

# Interannual variation in the moult cycle and size at double breeding of mature female western rock lobster (*Panulirus cygnus*)

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de Lestang, S., and Melville-Smith, R. 2006. Interannual variation in the moult cycle and size at double breeding of mature female western rock lobster (*Panulirus cygnus*). – ICES Journal of Marine Science, 63: 1631–1639.

The moult cycle of mature female *Panulirus cygnus* was examined from data recorded over 32 years at four sites along the coast of Western Australia. A repeating trend for mature females was inferred from samples taken between 15 November and 15 August. Setae were present on the endopodites of all large females from June until February–March; between March and June the proportions of females with setae declined sharply as about 80% moulted into a non-setose phase. Females that did not undergo this moult in February remained setose throughout the “normal” non-setose period before moulting and producing a new set of setae by midwinter. New or eroded spermatophores were present on most large females between November and January, but their presence declined sharply during the February–March moult, to be absent by May. The percentage of mature females that bypassed the non-setose moult varied markedly from 1% to 40%, and was well correlated with mean water temperatures in January and February. The proportion that did not undergo a moult increased when these months were cool but decreased when they were warm. The size (carapace width) at which females carry two batches of eggs in one breeding season (double breeder) declined progressively from 96.6 mm to 84.1 mm with decreasing latitude (32°S to 28°S), and further declined at the offshore Abrolhos Islands (29°S) to 78.7 mm. The implications of these findings are discussed in relation to management measures designed to protect females in a setose condition.

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Keywords: double breeding, moult cycle, *Panulirus cygnus*, water temperature.

Received 28 November 2005; accepted 6 June 2006.

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## Introduction

The fishery for western rock lobster (*Panulirus cygnus*) is Australia's most valuable single-species one (worth about AU\$250–350 million annually), with annual catches averaging 11 000 t. The species, which is endemic to Western Australia, is found predominantly in coastal waters from North West Cape (21°45'S) to Cape Leeuwin (34°22'S), in depths of less than 200 m (Gray, 1992).

Sustainability of this important fishery has been achieved by management regulations that include limited entry to the commercial fishery, effort controls, a closed fishing season from July to mid-November, a legal minimum size, and for females, protection of all animals with either ovigerous setae or above a specified size (Caputi *et al.*, 2000).

The single most important consideration in managing the fishery is that egg production be maintained at a safe level (Chubb, 2000; Hall and Chubb, 2001). Egg production is

monitored from both fishery-dependent and -independent data (Caputi *et al.*, 1995; Melville-Smith *et al.*, 1998). Indices, expressed as number of eggs per pot lift, are estimated for each locality using the relationship between female size, batch fecundity, and the number of batches produced within a season (Chubb, 1991). The size at which females start to carry two batches within a season is not known with certainty, and needs to be clarified for the production of more accurate egg-production indices.

It is also important to clarify the moult cycle of mature female *P. cygnus*, and particularly to establish the proportion of females that remain setose throughout the fishing season and are therefore protected from fishing. Females moult into a setose phase in June and July, prior to the spawning season. Following this moult, copulation takes place, resulting in a spermatophoric mass being attached to the sternums of receptive mature females. By September mated females begin to extrude their eggs, attaching them to ovigerous

setae located on endopodites beneath their abdomens (Chittleborough, 1976; Chubb, 1991). The eggs are fertilized during this process with sperm released from the scratching of the spermatophoric mass by the female's fifth pair of legs. Remnants of the spermatophoric mass remain until they are either covered by a second mating or sloughed off during moulting. The postspawning moult results in females entering a non-setose phase during the fishing season, generally February, although the time of year at which this occurs and the proportions of females that moult vary between years, mainly as a result of variations in environmental conditions, e.g. water temperature (Chittleborough and Thomas, 1969; Chittleborough, 1976; Chubb *et al.*, 1989). Greater knowledge of this moult cycle is important because the effectiveness of the legislation protecting females with ovigerous setae depends to some extent on the proportion of mature females that are fully protected from fishing throughout each part of the fishing season.

## Material and methods

### Sampling regime and measurements

To examine the moult cycle of mature female *Panulirus cygnus* on the west coast of Australia, data were collected during fishery-dependent commercial catch monitoring surveys (DCCM) at four localities (Fremantle, Lancelin, Jurien Bay, and Dongara; Figure 1) each year since 1972. Research staff aboard commercial vessels conduct the DCCM each month during the fishing season (15 November–30 June) in a range of fishing depths from 5 m to more than 80 m. The sampling regime is detailed in Caputi *et al.* (2000).

