Ocean circulation, Stokes drift and connectivity of western rock lobster (Panulirus cygnus) population

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Abstract
An individual-based model, incorporating outputs of a data-assimilating hydrodynamic model, was developed to investigate the role of ocean circulation in the recruitment processes of western rock lobster during its 9-11 month larval phase off the west coast of Australia. During austral summer, strong northward alongshore winds aid the offshore movement of early-stage model larvae from mid-shelf hatching sites into open ocean; during austral winter, eastward flows that feed the enhanced Leeuwin Current facilitate onshore movement of late-stage larvae towards near-shore habitats. Stokes drift induced by swells from the Southern Ocean is critical to retain larvae off the west coast. Diurnal migration and temperature-dependent growth are also important. Model larvae hatched in late-spring/early-summer grow faster due to longer exposure to warm summer temperature, which allows them to be transported towards the coast by the strong onshore flows in winter and reduces their natural mortality. Preliminary source-sink relationship indicates that the population was well mixed off the coast, with higher likelihood of settlement success from hatching sites in the north, mostly due to higher surface temperature. Weighted with the breeding stock distribution, area between 27.5°S-29.5°S, including the Abrolhos Islands, is the most significant hatching area to the success of settlement.

KEYWORDS: larvae, puerulus, Leeuwin Current, individual-based model, source-sink relationship
Introduction

Recruitment process for western rock lobster (*Panulirus cygnus*) fishery off the lower west coast of Western Australia (WA) have been found to be strongly influenced by the physical environment, with sea surface temperature (SST), the Leeuwin Current, and westerly winds being highly associated with interannual variation in puerulus settlements of western rock lobster off the coast. SST in February-April is found to be significantly correlated with puerulus settlements later in the year, and with a stronger southward-flowing Leeuwin Current, puerulus settlements in the southern locations tend to be relatively higher (Caputi et al. 2001). Westerly winds in late winter-spring also affect puerulus settlements (Caputi et al. 2010a). Puerulus settlements are in turn well correlated with lobster catches three to four years later (Caputi et al. 1995, de Lestang et al. 2009a) which generate revenues up to AU$200-300 million annually.

The very low puerulus settlements recorded in the 2007/08 and 2008/09 seasons (with 2008/09 being the lowest in 40 years) have not followed the historical environmental correlations and indicates the need for an improved understanding of the recruitment process in this nationally significant fishery. The breakdown in the historical correlations between environmental factors and puerulus settlements suggests that other unidentified physical factors may play a role. It has also raised the possibility that breeding stock, although at historically acceptable levels across most of the fishery (de Lestang et al. 2009b) may in some way have contributed to the settlement downturn. In particular, there is a need to better understand the source-sink relationship i.e. contributions to recruitment (puerulus settlements) from breeding stocks in different sections of the fishery. To address these specific issues, an individual-based model (IBM) approach has been adopted, taking advantage of our
improved oceanographic knowledge, the availability of a state-of-art data-assimilating hydrodynamic model, and a thorough review of larval behaviours of western rock lobster. This modelling approach as it is the only practical method to assess the possible impact of regional depletion of breeding stocks, or identify the combination of oceanographic factors, which may have caused the unprecedented low settlement that occurred in 2007/2008 and 2008/2009.

Individual-based models (IBM) that embed biological particles into simulated ocean circulation fields have been shown to have the capacity to provide important insights into potential patterns of transport and connectivity in populations of marine organisms with planktonic life stages (Cowen et al. 2006; Paris et al. 2007). An IBM has been used to investigate larval transport and connectivity patterns in the Gulf of Maine lobster population and found that abundance patterns of competent (to settle) model larvae closely resemble observed, alongshore patterns of lobster settlement density, so that connectivity and potential transport mechanisms can be assessed (Xue et al. 2008; Incze et al. 2010).

The first IBM developed to investigate the larval phase of the western rock lobster incorporated satellite-based ocean currents and larval behaviour and was capable of moving significant numbers of early-stage larvae (phylllosoma) offshore from breeding areas along the continental shelf and returning them to the west coast as puerulus some 9-11 months later (Griffin et al. 2001). While this model was a major step forward in the oceanographic sense, the authors noted that their model involved a number of simplifications and was not able to fully replicate the observed geographic distribution of puerulus settlements or the interannual variability in settlements.
In this study, the Griffin et al. (2001) model framework has been expanded based on recent developments in ocean models (Schiller et al. 2008) and satellite data. The new IBM also takes into account information from a review of the historical and recent *P. cygnus* literature on the behaviour of the phyllosoma and puerulus stages. The results from the IBM have been assessed for realism against the spatial and temporal distributions of the phyllosoma larvae from historical field surveys and the general puerulus settlement patterns along the WA coastline (Phillips et al. 1979; Caputi et al. 2001; Caputi et al. 2010b). The outputs from the IBM have been used to provide a preliminary assessment of the source-sink relationship between regional breeding stocks and puerulus settlement across the fishery and the key factors that may be affecting this relationship.

### Physical environment off the west coast of Western Australia

The poleward-flowing Leeuwin Current dominates the ocean circulation along the coast of Western Australia (WA). This atypical eastern boundary current deepens the thermocline and nitrocline off the coast of WA (Thompson 1984), suppressing productivity on the continental shelf and causing the oligotrophic marine environment off the coast (Koslow et al. 2008). Seasonal variations in the strength of the Leeuwin Current are predominantly driven by seasonal variations of surface winds off the west coast of WA (Smith et al. 1991; Feng et al. 2003). During the austral summer, strong southerly to south-easterly winds prevail, while during the winter half of the year the winds are much weaker and are from the west to south-west particularly in the southern section of the coast (Figure 1). The Leeuwin Current is therefore stronger during the austral winter compared with the austral summer, when pulses of northward winds balance the
meridional pressure gradient that drives the Leeuwin Current. These summer winds also drive the episodic northward inshore currents (Cresswell et al. 1989), and offshore (westward) surface Ekman transport (Figure 2). In addition to the Leeuwin Current, the west coast is significantly influenced by open ocean waves (swells), mostly arriving from the southwest due to storm activities in the Southern Ocean. In winter, strong westerly winds associated with storm fronts occur off the lower west coast, so that the wave energy is also stronger during the austral winter, with a significant wave height magnitude of 4-5 m in the area of the lobster settlement compared with typically less than 3 m in the summer (Figure 1).

