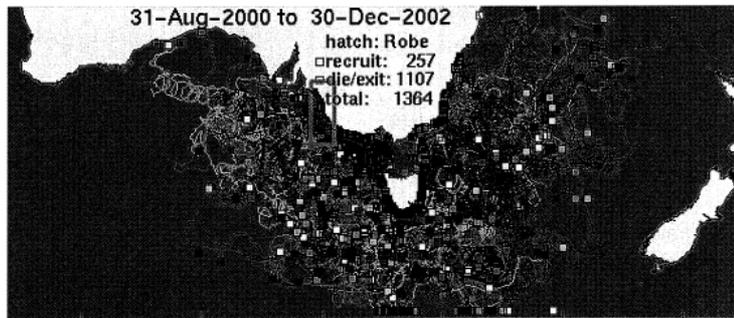
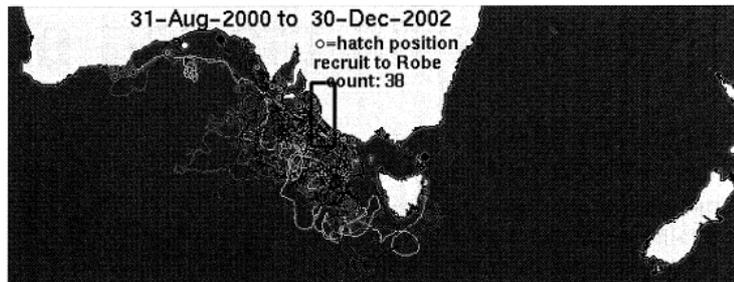
- The model predicts that increasing the spawning biomass in Tasmania's northern waters, where it is low, would produce benefits, with the best results likely to come from increasing spawning around Flinders Island, because fewer larvae appear to survive the west to east drift through shallow Bass Strait from the King Island region

Paradoxically, though the model provides crucial insights into the relationship between local egg production and larval movement, it cannot predict annual recruitment at any location.

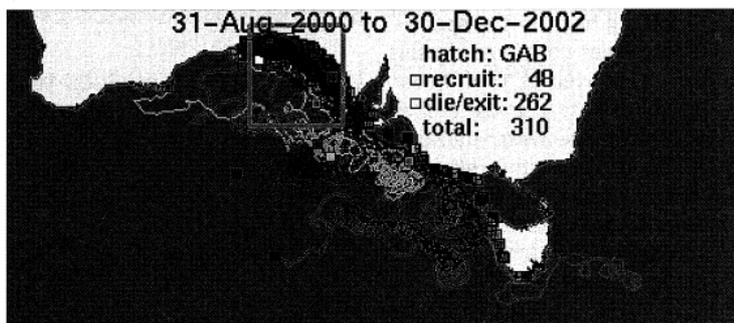
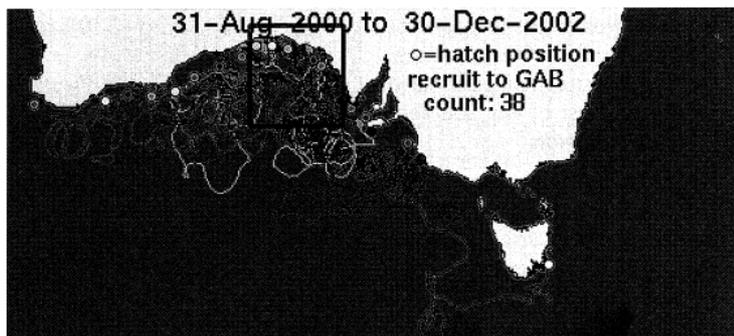
Verified against real data from puerulus collectors, it accurately predicts seasonal settlement peaks, but the big annual fluctuations in southern rocklobster recruitment - and their causes - remain a mystery. This suggests important biological processes contributing to settlement have yet to be discovered and understood.

So solving this puzzle becomes the next challenge, along with developing the ability to model future changes in ocean current behaviour likely to result from global warming and the consequent effects they will have on dispersion and settlement.

**MORE: Barry Bruce, email Barry.Bruce@csiro.au; Russell Bradford, email Russ.Bradford@csiro.au; David Griffin, email David.Griffin@csiro.au**  
See also Lobster insights in this edition's Final reports.



Source and supply for the Robe region in South Australia's Southern Zone - one of the species' major spawning areas - as shown by the model.