The data used to determine the size (carapace length) at which a female produces two broods of eggs per spawning season (i.e. becomes a "double breeder") were collected during the 2002 fishery-independent breeding stock survey (IBSS). This survey has been made annually at three sites (Lancelin, Dongara, and Abrolhos Islands), and intermittently at three others (Fremantle, Jurien Bay, and Kalbarri) since 1992. All six locations were surveyed in 2002. The survey is undertaken over ten days during the last new moon before the commercial lobster-fishing season starts (15 November), when the largest number of females bear eggs (Chubb, 1991). The water depths surveyed range from 25 m to 70 m at the five coastal locations, and from 10 m to 60 m at the Abrolhos Islands. Details of the sampling regime are given by Chubb (2000).

In both surveys, the carapace length (CL) of each female lobster was measured to the nearest millimetre. This dimension is defined as being from the anterior edge of the carapace between the preorbital spines down the mid-dorsal line to the posterior edge. The presence of setae on the endopodites (Figure 2), external ova attached to these setae, and spermatophoric masses (new or eroded) attached to the fifth abdominal segment, were recorded. During the IBSS the developmental stages of female ovaries, as viewed

through the dorso-thoracic musculature, and whether a lobster had missing or newly regenerated appendages, were also recorded. For both surveys the presence of setae on the endopodites has been recorded since 1992.

Temperature measurements collected during the DCCM by a protected reversing thermometer at a maximum depth of 38 m were analysed by ANCOVA and standardized by location, month of capture, and water depth (m), to produce mean monthly bottom-water temperatures (MWT; °C) for each year. Monthly mean sea level (MSL) data (cm) for the port of Fremantle in Western Australia were obtained from the Flinders University Tidal Institute in Adelaide, and used as a proxy for the strength of the Leeuwin Current.

### Interannual variation in moulting of mature females

Data on the presence or absence of ovigerous setae on the endopodites have only been recorded since 1992. Therefore, to determine the moult cycle of females over the period 1972–2005, DCCM data on the presence of a spermatophoric mass deposit on females  $\geq 95$  mm CL, which is above the size at maturity (Chittleborough, 1976), were used to determine the proportions of mature female *P. cygnus* that moulted in February and March after mating and spawning; moulting results in the loss of all traces of spermatophoric mass deposits. The females were caught in water depths down to 76 m in April each year since 1972, in the northern (Jurien Bay and Dongara) and southern (Fremantle and Lancelin) regions of the fishery. The standardized proportion of mature, unmoulted, and therefore setose, females, relative to all females in the same size range in April, was determined by ANCOVA, using location as a factor and depth (m) as a covariate.

The relationship between the two sets of environmental measures (MWT and MSL) in the months just prior to and during the non-setose moult, i.e. those that may affect participation in this moult, and the incidence of females that did not moult in February and March was examined using regression analysis. Therefore, environmental measures recorded from November to March and combinations of these months were regressed against the proportions of large females with new or eroded spermatophores in April, using both an exponential decay (Leike, 2002) and a linear equation, with the resultant  $r^2$  values then being plotted. As both the exponential decay and the linear models had the same number of parameters (two), resultant  $r^2$  values could be used to determine which model provided the better description.

### Assignment of double breeding and analysis of data

Appendage damage significantly reduces the likelihood of mature female *P. cygnus* producing eggs (SdeL, unpublished data). Therefore, only females with undamaged appendages were used to determine the size at double