ENSO-related upper ocean variations propagate poleward as internal coastal Kelvin waves along the northwest to west WA coasts (Meyers 1996; Feng et al. 2003). These waves generate higher coastal sea levels (increasing the depth of the thermocline) and induce strong Leeuwin Current flows during the La Niña years. Conversely, lower sea levels (and shallower thermocline) and weaker Leeuwin Current occur during the El Niño years (Feng et al. 2003; 2005). Interannual variations of SST off the lower west coast are strongly affected by the Leeuwin Current advection (Feng et al. 2008). Anomalous SST in the tropical eastern Indian Ocean associated with an Indian Ocean Dipole (IOD) acts to trigger Rossby wave propagation in the upper troposphere and the development of easterly wind anomalies off the lower WA coast during the austral winter (Weller et al. 2011, personal communication). A positive IOD event is often associated with an enhancement of the Leeuwin Current in the year following the event (Feng et al. 2008).

**Recruitment processes for western rock lobster**

Spawning female lobsters through the main distribution of the stock along the lower west coast are typically found in depths from about 40 to 80 m, and are
associated with reef habitats (Melville-Smith et al. 2009). Exceptions to this general pattern are breeding in shallower depths through the Abrolhos Islands and on some deeper reefs north of the Abrolhos (Chubb et al. 1994). More than 50% of the breeding stock is distributed around the Abrolhos Islands region, 28-29°S (Figure 3b). There is a regular migration of immature lobsters from the inshore nursery reefs offshore to the offshore reef breeding areas in November-December each year. This offshore movement can also involve a significant northward movement where the migrating lobster reach the shelf edge and result in significant numbers of lobsters reaching the Big Bank area (~27°S) at the northern limit of the fishery (Chubb et al. 1994).

From the monthly catch rates of berried females (Chubb 1991) and allowing a one-month lag for the typical incubation time at summer temperatures (Chittleborough 1976), the monthly distribution of hatching of phyllosoma larvae are approximately 3, 15, 36, 23, 20 and 3% for the six months from October to March. During the summer hatching period, the strong alongshore winds, weak Leeuwin Current and weak wave energy aid the offshore transport of the early stage phyllosoma (Figure 2a). Offshore movement of the first stage phyllosoma has been estimated to occur at a minimum rate of about 5 km per day (Rimmer 1980).

Nine development stages in the phyllosoma phase have been identified (Braine et al. 1979), through a development period of about 9-11 months with variable time spent in each stage (Chittleborough and Thomas 1969, and Phillips et al. 1979). Phyllosoma typically undergo diurnal vertical migrations and descend to increasing daylight depths with age (Rimmer and Phillips 1979). At night phyllosoma move into the surface layers (less than 20 m) and tend to concentrate in the upper few metres, particularly under calm conditions, and then they descend to deep layers during
daylight (e.g. Figure 4). Moonlight level and sea state also significantly influenced the position of phyllosoma in the water column at night. Stage I phyllosoma spend more time close to the surface than at later stages as a result of a more positive phototactic response (Ritz 1972; Rimmer 1980).

The growth rate of the early stage phyllosoma was found to be temperature dependent (Marinovic et al. 1994). Liddy et al. (2004) compared growth rates of phyllosoma at 19, 22 and 25°C and suggested that growth from hatching to Stage III took about 60 days at 19°C, 36 days at 22°C and 28 days at 25°C. The optimal temperature for growth was suggested to be in the range 22° to 23°C, which is in keeping with the SST recorded in the area off the mid west coast where the phyllosoma spend much of their time (Phillips et al. 1979). These temperatures for optimal growth are also supported by Caputi et al. (2001) who showed that high puerulus settlement years were generally associated with higher February-April SSTs (in the areas occupied by the phyllosoma) of about 22 to 22.5°C, while low settlement years were typically associated with temperatures below 21°C.

The numbers of phyllosoma surviving over time will also be a function of the level of ‘natural’ mortality being experienced. While phyllosoma appear to be able to survive a wide range of oceanographic conditions between 21°S and 35°S (Chittlebrough and Thomas 1969), survival is likely to be influenced by temperature (i.e. ability to feed), which has a range of 28°C off the North West Cape in the north and 15°C off the south coast. Predation of phyllosoma by plankton feeding fish species is also likely, and is supported by observations that few phyllosoma apart from the hatching Stage I (or late larval stages) are found on the shelf, where fish (predator) abundance is highest. An indication of the likely natural mortality rate is provided by the phyllosoma catches from a series of surveys (Rimmer and Phillips...
which suggested a decline in numbers by about 85 to 90% over the 9-month period, corresponding to progression from Stage II to VIII. Metamorphosis of the Stage VIII phyllosoma to puerulus also requires a build up of nutritional reserves (Phillips and McWilliam 2008) so that the non-feeding puerulus has sufficient energy reserves to migrate to coastal settlement areas.

