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Reproductive cycle of the blue swimmer crab, *Portunus pelagicus*, off southern Australia

Martin S. Kumar*, Yongshun Xiao, Sonja Venema and Graham Hooper

South Australian Aquatic Sciences Centre, South Australian Research and Development Institute, 2 Hamra Avenue, West Beach, Adelaide, SA, Australia 5024. *Corresponding author, e-mail: kumar.martin@saugov.sa.gov.au

The proportion of berried (externally egg-bearing) females, fecundity, gonadosomatic index, and egg size of the blue swimmer crab *Portunus pelagicus* off southern Australia were examined by analysing data from samples of commercial catches using generalized linear models. Ovarian development was studied morphologically and histologically. Female blue swimmer crabs spawn from October to January and can spawn more than once per season. The fecundity of female blue swimmer crabs initially increased with carapace width, maximized at a carapace width of 134 mm, and decreased thereafter. Thus, fecundity increased 83.9% with an increase of carapace width from 105 to 125 mm, implying a single large female can produce as many eggs as two or more small females. The gonadosomatic index of female crabs from Spencer Gulf increased 2.4% from October 1998 to November 1998, increased an additional 15.9% by December 1998, and then decreased 62.3% to its minimum in January 1999. Gonadosomatic index also increased with $\frac{1}{3}$ power of their body weight. Thus, the commonly used gonadosomatic index is overly simplistic for blue swimmer crabs. Unlike tropical or subtropical female blue swimmer crabs which often continually spawn, those off southern Australia spawn only in certain times of the year. The implications of this work lead to suggestions for three management measures for the commercial fishery: maintaining the prohibition of catching berried females, extending the seasonal closure from October to January, and maintaining the current legal minimum carapace width of 110 mm.

INTRODUCTION

The blue swimmer crab *Portunus pelagicus* Linnaeus, 1766 is distributed throughout coastal waters of the tropical regions of the western Indian and the eastern Pacific Oceans (Kailola et al., 1993). In Australia, it occurs off Western Australia, Northern Territory, Queensland, New South Wales and South Australia, spanning tropical, subtropical and temperate waters. Investigator Strait is the southern limit of blue swimmer crab distribution (Kailola et al., 1993). In South Australia, there are important commercial and recreational fisheries in Gulf St Vincent and Spencer Gulf. Each Australian state adopts their own management strategies for the blue swimmer crab fishery, due to biology differing between states, reflecting regional differences in prevailing climatic conditions.

South Australia has a limited entry fishery, where access was based on fishers' historical catches. Output controls were also imposed in 1996, with the total allowable catch (TAC) allocated as a quota to pot and ground fish fishers, based on catches of the past five years. The TAC allocated to pot fishers was divided equally among all operators, whereas allocation to ground fish fishers was divided among all operators pro-rated on their respective catches of the past five years. Further management measures include the imposition of a minimum legal size of 110 mm in carapace width, a ban of fishing during the breeding–spawning season, and a prohibition of catching berried (externally egg-bearing) females. These three measures were implemented in 1985, when little biological information was available in temperate regions. Their effectiveness and the need for additional measures have never been evaluated.

Much work has been conducted on the reproductive biology of marine crabs, including anatomical changes in the spermathecae over the reproductive cycle of male *Callinectes sapidus* (e.g. Van Engel, 1990). Data on *P. pelagicus* include temporal changes in gonadosomatic index (Pillai & Nair, 1971; Rahaman, 1980), temporal changes in the proportion of berried females in the population (Dhawan et al., 1976), anatomical changes in the spermathecae over the reproductive cycle (Bawab & El-Sherief, 1988), size of sexual maturity (Campbell & Fielder, 1986; Sukumaran & Neelakantan, 1996), and sex ratio and fecundity (Sukumaran & Neelakantan, 1997). All these studies were confined to tropical areas. Aspects of the blue swimmer crab's reproductive biology have been studied in the subtropical Moreton Bay, Queensland (Sumpton et al., 1994). Few data are available for temperate regions, despite their increasing popularity as a seafood and economic importance as a commercial fishery. However, studies on the general biology of *P. pelagicus* in temperate regions of Australia suggest that its reproductive biology varies markedly between regions (Meaghar, 1971; Penn, 1977; Smith, 1982; Potter et al., 1983).

Knowledge of reproductive biology of marine animals is used in stock assessment and developing and evaluating strategies for fisheries management. The rate of harvest of adults depends heavily on the rate of recruitment into the fishery, which in turn depends on the rate of egg production in the population. Knowledge of egg production appears

to be most important for managing fisheries of marine invertebrates (Caddy, 1989) and fish (Rothschild, 1986; Koslow, 1992). General knowledge of the reproductive cycle, the timing of breeding and recruitment is also required.

In this paper, the proportion of berried females, fecundity, gonadosomatic index and egg size using generalized linear models is examined, and study the ovarian development morphologically and histologically, to understand the reproductive cycle of females.

MATERIALS AND METHODS

Proportion of berried females

Detailed protocol for data collection for studying the proportion of berried females is given in Xiao et al. (in preparation). Briefly, from 9 October 1996 to 25 February 1999, 933 random samples of blue swimmer crabs were taken from commercial pot catches on board commercial vessels and comprised up to 75–100% of the commercial pot catches. The sampled crabs were sexed, their carapace widths measured (to the base of the spines) to an accuracy of 0.5 mm, and it was recorded whether sampled female crabs were berried or not. Water depth, and time of fishing were also recorded.

This data can be used to examine the proportion of berried females among all commercially caught females. For this purpose, consider a random sample of female blue swimmer crabs, some of which may or may not be berried. Let random variable Y denote the berried status of a typical female, such that $Y = 1$ denotes the event that it is unberried with probability $P(t, m; w, d) = \Pr\{Y = 1|t, m; w, d\}$; $Y = 0$ denotes the event that it is berried with probability $1 - P(t, m; w, d)$. We model $P(t, m; w, d)$ as a function of time t due to observed temporal variations in unberried status of the blue swimmer crabs; as a function of month m and water depth d as blue swimmer crabs are inferred to undertake seasonal inshore and offshore migrations on a gradient of water depth. The function of carapace width w was also modelled because males generally grow faster and reach a larger size and because smaller crabs moult more frequently than larger ones.