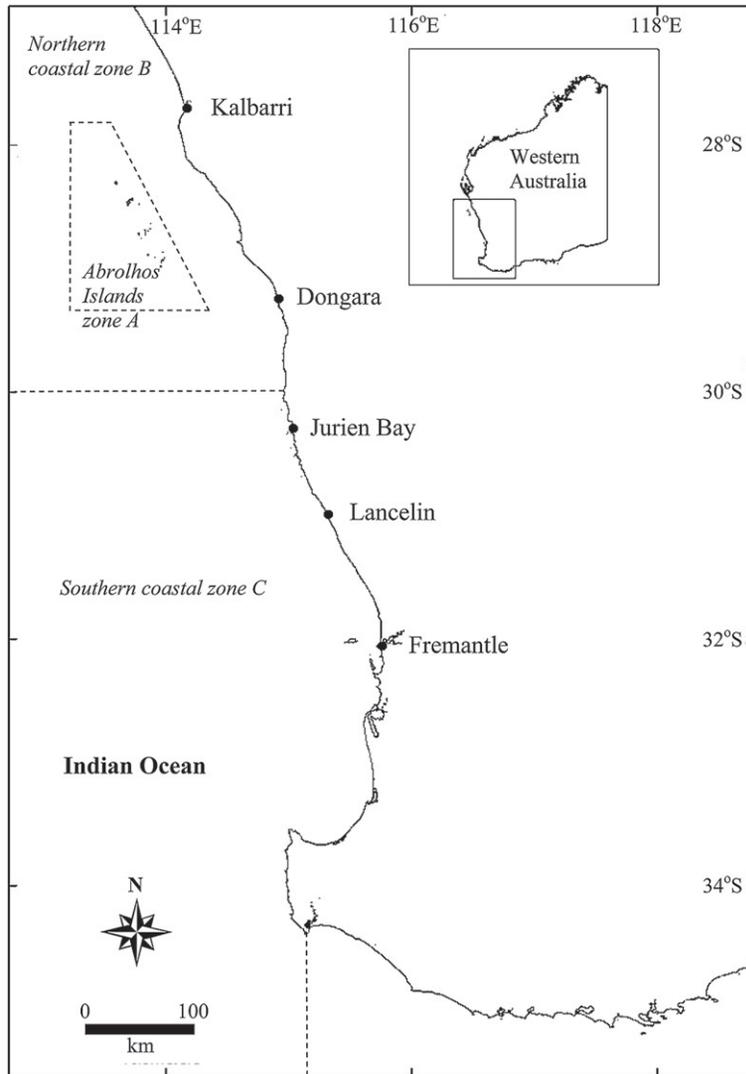


Figure 1. Management zones in the western rock lobster fishery and the locations of fishery-independent breeding stock surveys and commercial monitoring of the catch.

breeding. A female *P. cygnus* was considered to be a double breeder (DB) if, at the peak of the breeding season, October–November, she had either an external ova and an unused spermatophore; or a late stage external ova, no spermatophore, and a developing ovary; or no external ova, a used spermatophore, and a developing ovary (Melville-Smith and de Lestang, 2005).

At each location sampled during the 2002 IBSS, data on all female *P. cygnus* classified as DBs were analysed by logistic regression to determine the size at which 50% of spawning female lobsters breed twice in a spawning season ( $DB_{50}$ ). The data for each assemblage were analysed by a nonlinear regression subroutine in SPSS 11.5.0™, with the standard errors being derived from 100 bootstrap estimates. The equation used was:

$$P = P_{\max} / [1 + \exp(-\ln(19)(CL - DB_{50}) / (DB_{95} - DB_{50}))],$$

where  $P$  is the proportion of mature females at carapace length  $CL$ ,  $P_{\max}$ , which is constrained to be  $>0$  and  $\leq 1$ , is the maximum proportion of double breeders at  $CL_j$ , and  $DB_{50}$  and  $DB_{95}$ , respectively, are the  $CL$ s at which 50% and 95% of the assemblage breeds twice.

## Results

### Moulting cycle of mature females

The average moulting cycles of large ( $\geq 95$  mm), and therefore presumed mature, female *P. cygnus* in the northern and southern regions of the western rock lobster fishery were

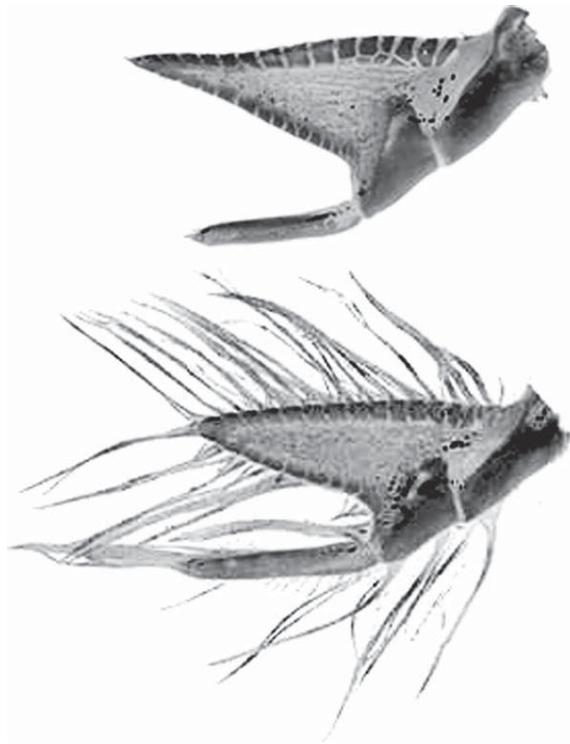


Figure 2. Non-setose (top) and setose (bottom) endopodites of female *Panulirus cygnus*.

similar (Figure 3a, b). In both regions the frequency of ovigerous females declined progressively each month from a maximum of ~70% in November and December to zero in March, with no ovigerous females caught by the end of sampling in August (Figure 3a, b). The average proportions of setose and mated females to all large females ( $\geq 95$  mm) in both regions remained at or close to 100% in all months from November until February, before both measures declined to ~20% in April. The contributions of mated females then declined further to essentially zero in May and June, while that of setose females increased in these months to 50% and 90% of all “mature” females, respectively (Figure 3a), owing to a moult in May. In both regions the frequency of mated females began to increase again to ~40% in July, then to 60–80% in August (Figure 3a, b).