While the westward wind-driven surface currents (0-20m) during the summer hatching season appears to be the mechanism to assist the offshore migration of the phyllosoma out into the eastern Indian Ocean, the eastward surface currents occurring during the austral winter appear to be the mechanism which facilitates the movement of late stage phyllosoma back to the shelf edge and allows them to metamorphose into puerulus and settle in the coastal habitats (Figure 2b).

Because most puerulus are found near or on the shelf break (Phillips and McWilliam 2008), it appears that successful metamorphosis mostly occurs when the Stage IX phyllosoma are carried close to the shelf break. The most likely trigger for metamorphosis is the nutritional state of the phyllosoma (Phillips and Pearce 1997), and satellite chlorophyll data show chlorophyll concentrations (likely to correspond to phytoplankton and zooplankton abundance) are highest along the edge of the shelf during late winter/spring (Feng et al. 2007; 2009).

Relatively few swimming stage puerulus have been caught and these were mostly captured at night on the shelf at subsurface levels between 15 and 25 m (Ritz 1972), and during new moon (Phillips et al. 1978). These records suggest that migration towards the coast occurs subsurface, although the largest catch recorded at night by Ritz (1972) was near the surface under storm conditions. Active swimming on the surface has been observed close to shore and near settlement habitats (Ritz 1972; Phillips and Olsen 1975). Because the puerulus stage does not feed, the time
available from metamorphosis to settlement on the coast, based on nutritional reserves (Lemmens 1994), is likely to be a maximum of about 21 days, assuming that the puerulus are swimming intermittently. Significant puerulus settlement has only been recorded in shallow reef and sea-grass areas in depths of less than 5 m (Jernakoff 1990), with high numbers occurring on artificial seaweed collectors between 25°S and 31°S (Figure 3a).

**Individual based model development**

**Physical models**

The Bluelink ReANalysis (BRAN) model used in this study is based on a global ocean model, OFAM (Ocean Forecasting Australia Model), and has been developed for the Australian region (Schiller et al. 2008). BRAN uses the European Centre for Medium-Range Weather Forecasts (ECMWF) reanalysis data for wind stress, and heat and freshwater flux forcing at the sea surface, and assimilates satellite altimeter and other in-situ data (Oke et al. 2008). BRAN was used to create a 1993 to May 2008 archive of daily values of ocean properties including ocean currents, salinity and temperature in 3 dimensions – resolved at 10 km horizontally and 10 m vertically (in the upper ocean i.e. to 300m) for the eastern Indian Ocean study region. For the recent period (i.e. from May 2008 to 2009) where BRAN was not available, an equivalent forecast product based on BRAN (G. Brassington, personal communication) has been used.

BRAN was selected as it appears to reasonably capture the average seasonal variations of the Leeuwin Current (e.g. Feng et al. 2010) along the west coast of Australia. The BRAN modelled currents and ocean temperature on seasonal and sub-seasonal (from days to weeks) time scales have also been validated with shipboard and mooring observations off the coast and shows that it has significant skills in
replicating the broader water movement off WA (A. Pearce et al. 2011, Personal communication). However, it appears that BRAN has underestimated the wind-driven surface currents, especially those on the continental shelf (e.g. Capes Current). To adjust for this anomaly, QuikScat satellite-derived wind data has been used to generate a correction to the BRAN surface currents. The QuickScat derived twice-daily global wind speed data at ¼ degree by ¼ degree resolution has been averaged into daily values and smoothed in time using a 7-point Hanning filter. The correction term was calculated using 1% and 3% of the wind speed and 20 degrees to the left of wind direction (e.g. Jenkins 1987) and applied to areas deeper and shallower, respectively, than 200 m. The correction is then interpolated onto the BRAN velocity grid and applied in the 0-20 m layer.

To further improve the surface water movements, the Wave Watch 3 model (WW3) incorporating significant wave height, wave period and direction data (Tolman 2002) has been used to derive Stokes drift velocities in the surface layer (0-20 m) off the coast of WA. For this purpose the WW3 data from 1997 onwards were converted to daily means, and then interpolated onto the BRAN velocity grid. In the wave propagation direction, the Stokes drift velocity can be calculated as:

\[ U_s = \frac{(ak)^2 C_p \cosh[2k(z + H)]}{2\sinh^2(kH)} \]

Here, \( C_p = \sigma / k \), is the phase speed of the waves (m/s), \( \sigma^2 = gk \tanh(kH) \), where \( a \) is the wave height (m), \( k \) is the wave number, \( z \) is the water depth which is zero at sea surface, and \( H \) is the ocean bottom depth. Using the WW3 data, \( a = H_s / 2 \), and
\[ \sigma = 2\pi / T_s, \] where \( H_s \) is the significant wave height, and \( T_s \) is the significant wave period (Monismith and Fong 2004).

**Individual based model of “super (larval) particles” and model runs**

Larval development stage, horizontal and vertical positions in the water column and mortality were represented by an individual-based model (IBM) of particles (groups of larvae, each particle represented a large number of individual larvae, following the method of Xue et al. 2008), and coupled with the physical model outputs. In the IBM, 10 particles were released daily at three depths at each 0.1° latitude along the coast between 22°S and 35°S. Equal numbers of particles were released in the model from 16 October of year (-1) to the 15 March of year (0) to cover the full hatching season. The three designated release depths were 40, 60, and 80 m, except in the Big Bank area (27°S) north of the Abrolhos Islands, where they were released in about 100 m, instead of 80 m (Figure 2a). Each particle in the model was developed through time according to the rate specified by the IBM, which takes into account the ambient temperature.