The probability that x individuals are unberried and $n - x$ individuals are berried in a random sample of n female blue swimmer crabs is given by the well-known binomial distribution, with a density function:

$$\binom{n}{x}(P(t, m; w, d))^x(1 - P(t, m; w, d))^{n-x},$$
$$x = 0, 1, 2, \ldots, n.$$

Again, the functional form of $P(t, m; w, d)$ must be specified for estimation of its parameters. Specifically, we assume that $P(t, m; w, d)$ is described by the logistic equation of the form:

$$P(t, m; w, d) = \frac{P_{\max}}{1 + \exp(-\{\mu + \alpha(t) + \delta(m, d) + \eta w\})} \quad (1)$$

or equivalently of the form

$$\text{logit}(P(t, m; w, d)) = \ln\left(\frac{P(t, m; w, d)}{1 - P(t, m; w, d)}\right) = \mu + \alpha(t) + \delta(m, d) + \eta w$$

where $P_{\max}$ is the maximum proportion of unberried female blue swimmer crabs; μ is a constant; $\alpha(t)$ is the (relative) effect of time t on the proportion of unberried female blue swimmer crabs; $\delta(m, d)$ is the (relative) effect of water depth of d in month m on the proportion of unberried female blue swimmer crabs; and η is the effect of carapace width w on the proportion of unberried female blue swimmer crabs.

If $\alpha(t) = C + A\cos((2\pi/T)(t - t_\phi))$, where C is the mean annual effect of time t on the proportion of unberried female blue swimmer crabs, t is still the time of year, A, $T(= 365.243\,\text{d})$ and t_ϕ are, respectively, the amplitude, period and time shift of the sinusoidal change of the proportion of unberried female blue swimmer crabs, equation 1 becomes:

$$P(t, m; w, d) = \frac{P_{\max}}{1 + \exp(-\{\mu + \xi x_1 + \rho x_2 + \delta(m, d) + \eta w\})} \quad (2)$$

or equivalently

$$\text{logit}(P(t, m; w, d)) = \ln\left(\frac{P(t, m; w, d)}{1 - P(t, m; w, d)}\right) = \mu + \xi x_1 + \rho x_2 + \delta(m, d) + \eta w$$

where parameter C is absorbed into parameter μ,

$$x_1 = \sin\left(\frac{2\pi t}{T}\right), \quad x_2 = \cos\left(\frac{2\pi t}{T}\right),$$

$$\xi = \sin\left(\frac{2\pi t_\phi}{T}\right), \quad \rho = \cos\left(\frac{2\pi t_\phi}{T}\right),$$

$$A = \sqrt{\xi^2 + \rho^2}, \quad t_\phi = \frac{T}{2\pi}\left\{n\pi + \tan^{-1}\left(\frac{\xi}{\rho}\right)\right\}, \quad n = 0, \pm 1, \pm 2, \ldots$$

Now, the parameters can be estimated by the maximum likelihood method, i.e. by maximizing the total likelihood for all samples

$$\prod_j \binom{n_j}{x_j}(P(t_j, m_j; w_j, d_j))^{x_j}(1 - P(t_j, m_j; w_j, d_j))^{n_j - x_j}, \quad x_j = 0, 1, 2, \ldots, n_j$$

or, computationally more efficiently, by maximizing the total log-likelihood function (ignoring a constant term)

$$LL = \sum_j x_j \ln(P(t_j, m_j; w_j, d_j)) + (n_j - x_j)\ln(1 - P(t_j, m_j; w_j, d_j)), \quad x_j = 0, 1, 2, \ldots, n_j. \quad (3)$$

In our estimation, we assumed that $P_{\max} = 1$, because no female crabs are berried at certain times of the year. Under this assumption, eqns 1 and 3, or eqns 2 and 3, become a generalized linear model; its parameters can again be estimated by use of a SAS Procedure Genmod

(SAS Institute, Inc., 1996), with a binomial distribution and a logit link function. From estimates of parameters ξ and ρ in eqn 2, and their variances and covariances, parameters A and t_ϕ, and their variances can be calculated following Xiao et al. (in preparation).

Fecundity, gonadosomatic index, and body weight versus carapace width of females

Fecundity of a female crab is defined as the number of eggs carried externally in its abdomen. Fecundity can be affected by many factors, including size, area of distribution, and time of year. Random samples of female blue swimmer crabs were taken from commercial catches from Gulf St Vincent and Spencer Gulf from 16 October 1998 to 28 January 1999. Each female was measured for carapace width to the nearest mm with callipers, body weight measured to the nearest 0.1 g with an electronic balance (Mettler AE 2000), external egg mass was carefully removed and weighed to the nearest 0.1 g, the number of eggs counted by an image analyser (Video Pro 32, Leading Edge Pty. Ltd), and the average size of eggs measured to the nearest 1 μm. At least five samples of eggs were taken from each ovary for counting and measurement of diameter. Fecundity or total number of eggs cannot be calculated uniquely. In our calculations, we assumed that $N_i/W = n_i/w$, or $N_i = Wn_i/w$, where W is the total weight of an ovary, w_i weight of the ith sample, n_i number of eggs in the ith sample, and N_i total number of eggs in the ovary as predicted by the ith sample, $i = 1, 2, \ldots, m$, and used N_is directly in data analysis.

We model the fecundity of female blue swimmer crabs $f(t; w)$ as a function of time t and carapace width $w = w(t)$ by a simple generalized linear model of the form:

$$f(t; w) = \mu\alpha(t)w(t)^\beta \exp\{-\gamma w(t)\}\varepsilon(t; w), \quad (4)$$

where μ is a constant; $\alpha(t)$ is (relative) effect of time t on the fecundity of female blue swimmer crabs; $w = w(t)$ is the carapace width of female blue swimmer crabs at time t; β and γ characterize the effect of the carapace width of female blue swimmer crabs on their fecundity; and $\varepsilon(t; w)$ is the error in fecundity of female blue swimmer crabs, and is a function of time t and carapace width w.

In this model, we included time t, because blue swimmer crabs are batch spawners in a spawning season; and included carapace width w, as larger crabs generally carry more eggs but a large (old) crab may actually carry fewer eggs due to its age. A similar model was used by Prager et al. (1990) to study the fecundity of *Callinectes sapidus* in Chesapeake Bay.