#### Annual variation in the moulting of mature females

The proportions of large ( $\geq 95$  mm CL) mated females in April ranged from 1% to 41% of the sampled population in different years (Figure 4). Low incidences (<5%) of mated females were recorded in the years 1973–1975, 1978, 1989, 1990, 1992, and 1997, while high incidences (>20%) were recorded in 1977, 1991, 1993, 1998, 2002, and 2004.

For both the exponential decay and linear models, standardized mean water temperatures for the combined months of January and February produced the highest  $r^2$  values (0.67 and 0.48, respectively) with the proportions of mature females that had not moulted into a non-setose phase (Figure 5a, b). The mean sea level correlations were too weak to be useful (Figure 5a, b).

The best relationship between the proportions of large mated females in April ( $P_M$ ) and standardized water temperature ( $T$ ) averaged for the months of January and February is described by the exponential decay equation  $P_M = 1.37E + 12 \exp(-T/0.721)$  (Figure 6). This model shows that, with lower water temperatures in mid-late summer, the proportion of female *P. cygnus* that moult into a non-setose phase after spawning decreases exponentially. This time period is towards the end of the egg-bearing season, just before the expected time of moulting.

#### Size at double breeding and the setose moult

The carapace lengths at which 50% of multiple spawning female *P. cygnus* produce two broods of eggs within a breeding season ( $DB_{50}$ ) were estimated from the 2002 IBSS (Figure 7). The lengths declined progressively with decreasing latitude along the coast and then offshore to the Abrolhos Islands, with the  $DB_{50}$  recorded at Fremantle (96.6 mm) being the largest, then Lancelin (90.4 mm), Jurien Bay, Dongara, and Kalbarri (all about 85 mm), and finally the Abrolhos Islands (78.7 mm). This progressively declining trend along the coast and to the offshore islands is similar to, but consistently greater (~10 mm) than, the trend of size at first maturity recorded for the species (Table 1).

The maximum percentage of females assigned as double breeders never reached 100%, even in the largest size classes, and varied markedly between locations. The Abrolhos Islands recorded the highest percentage of lobsters assigned as double breeders (79%), followed by Lancelin (70%), Kalbarri (57%), Dongara (52%), Fremantle (50%), and Jurien Bay (35%) (Figure 7).

The carapace lengths of females that do not moult into a non-setose phase did not differ between years (Kolmogorov–Smirnov,  $p > 0.05$ ). Therefore, to ascertain whether those females breed once or twice per season, the cumulative frequencies of females in 5-mm size classes that were classified as either single or double breeders were plotted with the cumulative frequency of mated females in April, pooled over the past 32 years (1972–2003) (Figure 8a, b). In both northern and southern zones, the cumulative frequency of mated females in April was, for corresponding size classes, significantly lower (Kolmogorov–Smirnov, all  $p < 0.01$ ) than that of either single- or double-breeding females in that size class. This indicates that lobsters that still show signs of mating by April, i.e. those that do not moult into the non-setose phase, are generally larger than double-breeding females (Figure 8).