The use of uniform releases of particles by both latitude and spawning depth zones in the IBM was adopted to allow for further investigation of a number of biological factors potentially influencing settlements. This was achieved through post-model analysis of a much smaller dataset of only the successfully settled particles, which allowed rapid investigation of the impacts of a range of factors such as time of hatching, release depth, spawner abundance etc. In order to simplify the modelling and reporting, a new ‘category’ system was devised to represent groups of phyllosoma and puerulus stages that could be assigned similar biological characteristics/behaviour in the model. Category A, B, and C particles represent the early (stages I, II and III), mid (IV, V, VI), and late (VII, VIII, IX) stages of
phylllosoma, respectively. Natant (or swimming) puerulus were designated as D1 particles and the settled puerulus as D2. Category A was further separated into A1 (stage I-newly hatched phylllosoma) and A2 (stages II, III). Category C was separated into C1 (stage VII, VIII) and C2 (stage IX) where an extended period waiting for metamorphosis could occur in the model. The average durations for each particle category in the IBM were set to approximate field observations (Chittlebrough and Thomas 1969; Phillips et al. 1979; Table 1).

Following the approach of Griffin et al. (2001), particles in the IBM spend 8 hours in the surface layer at night, 8 hours at depth during the day, and 8 hours (4 hours descending and 4 hours ascending) in transitions (Table 1; Figure 4). After hatching, the first category particles (A1) stay in the surface 20 m at all times. For all later categories, three vertical profiles of particle distributions in the upper 20 m are used when applying wave-induced Stokes drift movements: Distribution I assumes evenly distributed particles in the surface-20m layer, while Distributions II and III have exponential vertical distributions by assuming particles have skewed distribution towards the sea surface (Table 1) as occurs during calm conditions at night. To simplify the IBM, the effects of sea state and lunar cycle on vertical distributions of phylllosoma have not been included in the model at this stage.

To assess the effect of temperature on growth, the model has incorporated temperature-dependent growth for category A, B and C1 particles as follows:

\[ G_s = \frac{(T - T_0)}{P(T_i - T_0)} \]

where \( T \) is the 0-30 m average BRAN temperature that particles experience, \( T_0 \) and \( T_i \) are the nominal minimum and average temperatures that the particles experience.
during each category of their life cycle, and $P_i$ is the number of days that the particles spend during each category at the nominal temperatures (Table 2). On average particles are able to reach category C2 in 270 days; at a warmer average temperature of 23°C it takes about 240 days and at 20°C it takes about 315 days. There is no growth if the temperature is below 15°C, and the growth rate does not increase further if the temperature is above 26°C. Constant growth is assumed for category C2 and D1 has a maximum life of 21 days, or until they reach shallow habitat of <40 m to become D2 and are assumed to have successfully settled. Metamorphosis of C2 particles to D1 was triggered by any C2 particle intersecting the 200 m depth contour. D1 particles are assumed to swim directly toward the coast (i.e. 26 degrees north of east) during each 8-hour night, at a speed of 15 cm•s⁻¹. Any D1 particles that have not crossed the 40 m-depth contour during a 21-day period will perish. The maximum age of the particles is 420 days.

The advection scheme used in the IBM is 4th-order Runge-Kutta method, and the horizontal diffusivity, $K_m$, is assumed to be 1 m²•s⁻¹, in order to add extra diffusivity in the IBM, which is usually underestimated in the offline particle tracking. The IBM uses a 1-hour time step to calculate particle movement. The simulation of the WRL puerulus settlement processes have been undertaken for nine settlement seasons, from 2000/2001 to 2008/2009 which represents a range of years of good and poor settlement. For each settlement season, the model simulation is carried out for the period of 16 October of Year (-1) to 31 March of Year (+1) which represents the approximate start of the egg release and the end of the puerulus settlement recorded in the field, respectively.

The model was run with all particles being of equal rank and experiencing limited mortality. Category A particles are allowed to survive on the shelf for up to 15
days while instant mortality is applied to categories B and C1 when they come onto
the shelf. Category A to C particles can survive in ambient temperatures <16°C
(<15°C), but perish if they are there for more than 14 (7) days. Also if the particles
move out of the model domain, 18-40°S, 101-129°E, they are assumed to have
perished.

From the IBM outputs, an average of 1758 particles or about 0.3%, were
recorded as settling on the coast out of a total of 585,000 released each settlement
season. A smaller number of particles, 19 on average, also settled onto the south coast
each season. Among the unreturned particles, about 442,500, or 75.6%, died at A1, as
shelf currents were unable to move them offshore within the 15 days survival limit.
The total mortality on the shelf/land for particles in all categories was about 90.8%
and 3.7% of the particles were also lost by drifting out of the model domain. A further
4.0% of particles did not reach a position to undergo metamorphosis to D1 within the
420-day survival limit and about 1.4% of total released particles remained ‘alive’
within the model domain at the end of the IBM simulation.

The IBM results on successful settlements (time, location) were stored and
processed post-model run by weighting (multiplying) hatching rates and natural
mortality rate. The post-model processing include: (1) weighting the particles at the
time of their release according to monthly hatching rates, (2) applying an additional
mortality term (to incorporate a background level of ‘natural’ mortality) as a function
of category A duration (between 60 and 120 days), with an e-folding time scale of 15
days, and (3) latitudinal distribution of breeding stock (numbers hatching) as in Figure
3b.

**Assessment of IBM outputs**
Seasonal and spatial distribution of IBM particle categories

Particle abundance of individual categories from the IBM (Figure 5) compared well with monthly phyllosoma patterns observed during 1973-1977 (Phillips et al. 1979). Peak particle numbers for category A occurred in February (i.e. the end of the hatching season) in the model domain, and had largely disappeared after May. The peak numbers of category B occurred in April, though significant numbers were present between February and June. Very few of these middle stages were taken in field surveys, however their field presence ceased at about the same time as category B particles in the model, i.e. they had largely disappeared by September. C1 particles peaked and became dominant in June-July, and C2 particles first started to appear in May-June and reach peak numbers in October-November. Small numbers of D1 particles started to appear in the model domain in June and their peak occurrence was in September. The monthly occurrence of D1 particles was consistent with puerulus collector data with most of the model settlement occurring before December (Figure 3a). The average particle duration to settlement was 307 days, or about 10 months, which is consistent with the observed period from peak hatching (December) to the peak of puerulus settlement (September). The peak distribution of particle settlement occurs between 270 and 330 days, or 9-11 months which is also consistent with the field data.