Instead of directly modelling the gonadosomatic index of female blue swimmer crabs, we model their ovary weight $f(t; w)$ as a function of time t and body weight $w = w(t)$ by a simple generalized linear model of the form:

$$f(t; w) = \mu\alpha(t)w(t)^\beta\varepsilon(t; w), \quad (5)$$

where μ is a constant; $\alpha(t)$ is (relative) effect of time t on the ovary weight of female blue swimmer crabs; $w = w(t)$ is the body weight of blue swimmer crabs at time t; β is (approximately) the relative increase in ovary weight for 1% increase in body weight of blue swimmer crabs; and $\varepsilon(t; w)$ is the error in ovary weight, and is a function of time t and body weight w.

In this model, we included time t, on account of changes of ovary weight with time because blue swimmer crabs are batch spawners in a spawning season and earlier spawned batches generally have more eggs than later ones; and included body weight w, because larger crabs generally have larger ovaries. This indirect approach of calculating the gonadosomatic index tests the hypothesis that gonadosomatic index is independent of body weight (i.e. $\beta = 1$) and gives more flexibility in the model.

We also used eqn 5 to model the body weight of female crabs $f(t; w)$ as a function of time t and carapace width $w = w(t)$. For this purpose, μ is a constant; $\alpha(t)$ is (relative) effect of time t on the body weight of female blue swimmer crabs; $w = w(t)$ is the carapace width of blue swimmer crabs at time t; β is (approximately) the relative increase in body weight for 1% of increase in carapace width of blue swimmer crabs; and $\varepsilon(t; w)$ is the error in body weight of female blue swimmer crabs, and is a function of time t and carapace width w. In this model, we included time t again, as ovary weight changing with time as blue swimmer crabs are batch spawners in a spawning season and earlier spawned batches are generally larger than later ones; and carapace width w, because the larger the crabs, the heavier they are.

Similar models have been used in many other contexts (e.g. Xiao, 1998). Parameters in eqns 4 and 5 can be estimated from observed fecundity (or ovary weight), time, and body weight (or carapace width) by the maximum likelihood method. This method makes appropriate assumptions about the distribution of errors observed in fecundity (or ovary weight or body weight) $f(t; w)$. Three assumptions were made about the distribution of errors of $f(t; w)$, i.e. independent log-gamma, log-normal, or log-negative binomial distribution. All computations were affected by the SAS Procedure Genmod (SAS Institute, Inc., 1996).

Egg diameter

The above data can also be used to examine changes in egg diameter. For this purpose, we consider the egg diameter $f(t, a; w)$ as a function of time t, area a and carapace width $w = w(t)$, of the form:

$$f(t, a; w) = \mu\alpha(t)\delta(a)w(t)^\beta \exp\{-\gamma w(t)\}\varepsilon(t, a; w), \quad (6)$$

where μ is a constant; $a(t)$ is (relative) effect of time t on the egg diameter; $\delta(a)$ is (relative) effect of area a on the egg diameter; $w = w(t)$ is the carapace width of female blue swimmer crabs at time t; β and γ characterize the effect of carapace width on their egg diameter; and $\varepsilon(t, a; w)$ is the error in egg diameter and is a function of time t, area a and carapace width w.

In this model, we included time t, for temporal variation during spawning season; included area a because of possible geographic differences in egg diameter; and included carapace width w, because the larger the number of eggs a crab carries, the smaller their diameter, and larger crabs generally carry more eggs but a crab which is too large may actually carry fewer eggs because of its age.

Parameters in eqn 6 can be estimated from the observed egg diameter, time, fishing area, and carapace width by the maximum likelihood method by making appropriate assumptions about the distribution of errors in observed egg diameter $f(t, a; w)$. Three assumptions were made about the distribution of errors of $f(t, a; w)$, i.e. independent log-gamma, log-normal, or log-negative binomial distribution. All computations were affected by the SAS Procedure Genmod (SAS Institute, Inc., 1996).

Ovarian development

A random sample of at least 40 female crabs was collected from Gulf St Vincent and Spencer Gulf. Additional ones were included to cover as wide a carapace width range as possible. All crabs were frozen on-board commercial vessels, and brought back to the laboratory to study their ovarian development. Immediately after each field trip, crabs were measured in the laboratory for carapace width to the nearest 0.1 mm with callipers, weighed to the nearest 0.1 g with an electronic balance (Mettler AE 2000), dissected for removal of their ovaries, weighed to an accuracy of 0.1 g, and macroscopically staged. Five morphological macroscopic stages were recognized (Sumpton et al., 1994).

These macroscopic stages were verified microscopically by observing samples of fresh oocytes and histological slides of a randomly selected sample of ovaries in each maturity stage. Fresh oocytes were removed from an ovary, spread on a microscope slide, and examined under a dissecting microscope (×12–50). Colour photographs were used to record the appearance of fresh oocyte samples. This technique allowed fresh oocytes to be compared with histological slides in assessing gonad maturity stage. For histological preparation, ovary samples were fixed in Bouin's solution, soaked in water for 24 h, dehydrated in 99% ethanol, cleared in 99% toluene, embedded in paraffin, sectioned to 78 μm in thickness, and stained with haematoxylin.

RESULTS

Temporal changes in surface water temperature

Sea surface water temperatures at the sampling sites varied seasonally, with an annual maximum of 23.52 ($\pm$0.09)°C in late January (27.30 $\pm$ 0.65 d), a minimum of 11.64 ($\pm$0.06)°C in late July, and a mean of 17.58 ($\pm$0.04)°C (Figure 1).

Proportion of berried females

Fitting of eqns 1 and 3, and eqns 2 and 3 (SAS Proc Genmod, SAS Institute, 1988), to data from monthly random samples of commercial blue swimmer crab catches yielded a log-likelihood of -7743.8, a deviance of 4881.2, 4842 df, and N=4858. Because the deviance divided by its associated degrees of freedom is 1.0081, being quite small for such a large set of data, the goodness of fit of eqns 2 and 3 seemed reasonable.