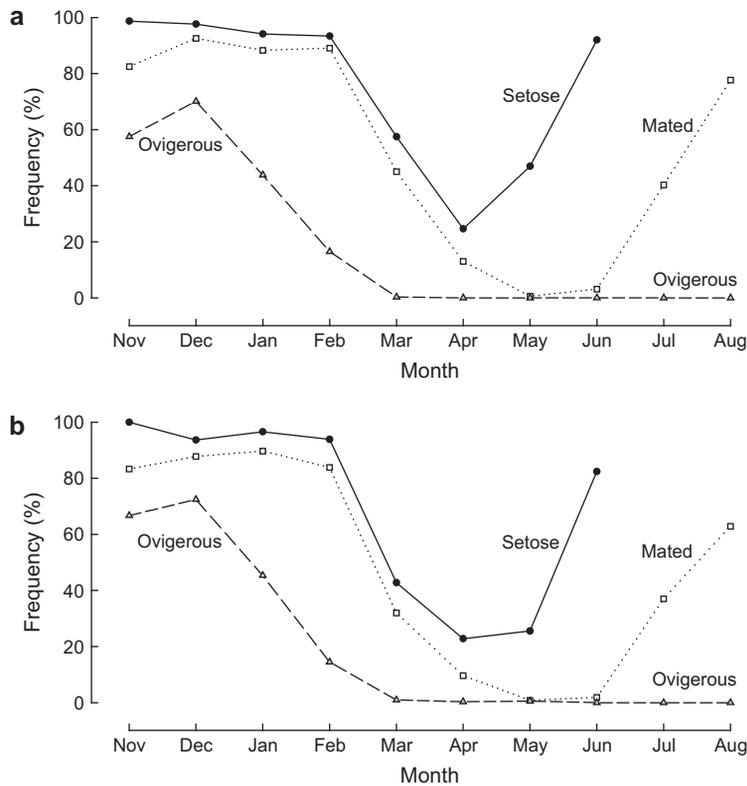


Figure 3. Mean monthly percentages of large ( $\geq 95$  mm) setose, mated, and ovigerous female *Panulirus cygnus* sampled during commercial monitoring surveys in (a) the northern and (b) the southern zones of the western rock lobster fishery between 1972 and 2005.

### Discussion

The different proportions of setose, ovigerous, and mated females in commercial samples throughout the season provide a reliable indication of the moulting and mating cycles of mature female *P. cygnus* (Figure 3). The sharp decrease in the proportion of setose and mated lobsters in February and March indicates that most ( $\sim 80\%$ ) breeding females moult into the non-setose phase then. The disappearance of females with new or eroded

spermatophores in samples from May onwards indicates that those animals ( $\sim 20\%$ ) that did not moult in February or March moulted by May. The high proportion of setose females in June indicates that those that moulted into a non-setose condition in February and March moult back into setose condition in preparation for the next breeding season by June. The increase in females with new spermatophores in July and August is two months ahead of when external eggs are produced in mid-spring (Chubb, 1991).

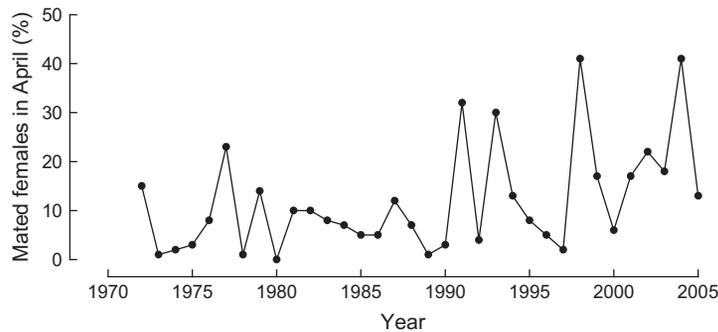


Figure 4. Percentage of large ( $\geq 95$  mm) mated female *Panulirus cygnus* sampled throughout the fishery during April from 1972 to 2005.