The spatial pattern of daily visits of successfully settled particles has the highest rate between the Abrolhos Islands and Fremantle (28-32°S; Figure 6a and 6b). While most particles were located in the offshore regions, early D2 settlers near North West Cape (22°S), Shark Bay (26°S), Abrolhos, Jurien, and Fremantle were also indicated in the daily visit pattern. The total (successful and unsuccessful) particle distribution resembled the observed phyllosoma distribution in June-July period.
(Figures 6c and 2b). It appears that particles west of 108°E or north of 24°S during June-July are less likely to return to coastal regions, despite the high concentrations of phyllosoma found in these areas during historic surveys (data from Phillips et al. 1979 superimposed on Figure 2b).

**Factors affecting IBM particle settlement**

Time of hatching was found to influence settlement success. The IBM results, with equal daily particle releases (unweighted), suggest that settlement success rate was highest for particles released in October (half month) and declined through to March. The majority of successfully settled particles were released during the first half of the hatching season, i.e. from mid-October to December (Figure 7a). The early-released particles experience a longer period in the warmer temperatures during the summer season, which enables them to ‘grow’ faster and be at a stage able to metamorphose to puerulus, when the strongest onshore flows occur during the winter to early spring months. When the settled particle numbers are weighted with monthly hatching rates, the successful particles show a peak hatch time in December. More than three quarters of successful settlements were from November and December releases (Figure 7b). This pattern was only slightly changed by the additional inclusion of the particle duration (mortality) weighting.

Release latitude in the IBM also affects success of particle settlement. The un-weighted distribution of settling particles shows two major source areas, a northern area between 23° and 25°S and a larger southern area between about 28°S and 34°S. Within the southern release area two distinct peaks also occur around 28°S and 33°S (Figure 8a). After weighting to take into account the observed monthly hatching pattern there was little change in this pattern. However when particle duration mortality was also taken into account the success rate in the northern area is enhanced.
and a general decrease in settlement success from north to south becomes evident (Figure 8b). The declining trend in success from north to south appears to result from the particles released in the north experiencing high temperatures and therefore having shorter overall pelagic larval duration. In comparison, particles released further south tend to experience colder temperature resulting in longer larval duration, and therefore receive a higher natural mortality in the model.

In order to compare with observed spatial patterns of puerulus settlement (e.g. Figure 3a), the IBM results are further scaled with the latitudinal distribution to the breeding stock as in Figure 3b. Whereas nearly 60% of the breeding stock is located near the Abrolhos region (28-29°S), about three quarters of the successful settlements were originated from that region after considering all the weighting factors (Figure 8c). Also noticeably the shelf regions north of 27°S and south of 32°S are no longer significant sources of successful particle settlements. When scaled by the latitudinal breeding stock distribution, the successful rate for the December releases was also further enhanced (Figure 7c).

Comparison of the successful settlement rates for particles released at different depths suggests that the success rates were much higher for 60 and 80/100 m releases compared with those in 40 m, as particles released at inner shelf depth take longer to exit the shelf and are therefore subject to additional mortality in the model. The low likelihood of successful returns for particles released at Northwest Cape (22°S), near Shark Bay (26°S), and off Cape Leeuwin, 34°S (Figure 8b) is due to particles being only released very close to the coast at these locations and therefore have a greater chance of hitting the coast (Figure 2a).

The un-weighted data showing the latitude of model puerulus settlements suggests that the mean latitude for successful settlement is at about 30.4°S, with the
main settlement region centred between the Abrolhos (28-29°S) in the north and Perth (32°S) region in the south (Figure 9a). There are also three other regions where peaks occur i.e. Coral Bay (23°S), South of Shark Bay (26°S), and near the Capes (34°S) region. This distribution bears some similarity to the spatial distribution derived from puerulus collectors, with the exception of the settlement south of 32°S that is consistently low (e.g. Figure 3a). Weighting the model settlements with monthly hatching rate does not modify the settlement pattern significantly, whereas adding the weighting factor of pelagic larval duration mortality, the likelihood of successful settlement in the north has increased, while the successful settlement in the south has reduced (Figure 9b). The overall settlement structure under this arrangement has more resemblance to the spatial distribution from puerulus collector observations, which may indicate the importance of environmental effects of growth/survival on the particle settlement. The scaling with the latitudinal breeding stock distribution gives more weight to the settlements between Abrolhos (28-29°S) and Perth (32°S) (Figure 9c), but retains the over representation of settlement in the southern Capes (34°S).

The daily pattern of settlement from the IBM suggests that particles begin settling in June and continue until March (not shown), as indicated in D1 distribution in Figure 5. After applying the weighting and scaling factors, most of the particle settlement occurs from August to December, with a distinct peak occurring in September-October north of Abrolhos (28-30°S) and a broader peak spanning from September to almost December in the south (30-32S°) (Figure 10). The difference in IBM settlement patterns between the north and south reflects the relative advantages of fast growth by phyllosoma which are released and therefore spend more time in the high ambient temperature in the offshore north region, as reflected in the puerulus collector observations (e.g. Figure 3a).
The post-model analyses elucidate the dual role of ocean temperature on the particle settlements in our model. High temperature results in increased growth rate such that the stage of particle development has advanced sufficiently to allow for successful later settlement if they are transported into coastal regions by the strong onshore ocean current during the austral winter. Faster growth with higher temperatures, also reduce the particle duration which lowers the natural mortality, which is applied to all particles from age 300 days onwards. These temperature effects enhance the success rate for more northern releases i.e. into warmer waters, and cause relatively more particles to settle earlier in the settlement season.