A significant annual variation in the proportion of unberried females of all female crabs in commercial catches in both Gulfs was detected, with $\hat{\xi} = 0.56(\pm 0.09)$, $\chi^2_{0.0001}(1) = 35.8$; $\hat{\rho} = -3.53(\pm 0.15)$, $\chi^2_{0.0001}(1) = 588.7$; $\mathrm{Cov}(\hat{\xi}, \hat{\rho}) = -0.005258$. Such estimates of ξ and ρ, and their variances and covariances

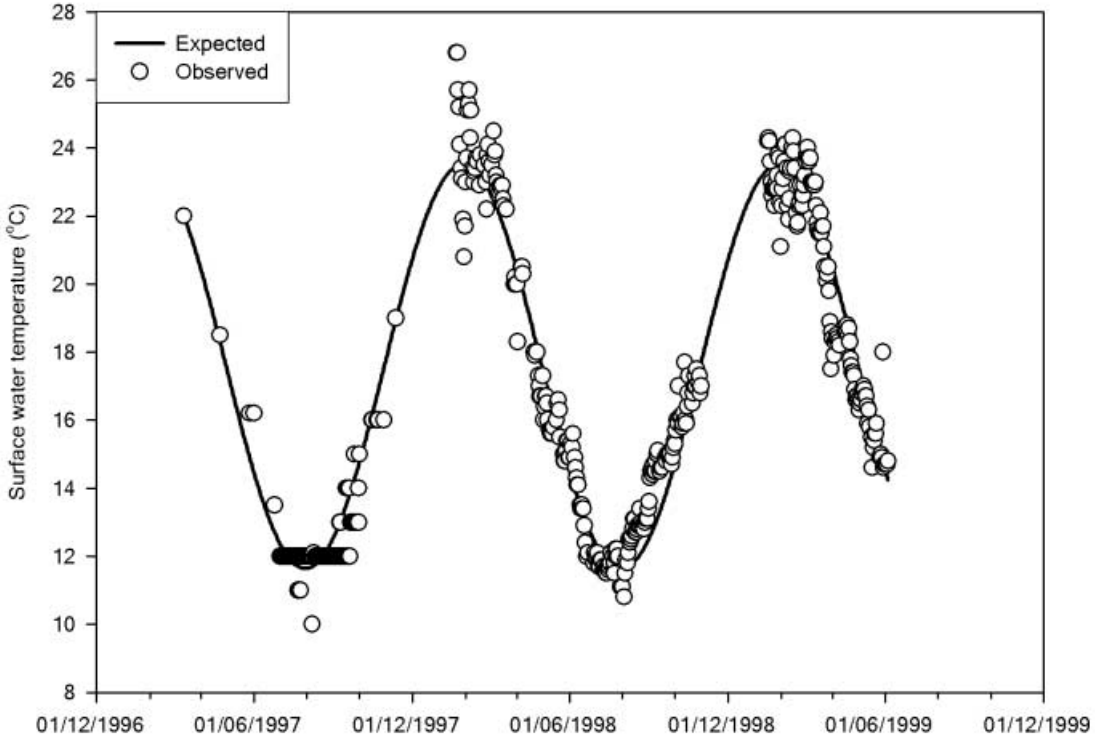

Figure 1. Observed (circle) and expected (solid line) temporal variation in the sea surface water temperatures at the sampled sites off South Australia.

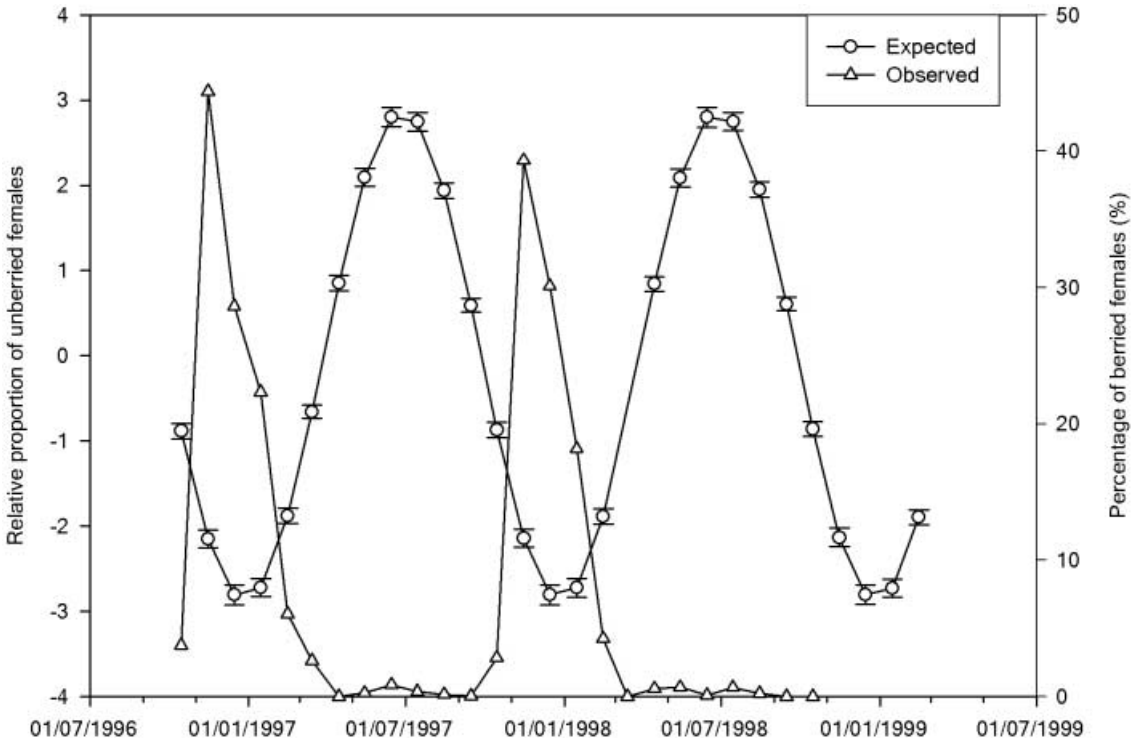

Figure 2. Temporal variation in the approximate relative proportion of unberried (circle) female blue swimmer crabs in commercial catches and in the proportion of berried (triangle) ones in raw commercial catches off South Australia.