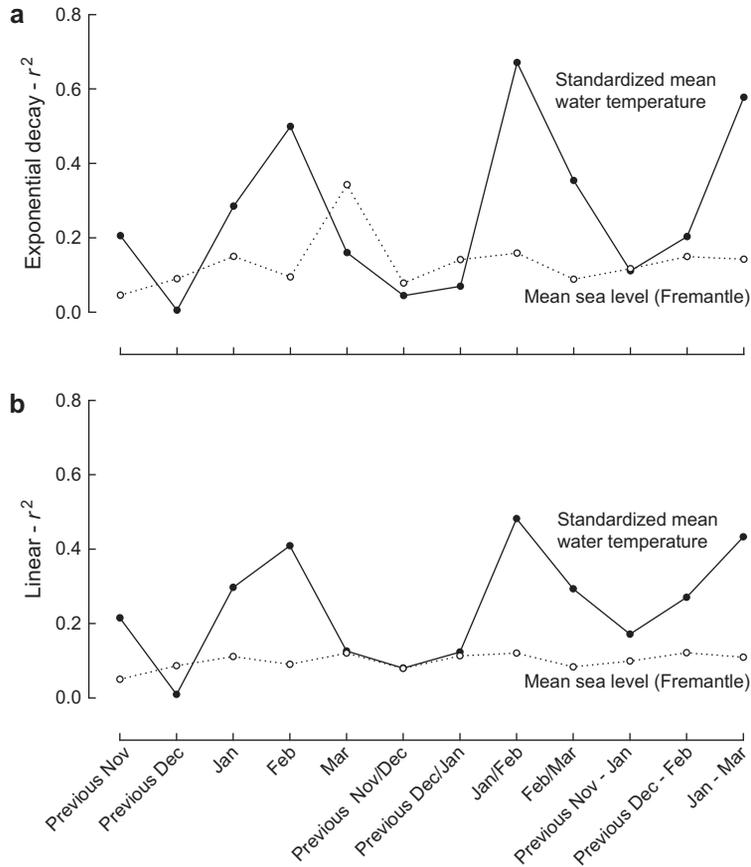


Figure 5. Values of  $r^2$  from (a) exponential decay and (b) linear regressions between the incidence of large ( $\geq 95$  mm) mated female *Panulirus cygnus* in April and annual values, individual months and subsets of months of standardized mean water temperatures ( $^{\circ}$ C), and mean monthly Fremantle sea levels (cm).

The ability of mature females to moult out of setose condition outside the breeding season is common to numerous other spiny lobster species, for example *Jasus edwardsii* (MacDiarmid, 1989), *Jasus lalandii* (Paterson, 1969),

*Panulirus japonicus* (Nakamura, 1940), and *Panulirus argus* (Sutcliffe, 1953).

The large numbers of reproductively active females not moulting into a non-setose phase in late summer appear

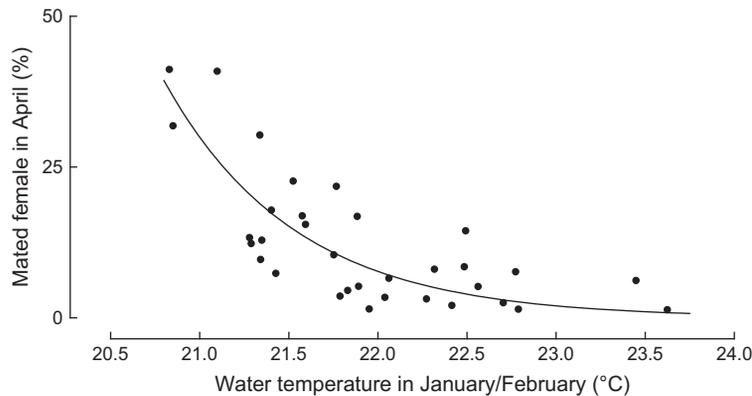


Figure 6. Exponential decay regression between the annual incidence of large ( $\geq 95$  mm) mated female *Panulirus cygnus* in April and the annual standardized mean bottom-water temperature for January and February (combined) of that year.

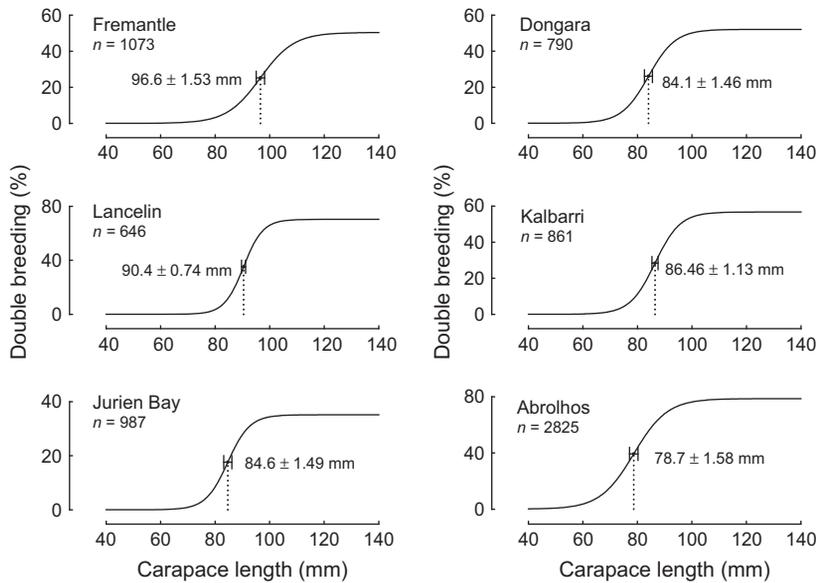


Figure 7. Logistic regressions fitted to the percentage of double-breeding female *Panulirus cygnus* at different carapace lengths in six locations in Western Australia, based on data collected during the 2002 Independent Breeding Stock Survey.  $DB_{50} \pm 1$  s.e. denotes the size at which 50% of the assemblage is mature, and  $n$  is the sample size.

to be linked to cool water temperature towards the end of the egg-bearing season. Chittleborough (1976) showed that the development time of fertilized eggs of *P. cygnus* increased exponentially from about 26 days at 25°C to 70 days at 19°C. It is therefore likely that females that become ovigerous late in the spawning season during a year when water temperatures are cool, may not have sufficient time to develop and release their eggs prior to the synchronous non-setose moult in February and March. Further, females that produce two batches of eggs in a spawning season would be more likely to extrude their last (second) batch of eggs later in the season than would the single breeders that extrude only one batch of eggs. It therefore follows that the females most affected by cool water towards the end of the spawning period are the larger females, i.e. those that are more likely to produce two broods of eggs each season. It is not possible to measure this directly by examining the numbers of egg-bearing females then, because most will be bearing eggs in a late stage of development, and females in such a condition have an extremely low catchability (Waddington *et al.*, 2005).