**Source-sink relationship of particle settlements**

To assess the source (hatching) and sink locations (puerulus settlement) along the coastline the successfully settled particles from uniform releases have been grouped according to their release and settlement latitudes. These ‘source-sink” data from the model, averaged over the nine years have then been weighted with monthly hatching rates and ‘natural’ mortality linked to category A duration, to provide a preliminary view of the relative success of sources throughout the full latitudinal species range (Figure 11a).

These data suggest that two areas of the coast have the potential to be major sources of successful settlement: a northern area, between 23°30’S and 25°30’S (between North West Cape (NWC) and northern Shark Bay), and a southern area between 27.5°S and 33°S. Within the southern area, the section of the mid west coast between 28° and 29°S (including the offshore Abrolhos region) was the most significant source region. Further, particles released from the northern source area were likely to supply successful settlements all along the coast, i.e. from NWC to Cape Leeuwin, with peaks in the Shark Bay and Geraldton/Abrolhos regions.
Particles released off mid west coast region were more likely to result in settlements in a broad area south of 28°30′S, but with a peak on the coast around 29°S i.e. in the area including the offshore Abrolhos Islands. In general, particles released at any point along the coast were more likely to return to the same region or further south, than settle north of their release location. These IBM results showing that northern released particles are more likely to result in successful settlements are a reflection of the influence of the southward-flowing Leeuwin Current in the model.

To further assess the source-sink relationship for the stock, the sources of particle settlement were scaled to take into account the general latitudinal distribution of breeding stock (e.g. Figure 3b). This weighting results in the southern source region between 27.5°S (Kalbarri) and 31.5°S (Lancelin), becoming the main and only section of the coastline to generate significant particle settlement (Figure 11b). That is, very low breeding stock abundance from Shark Bay north (25°S) to NWC (22°S), an area on the edge of the stock’s geographic distribution, removes this area as a source of significant model settlement. While all of the southern source sites are important within the general southern region, the release latitudes between 27.5°S and 29°S are shown to be the more important sources of particle settlement for all coast regions. This northern section of the southern source region includes the offshore Abrolhos Islands which have relatively high breeding stock levels (Chubb 1991) and contain a major part of the breeding biomass. These areas, being close to the edge of shelf, are also more likely to be the source of successfully settling particles in the model.

Effects of Stokes drift

To assess the overall effect of the surface waves, a parallel IBM run has been carried out removing the wave-induced Stokes drift in the model. For this assessment
we compare the winter particle distributions and settlement locations generated by the two simulations (i.e. with and without Stokes drift effects).

With Stokes drift, the latitudinal distributions of the category C particles in June-July are centred around 22-33°S (e.g. Figure 6c), largely consistent with late Stage [VI to IX] phyllosoma spatial distributions (Rimmer and Phillips 1979). Without Stokes drift effect, the category C particles have a more southern distribution, skewed toward 30-32°S (not shown). The average latitudes of all category C particles during this period are 27.6°S and 28.6°S for the IBM simulations with and without Stokes drift, respectively, so that the net effect of Stokes drift is to shift the particle population by about a 100 km northward, and retain the particle population off the west coast.

As a consequence of the northward shift of the category C particle distribution (due to Stokes drift), the mean latitude of settling particles (category D1) is at 29.7°S, more than 150 km northward compared with the simulation without Stokes drift (Figures 12a and 12b). With the Stokes drift effect, the central region of the settlements is located between the Abrolhos and Fremantle and the settlements in the southern Capes region are significantly reduced. The model outputs are more consistent with the puerulus collector data (Figure 12c), compared with the simulation without Stokes drift. Although the model fails to settle particles between 24-25°S, (puerulus settlement in this area has only been recorded over a short period), the model with Stokes drift has relatively high settlement near Shark Bay. Overall, the model has overcome one of the significant issues of settlement being too far south in the previous model (Griffin et al. 2001).

Another significant effect of including the Stokes drift in the IBM is that the total number of surviving category C particles in June-July is about 60% higher.
without Stokes drift, compared to with Stokes drift. This indicates that the onshore wave action during the summer hatching period of the particles (Figure 1c) traps more newly hatched particles on the shelf and increases their overall mortality. On the other hand, there were similar total particle numbers settling in these two simulations (not shown), which indicates that including Stokes drift results in higher winter onshore wave action driving more particles toward the coast and this compensates for the increased mortality at time of hatching. Thus, variations and changes in the wave climate in the Southern Ocean may affect their overall effects on particle settlement rate off the coast.