imply that $\hat{A} = 3.57\ (\pm 0.15)$ and $\hat{t}_\phi = 173.46(\pm 1.41)$d. Notice that $\hat{t}_\phi$ takes a value of 173.46 (=365.25/2−9.17) d, because the principal value of $(T/2\pi)\tan^{-1}(\hat{\xi}/\hat{\rho})$ on the interval $(-\pi/2, \pi/2)$ is −9.17 d, and $\hat{\xi} > 0$ and $\hat{\rho} < 0$. Because $P(t, m; w, d)$ in eqns 1 or 2 increases with any quantity on its right-hand side, the proportion of unberried females in commercial catches increased from a minimum at time $t = \hat{t}_\phi = 356.1$ d (22 November) when $\cos((2\pi/T)(t-\hat{t}_\phi))$ is a minimum to a maximum at time $t = \hat{t}_\phi = 173.46$ d (21 May) when $\cos((2\pi/T)(t-\hat{t}_\phi))$ is a maximum, and then decreased at time $t = \hat{t}_\phi = 356.08$ d (22 November) when $\cos((2\pi/T)(t-\hat{t}_\phi))$ is a minimum for another cycle (Figure 2). The trend is reversed for the proportion of berried female crabs; it decreased from a maximum at time $t = \hat{t}_\phi = 356.08$ d (22 November) when $\cos((2\pi/T)(t-\hat{t}_\phi))$ is a minimum to a minimum at time $t = \hat{t}_\phi = 173.46$ d (21 May) when $\cos((2\pi/T)(t-\hat{t}_\phi))$ is a maximum, and then increased at time $t = \hat{t}_\phi = 356.08$ d (22 November) when $\cos((2\pi/T)(t-\hat{t}_\phi))$ is a minimum for another cycle. This trend is also obvious in grouped (by month) monthly random samples of commercial catches of blue swimmer crabs.

The proportion of unberried females also increased with water depth in March, April, July and December, while decreased in May, August, September and November, and remained unchanged in January, February, June and October (Figure 3). Finally, the proportion of unberried adult females increased with carapace width ($\hat{\eta} = 0.0125\ (\pm 0.0018)$, $\chi^2_{0.0001}(1) = 48.0$) possibly as a result of maturity moult, mating at moult and/or multiple moults in their mature stages of life.

Fecundity, gonadosomatic index, and body weight versus carapace width of females

Under the assumptions that the errors in $f(t; w)$ follow independent log-gamma, log-normal, or log-negative binomial distribution, fitting eqn 4 to data from monthly random samples of commercial catches of blue swimmer crabs from Spencer Gulf yielded very similar results (Table 1). Specifically, the fecundity of female crabs increased, somewhat gradually, from October 1998 to December 1998, and decreased 46.8% to reach its minimum in January 1999. Fecundity initially increased with carapace width ($\hat{\beta} > 0$), maximized at a carapace width of $\hat{\beta}/\hat{\gamma} \approx 134$ mm, and decreased thereafter. These results are reliable, since the goodness of fit of eqn 4 was appropriate for all three distributions. The value of R^2 is 0.76 for log-normal distribution; the deviance divided by its associated degrees of freedom is 0.064 for log-gamma distribution and 0.15 for log-negative binomial distribution.

Similarly, under the assumptions that the errors in $f(t; w)$ follow independent log-gamma, log-normal, or log-negative binomial distribution, fitting eqn 5 to data on ovary weight as a function of time and body weight collected from monthly random samples of commercial catches of blue swimmer crabs from Spencer Gulf yielded very similar results (Table 1). The gonadosomatic index of female crabs increased 2.4% from October 1998 to November 1998, increased a further 15.9% by December 1998, and decreased 62.3% to reach its minimum in January 1999. Also, because female ovary weight increased with $\hat{\beta} \approx 1.3345 \approx 1\frac{1}{3}$th power of their body weight, their gonadosomatic index increased with $\frac{1}{3}$th

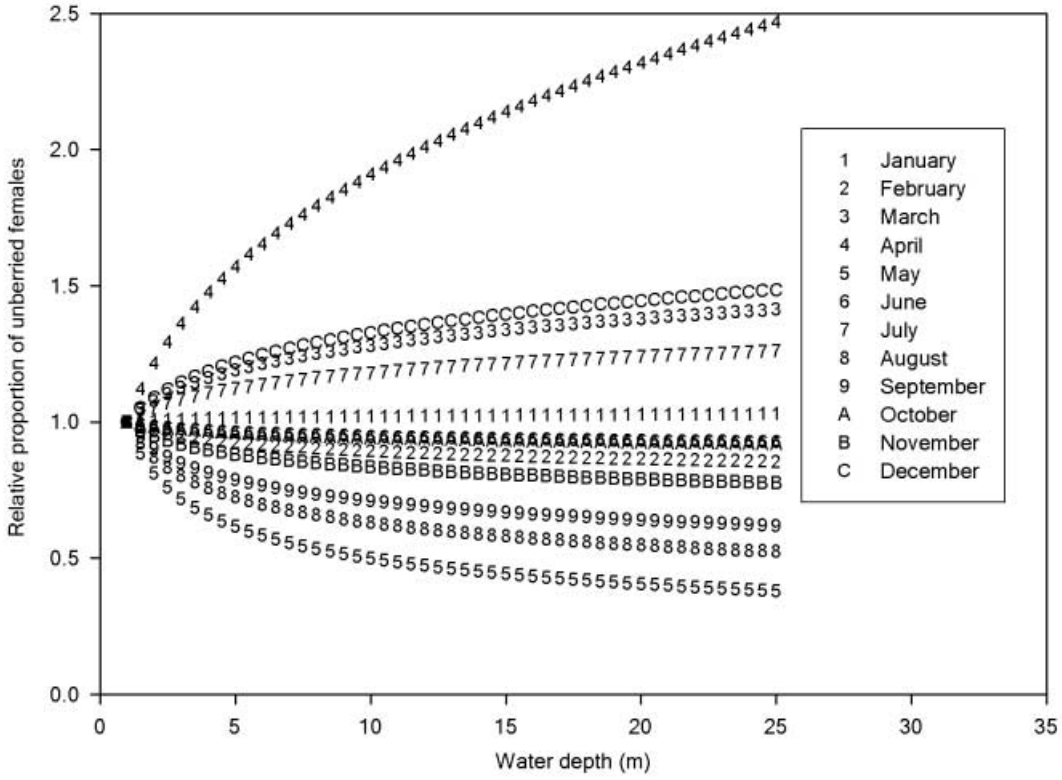

Figure 3. Temporal change of the (approximate) relative proportion of unberried female blue swimmer crabs in commercial catches off South Australia as a function of water depth.