At each location, the double-spawning females were always the larger lobsters sampled. This is consistent with previous findings for *P. cygnus* (Chittleborough, 1976; Chubb, 1991), and for other species of this genus (Berry, 1971; Briones-Fourzan *et al.*, 1981; MacFarlane and Moore, 1986; Briones-Fourzan and Lozano-Alvarez, 1992; Gomez *et al.*, 1994). However, the sizes recorded by Chubb (1991) at which 50% of *P. cygnus* became double breeders ( $DB_{50}$ ), at Two Rocks (between Fremantle and Lancelin; ~80 mm), Dongara (~93 mm), and Abrolhos Islands (~63 mm), were all markedly different from those recorded in the present study (Table 1, Figure 7). These differences arise because Chubb (1991) visually classified lobsters with an eroded spermatophoric mass, external eggs, and a developing ovary as multiple (i.e. double) breeders. Recently, however, Melville-Smith and de Lestang (2005) showed that an ovary classified as “developing” in this situation is more likely a “spent” ovary containing residual atretic oocytes which make it appear yellow and developing, and so is only a single breeder. Furthermore, the  $DB_{50}$  recorded by Chubb (1991) for

Table 1. The size at which 50% and 95% of female *Panulirus cygnus* produce one (SB; Melville-Smith and de Lestang, in press) and two batches (DB) of eggs per spawning season at six locations along the west coast of Australia.

Parameter	Fremantle	Lancelin	Jurien	Dongara	Kalbarri	Abrolhos
$SB_{50}$	$87.5 \pm 0.22$	$82.2 \pm 0.34$	$81.4 \pm 0.32$	$74.9 \pm 0.49$	$77.2 \pm 0.34$	$65.0 \pm 0.27$
$SB_{95}$	$92.8 \pm 0.57$	$89.6 \pm 0.87$	$90.6 \pm 1.00$	$88.1 \pm 1.26$	$87.5 \pm 0.86$	$76.3 \pm 0.51$
$DB_{50}$	$96.6 \pm 1.52$	$90.4 \pm 0.74$	$84.6 \pm 1.49$	$84.1 \pm 1.46$	$86.5 \pm 1.13$	$78.7 \pm 1.58$
$DB_{95}$	$114.8 \pm 3.82$	$100.8 \pm 2.05$	$96.5 \pm 3.50$	$98.6 \pm 4.54$	$100.0 \pm 3.48$	$96.8 \pm 3.63$

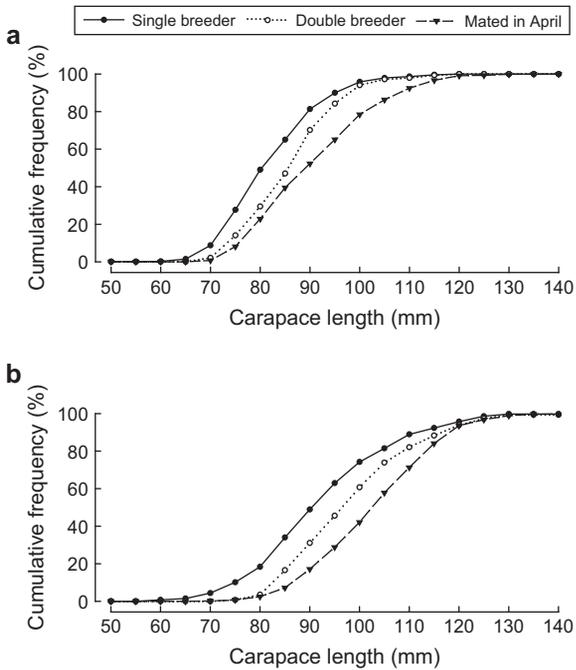


Figure 8. Cumulative frequencies (%) of single and double breeders and of mated female *Panulirus cygnus* recorded in April in sequential 5-mm CL classes in (a) the northern and (b) the southern zones of the western rock lobster fishery.