The modelled pattern of particle settlement along the coast (Figure 12a) is generally consistent with the observed puerulus settlement distribution (Figure 12c) and catches in the fishery. Additionally, it also shows a series of peaks, which are consistent both with and without the Stokes drift effect (Figures 12a and 12b). These distinct peaks in IBM settlement, suggests that the particles are not being randomly distributed along the coast and oceanographic factors other than wave action are involved. One likely cause of these peaks or distinct bands in the particle settlement along the coast are the observed surface eastward jets in the southeast Indian Ocean, e.g. the Eastern Gyral Current (off NWC), the broad eastward flow in the south subtropical Indian Ocean (off Abrolhos-Perth) and the South Indian Countercurrent (off the Capes). The other likely cause is the semi-permanent meander structure in the Leeuwin Current (e.g. Figure 2b). Both factors would have been incorporated in the IBM through the BRAN inputs. The potential impact of these factors will be investigated when the IBM is further developed to examine interannual variability in puerulus settlement.
Discussion

An improved individual-based model (IBM) for investigating phyllosoma transport and puerulus settlement processes for western rock lobster stock has been developed. Innovations include the use of daily outputs from a hydrodynamic model to provide the 3-dimensional wind and density driven horizontal velocity fields, corrected with additional surface Ekman flows and Stokes drift. As in the Griffin et al. (2001) model, advection alone did not produce a realistic distribution of particle settlement relative to puerulus collector catches along the coast. The Stokes drift effect due to surface waves was found to be a key factor in maintaining the latitudinal position of particle population, overcoming the problem in the previous model of too many particles being swept onto the south coast and out of the natural settlement zone. Similarly, the increased growth and subsequent increased survival of the phyllosoma associated with water temperature was an important component of the model, which resulted in a more realistic distribution of particle settlement along the coast.

The modelling indicates that early phyllosoma release (mid-October to December) is likely to result in a greater chance of survival to puerulus than late release (January to mid-March). These early-release particles experience a longer period of warmer temperatures during the summer, which enables them to grow faster and hence increase their survival to the settling stage. The potential positive effects of warmer water temperatures and early hatching on the model puerulus settlement are supported by the relationship between the annual level of puerulus settlement and average day of the year that settlement occurs (Caputi et al. 2001). That is, good settlement (e.g. 50% above average) in a year is associated with a peak in settlement about one month earlier compared with a low settlement year.
The outputs from the model in the nine years simulated, also suggest a
decreasing trend in the likelihood of settlement success from releases north to south.
This appears to result from the model particles released in the north tending to
experience higher temperature and therefore have shorter overall durations, compared
with those released further south. After scaling for the latitudinal distribution of
breeding stock, the model suggests that the coastline between Kalbarri and Fremantle
is the major source area for the entire coast, and within this area the region from
27.5°S-29.5°S, which includes the Abrolhos Islands clearly becomes the most
significant source of particle settlement.

Further Development

While the IBM model settlement outputs with the Stokes drift are now much
closer to the patterns observed for the field, the model continues to settle more
particles on the southern section of the west coast near Cape Leeuwin, than occurs at
the field collector sites. A number of aspects of larval behaviour in the IBM can be
further improved to help replicate the interannual variation in puerulus settlement
which is the main focus of the next stage of development of the IBM. The 8-hour
block distribution approach used to simplify the diurnal vertical migration may be
underestimating the vertical extent of larval distribution during the daytime and could
be improved by shorter time steps. The effects of sea state (wind and wave) and
moonlight level on the diurnal movements and distribution of phyllosoma in the
surface layers at night have also been shown to be significant (Rimmer and Phillips
1979). Incorporation of sea state and moonlight levels in the model has the potential
to move the phyllosoma depth distributions to slightly deeper levels at night but may
also result in the daytime depth arc being moved downward during the bright
moonlight periods. All of these additional phyllosoma behaviour related factors have
the capacity to alter particle movements in the IBM and potentially improve its ability
to replicate interannual variability in settlement. Similarly, most of the ‘natural’
mortality in the current IBM, occurs through particles failing to move off the shelf
after hatching and then again at the end of the cycle through failing to settle. Further
development of this aspect of the IBM is necessary and could also help address the
interannual variability issue.

The eastern Indian Ocean area, where the phyllosoma spend most of their
development time (Phillips et al. 1979), has extremely low productivity, which
suggests that phyllosoma growth may be food limited which is in turn likely to be
linked to the success of metamorphosis to the non-feeding puerulus stage (Phillips and
McWilliam 2008) and successful settlement. The model currently uses interception
with the 200 m depth isobath (shelf edge) as a proxy for food availability and the
trigger for metamorphosis, but does not include any direct measures of ocean
productivity/food. Field survey data (Tranter and Kerr 1969) has indicated that
chlorophyll a peaked in the region in May/June, with zooplankton peaking 2-3
months later in August/September. Satellite monitoring data has confirmed this
general seasonal pattern that chlorophyll levels are highest in winter months,
suggesting that zooplankton will peak in spring, assuming the lag in zooplankton
abundance by Tranter and Kerr (1969). Satellite data (Caputi et al. 2010b) has also
indicated that chlorophyll levels are higher on the shelf at all times, but with
considerable seasonal variability. The incorporation of both seasonal and interannual
parameters for productivity based on satellite chlorophyll monitoring could
significantly improve the model’s response to environmental changes and potentially
its ability to replicate interannual variability in puerulus settlement.
Acknowledgements

Funding support for the project from the Fisheries Research and Development Corporation, the Western Australian Department of Fisheries (DoF) and CSIRO Marine and Atmospheric Research is gratefully acknowledged. The authors would also like to acknowledge the participants of the two workshops involved in the development of this project, particularly the contributions of the reviewers, Dr Bruce Phillips and Dr David Griffin. Also acknowledged are the significant contributions to the project from: the Bluelink (BRAN) model developers in CSIRO and Australian Bureau of Meteorology, the Satellite data providers e.g. NASA, WW3 model, Western Australian Marine Science Institution (WAMSI) and CSIRO Wealth from Oceans National Research Flagship. Finally, the authors also thank the internal reviewers at CSIRO and the Western Australian Fisheries and Marine Research Laboratories (DoF), Drs Rick Fletcher and Mervi Kangas, and three anonymous reviewers. We thank Drs Huijie Xue and Alejandro Sanchez for sharing some of their programming codes.

References


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Table 1: Depth ranges of diurnal vertical migrations by larval stage and time of day.