Table 1. *Estimates of parameters and their standard errors (SE) in eqns 4–6 under the assumption that each dependent variable follows log-normal distributions with a constant variance. Equation 4 characterizes the fecundity of female blue swimmer crabs as a function of time and carapace width; eqn 5, ovary weight as a function of time and body weight; eqn 5, body weight of female blue swimmer crabs as a function of time and carapace width; and eqn 6, egg diameter as a function of time, geographic region, and carapace width. Blank indicates inapplicable.*

Equation	Dependent variable	Parameter	Estimate (SE)	t	P
4	Fecundity	$\log(\mu)$	−23.18 (6.68)	−3.47	0.0007
		$\log(\alpha(\text{Oct 1998}))$	0.08 (0.10)	0.83	0.4089
		$\log(\alpha(\text{Nov 1998}))$	0.25 (0.10)	2.52	0.0126
		$\log(\alpha(\text{Dec 1998}))$	0.40 (0.09)	4.25	0.0001
		$\log(\alpha(\text{Jan 1999}))$	0.00		
		β	23.29 (4.80)	4.84	0.0001
		$\gamma(\text{cm}^{-1})$	1.72 (0.43)	−3.97	0.0001
5	Ovary weight	$\log(\mu)$	−4.20 (0.61)	−6.88	0.0001
		$\log(\alpha(\text{Oct 1998}))$	0.35 (0.10)	3.68	0.0009
		$\log(\alpha(\text{Nov 1998}))$	0.38 (0.10)	3.75	0.0008
		$\log(\alpha(\text{Dec 1998}))$	0.52 (0.11)	4.91	0.0001
		$\log(\alpha(\text{Jan 1999}))$	0.00		
		β	1.39 (0.10)	13.32	0.0001
5	Body weight	$\log(\mu)$	−2.12 (0.33)	−6.39	0.0001
		$\log(\alpha(\text{Oct 1998}))$	0.05 (0.04)	1.23	0.2281
		$\log(\alpha(\text{Nov 1998}))$	0.11 (0.04)	2.82	0.0086
		$\log(\alpha(\text{Dec 1998}))$	0.14 (0.04)	3.38	0.0021
		$\log(\alpha(\text{Jan 1999})$	0.00		
		β	3.14 (0.13)	23.96	0.0001
6	Egg diameter	$\log(\mu)$	12.15 (0.61)	19.88	0.0001
		$\log(\delta(\text{GSV}))$	0.10 (0.01)	14.51	0.0001
		$\log(\delta(\text{SPG}))$	0.00		
		β	−4.34 (0.41)	−10.47	0.0001
		$\gamma(\text{cm}^{-1})$	−0.37 (0.03)	−10.74	0.0001

power of their body weight. Consequently, the most commonly used gonadosomatic index is not a constant, as commonly believed, for blue swimmer crabs and undoubtedly many other animals, its use should be discouraged, and a generalized approach to its calculation should be adopted (see below). These results are reliable, because the goodness of fit of eqn 5 was similar for all three distributions. The value of R^2 is 0.88 for log-normal distribution; the deviance divided by its associated degrees of freedom is 0.034 for log-gamma distribution and 0.223 for log-negative binomial distribution.

Finally, under the assumptions that the errors in $f(t; w)$ follow independent log-gamma, log-normal, or log-negative binomial distribution, fitting eqn 5 to data on (total) body weight of female blue swimmer crabs as a function of time and body weight collected from monthly random samples of commercial catches of blue swimmer crabs from Spencer Gulf yielded very similar results (Table 1). The body weight of female crabs increased 6.6% from October 1998 to November 1998, increased a further 3.1% by December 1998, and decreased 14.6% in January 1999. Also, body weight increased with $\hat{\beta}$ 3.1th power of their carapace width. Thus, female gonadosomatic index increased with $\frac{1}{3}$th power of body weight, or approximately linearly with their carapace width. These results are reliable, because the goodness of fit of eqn 5 was valid for all three distributions. The value of R^2 is 0.96 for log-normal distribution; the deviance divided by its associated degrees of freedom is 0.005 for log-gamma distribution and 0.277 for log-negative binomial distribution.

Egg diameter

Under the assumptions that the errors in $f(t, a; w)$ follow independent log-gamma, log-normal, or log-negative binomial distribution, fitting eqn 6 to data from monthly random samples of commercial catches of blue swimmer crabs from both Gulfs yielded very similar results (Table 1). A significant seasonal variation in egg diameter of female crabs in commercial catches was found for all three distributions, and characterized by a somewhat continuous increase from mid-March to November and December, and then a sudden decrease (Figure 4). Also, the egg diameter of female crabs initially decreased with carapace width (because $\hat{\beta} < 0$), minimized at a carapace width of $\hat{\beta}/\hat{\gamma}$ 118 mm, and increased thereafter. Finally, significant difference in egg diameter occurred between both Gulfs, with Gulf St Vincent being $\hat{\delta}(\mathrm{GSV})/\hat{\delta}(\mathrm{SPG}) - 1$ 10.4% larger. Again, these results are reliable, because the goodness of fit of the proposed model was satisfactory for all three distributions, despite large variability. The value of R^2 is 0.52 for log-normal distribution; the deviance divided by its associated degrees of freedom is 0.079 for log-gamma distribution and 0.001 for log-negative binomial distribution.