Two Rocks, Dongara, and the Abrolhos Islands are the same as, or smaller than, the size at first maturity recorded by the same author for the same regions (Chubb, 1991), which casts doubt on the appropriateness of the criteria used to assign double breeding in this case.

Our data show that large mature females were able to produce multiple batches of eggs within a spawning season, although whether this was limited to two broods could not be determined directly. Anecdotally however, two broods do seem to be the maximum number *P. cygnus* is capable of producing per season. Chittleborough (1976) showed that when kept at a constant temperature and fed to excess, the maximum number of broods produced by female *P. cygnus* between moulting events was two.

The percentage of females classified as double breeders not reaching 100% at any of the six locations, even in the very large size categories, was expected. Clear identification of an individual female as a double breeder is only possible when they are sampled reasonably close to the middle of their spawning season (Melville-Smith and de Lestang, 2005). Small variations are likely to exist in the stimuli that initiate spawning between and within each location, resulting in spawning not being synchronous throughout the fishery. Consequently, it was not possible to sample all double-breeding females when they were in the middle of their spawning season. As a result, some double-breeding females sampled will always be identified incorrectly as single breeders. As it is likely that

misclassification results in the percentage of double breeders never reaching 100%, it seems probable that, at each location, the size at  $DB_{50}$  recorded in this paper not only describes the size at which 50% of double-spawning females are breeding twice, but also is a good estimate of the size at which 50% of females within the sampled population will breed twice.

This study has found that double-breeding female lobsters sampled at six locations during the 2002 IBSS are about 10-mm CL larger than females at first maturity recorded at the same locations (Melville-Smith and de Lestang, in press). As 2–3 mm is the average moult increment achieved by newly mature female lobsters (Morgan, 1977), and females of this size are expected to moult twice a year (Chittleborough, 1976; Morgan, 1977), it seems likely that newly mature females require a further two years of growth before they increase in carapace length by ~10 mm and attain the size at which they start to produce two batches of eggs in a season.

While  $DB_{50}$  may correspond to females two years older than their size at first maturity ( $CL_{50}$ ) at the same locality, it is unlikely that either size or age is directly responsible for this finding. It has been shown by Chittleborough (1974, 1976) that aquarium-held females kept at higher temperatures than in their natural environment (25°C) and fed to satiation can breed twice within an intermoult period from when they first mature, and thereafter breed repetitively without moulting into a non-setose (resting) phase.

The size at maturity of females has declined at all coastal sites since the 1970s (Melville-Smith and de Lestang, in press). It has not been possible to investigate whether  $DB_{50}$  has decreased over the same period, because ovarian development has been recorded only since 1992. Moreover, establishing whether a female is a single or a double breeder is very sensitive to the time of year she is sampled (Melville-Smith and de Lestang, 2005), and suitable IBSS data are not available for this purpose in most years. However if, as we have suggested,  $DB_{50}$  occurs on average two years after  $CL_{50}$ , then it could be assumed that  $DB_{50}$  has declined in a similar manner to  $CL_{50}$  since the 1970s. Incorporation of new  $DB_{50}$  estimates into the current egg-production indices will swing the relative contribution of eggs towards the larger size classes of female lobsters, further highlighting their importance to the sustainability of this fishery. Furthermore, the addition of slowly declining  $DB_{50}$  estimates will increase recent egg-production estimates relative to those determined for early periods, making the current position of these indices more positive.

There are important management implications resulting from identifying a relationship between water temperature and the likelihood of mature females moulting to the non-setose phase in February or March. A substantial portion of the commercial catch landed each year in March, April, and May are mature females that have moulted out of a setose condition. Cool waters in January and February would increase the protection provided to the breeding stock by

the “setose rule”, which was introduced as one of several management measures in 1993/1994 to limit fishing pressure on those females (Hall and Chubb, 2001). The Reynolds Sea Surface Temperature data set (Reynolds and Smith, 1994) records a slight increase in water temperatures on the western rock lobster grounds over the past 30 years. Such a trend can be expected to dilute the effect of the setose rule over time, by allowing more females to moult into the non-setose condition and becoming legal to retain. Conversely, the more frequent occurrences of ENSO events since the 1990s have resulted in a higher frequency of weaker Leeuwin Current years and hence cooler water temperatures (SdeL, unpublished data). This has resulted in the four highest percentages of setose females in April recorded since 1991.

## Acknowledgements

We thank the research staff and crew of the RV “Naturalist”, and Nick Caputi, Anthony Hart, Vivienne Mawson, James Penn, Rick Flecher, and Bruce Phillips, as well as the two anonymous reviewers for their valued suggestions on the manuscript. The work was undertaken as part of Fisheries Research and Development Corporation Project 2003–2005.

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