<table>
<thead>
<tr>
<th>Category A</th>
<th>Category B</th>
<th>Category C</th>
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</thead>
<tbody>
<tr>
<td>A1</td>
<td>A2</td>
<td>C1</td>
</tr>
<tr>
<td>Duration (days)</td>
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<td>60</td>
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</table>

**Day time (9:00-17:00)**
- 0-20m
- 10-100m\(^a\)
- 30-100m\(^b\)

**Transition time**
(17:00-21:00 and 05:00-9:00)
- 0-20m
- 0-100m
- 0-100m

**Night time (21:00-05:00)**
- 0-20m
- 0-60m\(^c\)
- 0-40m\(^d\)
- 0-20m

**Near surface profile**
- I
- I
- II
- III

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\(^a\) 50% of the larvae are in 10-50m and 50% in 50-100m

\(^b\) 50% in 30-60m and 50% in 60-100m

\(^c\) Stationary

\(^d\) Use one third of 0-100 m BRAN velocity to transport particles

\(^e\) 50% in 0-20m and 50% in 20-60m

\(^f\) 50% in 0-10m and 50% in 10-40m

\(^g\) I: even distribution; II and III: exponential distributions with e-folding scales of 10 and 3 m respectively
Table 2: Parameters used in the IBM growth equation

<table>
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<tr>
<th>Category</th>
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<th>$T_1$ (°C)</th>
<th>$T_0$ (°C)</th>
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<td>21.5</td>
<td>10</td>
</tr>
<tr>
<td>B</td>
<td>60</td>
<td>22.4</td>
<td>10</td>
</tr>
<tr>
<td>C1</td>
<td>120</td>
<td>21.4</td>
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**Figure captions**

**Fig. 1.** Surface wind speeds (a, b) and significant wave height (contour in metres) and direction (c, d) off the west coast of WA during the austral summer (December-February) and winter (June-August).

**Fig. 2.** Schematics of surface currents along the west coast of WA during (a) the austral summer (December-February) and (b) winter (June-August). The hatched area in (a) denotes the release sites of particles in the IBM and the hatched area in (b) denote the June-July distribution of high-abundance late stage phyllosoma from historical observations (adapted from Phillips et al., 1979). Note that the abundance distribution is not uniform in the region. The broad arrows in the figures denote general directions of particle transport by ocean currents during the two opposite seasons.

**Fig. 3.** (a) Average monthly settlement rates (2000/01 to 2008/09 settlement seasons) for western rock lobster (Panulirus cygnus) pueruli as percentages of total settlements (average number per collector shown to right of histogram) at each collector site along the west coast of Australia. Note: In 2005 the Shark Bay South Passage site was replaced by the Quobba site so the two have been treated as a one site average. (Note the Rat Island site is in the central group of the Abrolhos Is.). (b) Relative latitudinal contributions to overall breeding stock of western rock lobster (source: S. de Lestang).

**Fig. 4.** A schematic diagram representing the IBM model depths occupied by each category of phyllosoma and puerulus. The two lines are used to mimic the diurnal migration of the particles at each category and they represent the upper and lower depth (m) limits of particle distributions. D denotes daytime and N denotes nighttime. The stippled area denotes a depth zone below the Leeuwin Current or shelf bottom and particles are motionless in this layer.
Fig. 5. Nine-year average monthly counts of different categories of particles from November near the start of the hatching season to March near the end of settlement season. (Note: The D1 particle (puerulus equivalent) counts have been multiplied by 200 to enable the monthly pattern to be visible).

Fig. 6. June-July (a) spatial distribution and (b) latitudinal visit rates (visits per day in every 0.5° grid) of successfully settled particles averaged over the nine model years; and (c) latitudinal visit rates for all particles (both settled and unsettled).

Fig. 7. Release months for successfully settled IBM particles along the west coast of WA averaged over the nine model years: (a) unweighted distribution, (b) weighted for monthly hatching rate and for natural mortality at category A, and (c) same as (b) but with additional scaling using the breeding stock distribution in Figure 3b.

Fig. 8. Release latitudes (by half-degree grids) for successfully settled IBM particles along the west coast of WA averaged over the nine model years: (a) unweighted distribution, (b) weighted for monthly hatching rate and natural mortality, and (c) same as (b) but with additional scaling using the breeding stock distribution in Figure 3b.

Fig. 9. Settlement latitudes (by half-degree grids) for successfully settled IBM particles along the west coast of WA averaged over the nine model years: (a) unweighted distribution, (b) same as (a) but weighted for monthly hatching rate and for natural mortality, and (c) same as (b) but with additional scaling using the breeding stock distribution in Figure 3b.

Fig. 10. Monthly IBM particle settlement rates along two latitude bands (solid line: 28-30°S; dashed line: 30-32°S) during the settlement season (May-March) after weighted with monthly hatching rate, natural mortality for category A, and the latitudinal distribution of breeding stock.
**Fig. 11.** Source and sink relations along the west coast of WA in half degree latitude boxes for successfully settling IBM particles averaged over the nine model years: (a) weighted by monthly hatching rate and category A particle duration which affects the mortality rate, (b) same weighting as (a), but with additional weighting by the breeding stock distribution in Figure 3b. (Both plots are scaled by their maximum values).

**Fig. 12.** Latitudinal distribution of successfully settled IBM particles along the west coast of WA averaged over the 9 model years: (a) with Stokes drift incorporated in the IBM and (b) without the Stokes drift effect, and their comparison with observed settlements that are binned onto the half degree segments off the coast (c).
Figure 1
Figure 2
Figure 3
Figure 4
Figure 5
Figure 6
Figure 7
Figure 8
Figure 9
Figure 10
Figure 11
Figure 12