Ovarian development

Following morphological and histological examination of blue swimmer crab ovaries, five ovarian development stages (four internal and an external) were recognized, based mainly on change in ovarian colour resulting from

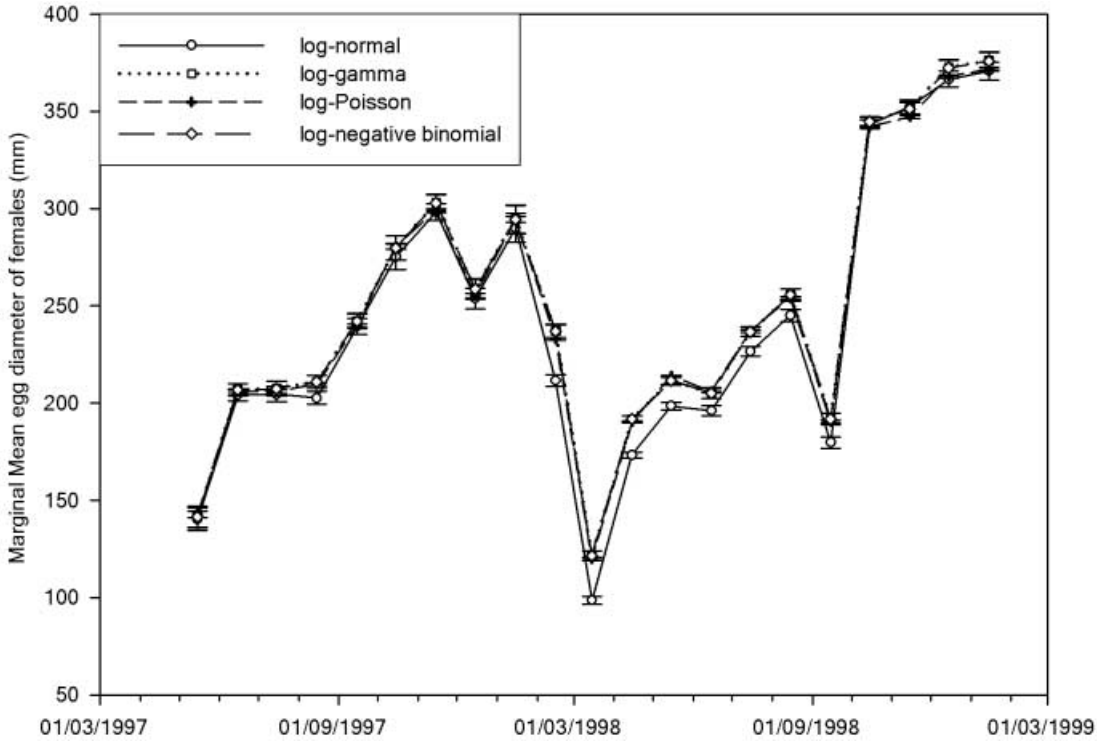

Figure 4. Temporal change of egg diameter of berried female blue swimmer crabs in commercial catches off South Australia.

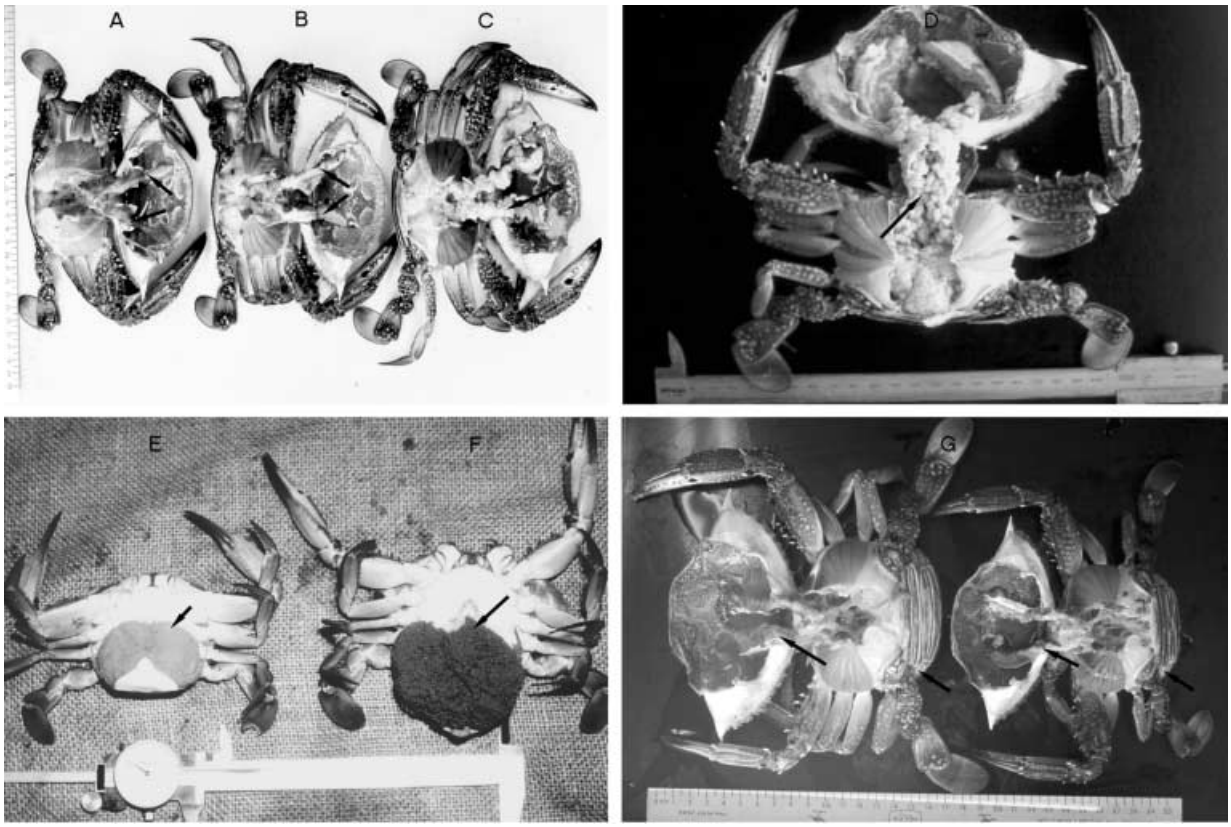

Figure 5. Ovarian stages (indicated by an arrow) of female blue swimmer crabs off South Australia: A, Stage 1; B, Stage 2; C, Stage 3; D, Stage 4; E, Stage 5 (berried females); F, embryonic development of berried females; G, evidence of batch spawning of female blue swimmer crabs off South Australia (two externally egg-bearing females with an internal ovarian developmental stage of 2–3 indicated by arrow).