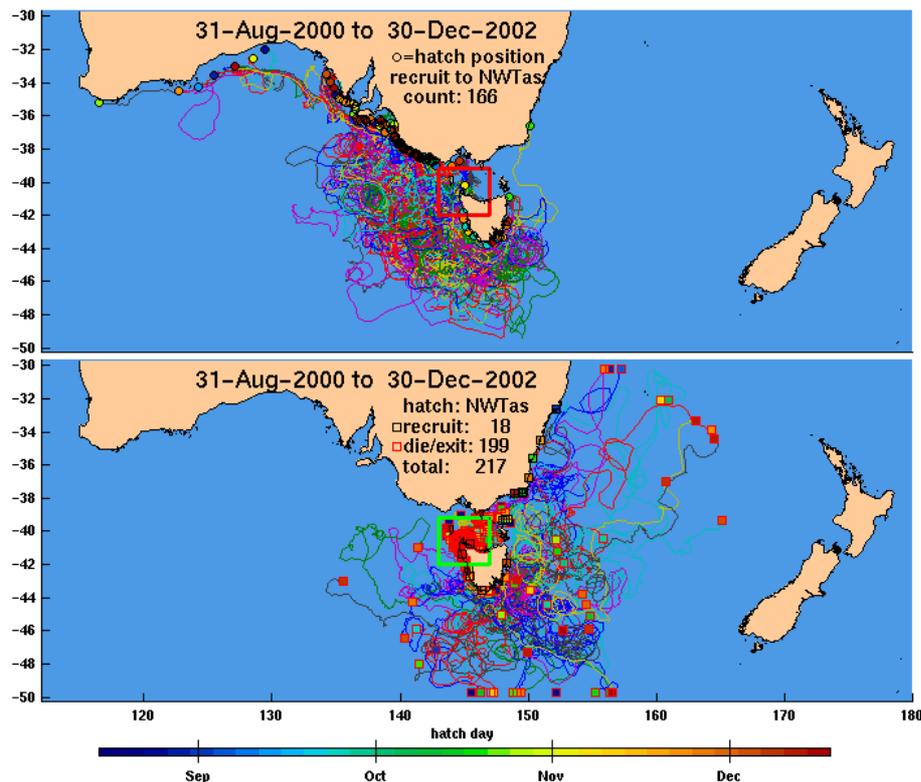
The model predicts where puerulus that successfully recruit within the red box come from and where rocklobster larvae that originate in the green box are transported to. This gives a region by region view of source and supply of recruits across the fisheries. The model keeps track of individual larvae and plots the paths - the connecting lines - that they travel.

## (V) TASMANIAN FISHING INDUSTRY NEWS - DECEMBER 2006/JANUARY 2007: P 5.

### Ocean model links lobster larvae and recruitment

A modelling project led by CSIRO has shed new light on larval transport and recruitment processes across Australia's southern rock lobster management zones.

The project linked a model of regional egg production, larval behaviour, growth and survival with the oceanographic circulation model, BLUElink, to simulate the transport and survival of larvae over a 10-year period.



BLUElinks off north-west Tasmania. The model predicts the source of puerulus that recruit to the red box, and the destination of larvae that originate in the green box. This gives a region-by-region view of source and supply of recruits to areas of the fishery. The model keeps track of individual larvae and plots their dispersal pathways.

This was the first biological application of the BLUElink model, an initiative of the Bureau of Meteorology, the Royal Australian Navy and CSIRO through the Wealth from Oceans Flagship.

After three months of supercomputing, the model revealed that while the seven rock lobster management zones across southern Australia are connected by larval transport, some zones have a relatively high degree of self-recruitment.

It also showed that some zones consistently produce more recruits to the total southern Australian population than others and that larval exchange between Australian and New Zealand stocks was minor.

Each management zone contributes to a swirling pool of larvae that can be transported hundreds of kilometres offshore. These larvae are either transported east where they

contribute to recruitment in zones further 'downstream' or find their way back to the zone from which they originated. In some cases, larvae recruited to zones to their west.

This mutually-beneficial transfer of larvae benefited all seven Australian management zones spanning the fishery, from Western Australia to New South Wales.

For Tasmania, the model predicts that although receiving recruits from South Australia and western Victoria, much of Tasmania's recruitment comes from its own waters. Tasmania's south-west stock – including the southern females that start spawning before they reach legal size – is predicted to contribute the majority of recruits.

The model further predicts that increasing spawning stock biomass in Tasmania's northern waters, where it is now low, will have benefits for the Tasmanian fishery. The benefits are likely to be maximised by increasing spawning stock biomass in the Flinders Island region. This is largely because fewer larvae appear to survive the west to east drift through shallow Bass Strait from the King Island region.

Paradoxically, though the model sheds new light on the relationship between local egg production and larval movement, it cannot predict annual recruitment.

Verified against real data from puerulus collectors, it accurately predicts seasonal settlement peaks, but the big annual fluctuations in southern rock lobster recruitment, and their causes, remain a mystery. This suggests important biological processes contributing to settlement have yet to be discovered and understood.

So solving this puzzle becomes the next challenge, along with developing the ability to model future changes in ocean current behaviour likely to result from global warming and the consequent effects they will have on larval transport and settlement.

*The project was funded by the Fisheries Research and Development Corporation and involved collaboration with the research agencies of five Australian states and New Zealand.*

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## **APPENDIX F: PRESENTATION OF RESULTS, ADDITIONAL FIGURES AND ANIMATIONS OF MODEL OUTPUTS.**

There is a CD-ROM available as part of this project report. Contact Barry Bruce ([Barry.Bruce@csiro.au](mailto:Barry.Bruce@csiro.au)) David Griffin ([David.Griffin@csiro.au](mailto:David.Griffin@csiro.au)) or Russell Bradford ([Russ.Bradford@csiro.au](mailto:Russ.Bradford@csiro.au)) or libraries at CSIRO Marine and Atmospheric Research for a copy if not included with this report.