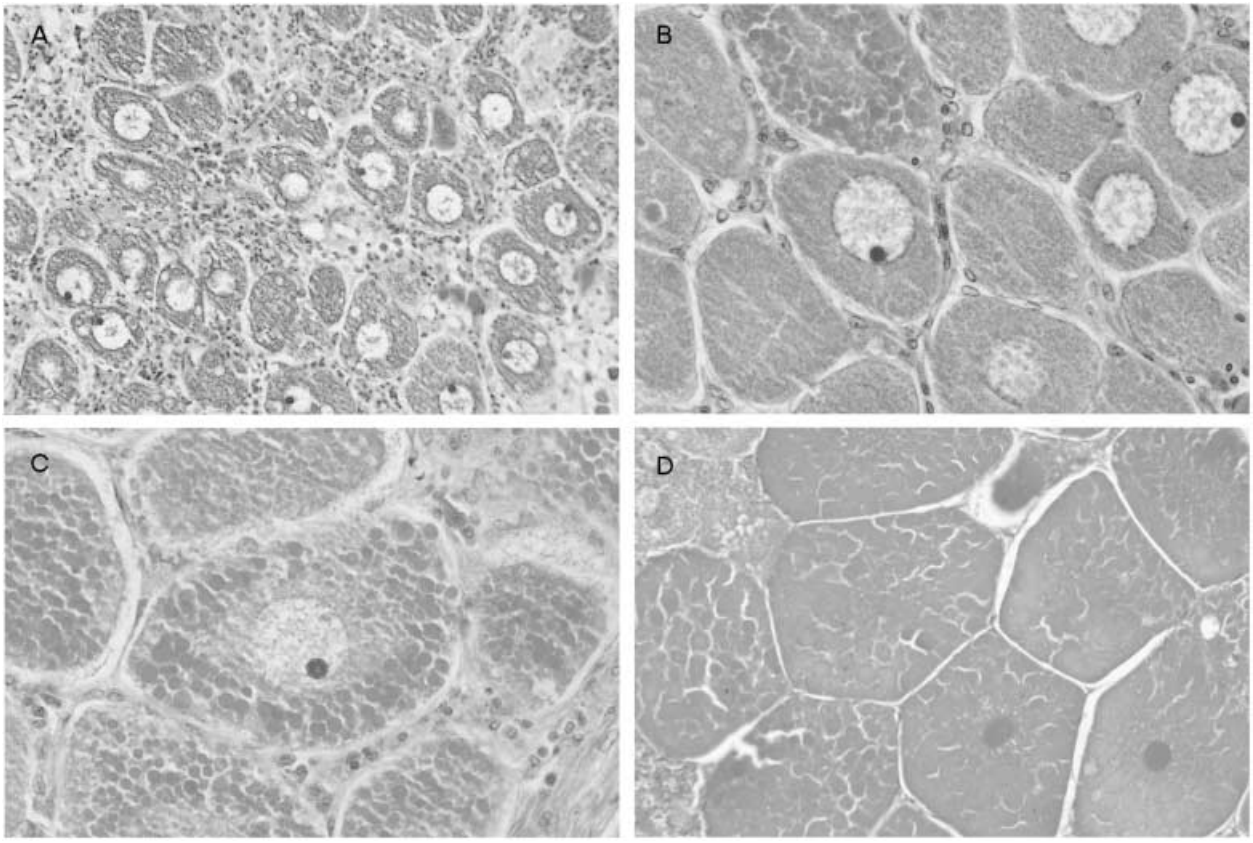

Figure 6. Histology of ovarian development of blue swimmer crabs off South Australia (×40): A, primary oocytes; B, maturing oocytes; C, mature oocytes; D, oocyte degeneration and reabsorption.

Table 2. *Summary of measurements characterizing five stages of ovarian development of the blue swimmer crab off South Australia.*

	Ovarian development stage				
	1	2	3	4	5 (Berried)
Reproductive state					
Number of individuals examined	14	39	64	15	40
Minimum carapace width (mm)	108.0	109.3	103.0	104.9	89.3
Carapace width (mm)	123.0 ±0.7	123.4 ±1.0	123.8 ±0.9	129.4 ±1.3	114.2 ±1.1
Body weight (g)	252.6 ±46.2	260.9 ±57.2	295.2 ±240.8	294.4 ±87.0	274.1 ±85.4
Percentage of ovarian cell stage					
1–100 μm	64.3 ±19.1	7.7 ±7.1	0	0	0
101–200 μm	35.7 ±29.0	69.2 ±27.3	14.1 ±25.8	0	0
201–300 μm	0	23.1 ±21.2	60.9 ±26.5	40.0 ±20.3	2.5 ±12.5
301–400 μm	0	0	23.4 ±24.8	60.0 ±18.3	92.5 ±23.7
$>$401 μm	0	0	1.6 ±16.7	0	5.0 ±15.5
Reproductive effort					
Number of individuals examined	0	5	4	4	40
Ovary weight (g)	0	3.4 ±0.9	7.0 ±3.1	17.6 ±2.6	54.8 ±22.2
Egg diameter (mm)	0	131.4 ±29.7	212.6 ±32.2	305.4 ±30.7	358.4 ±33.5
Number of eggs/g	0	82113 ±17922	66143 ±21926	38765 ±15799	23482 ±5974

yolk accumulation in the ova during development (Figure 5). Stage l, gonad immature, white or translucent (Figure 5A); Stage 2, gonad maturing, light yellow/orange, not extending into hepatic region (Figure 5B); Stage 3, gonad maturing, yellow/orange not extending into hepatic region (Figure 5C); Stage 4, gonad mature, dark yellow/orange extending into hepatic region (Figure 5D); Stage 5, berried females: females bearing fully mature eggs (pale to dark yellow eggs) externally (Figure 5E). After extrusion during oviposition, eggs are attached to the setae on the endpod of the pleopods. As embryonic development continued, the berry (external egg mass) changed colour to yellowish grey (Figure 5E,F).

Like the proportion of berried females (Stage 5) (Figure 2), the proportion of females at ovarian development Stages l–4 varied seasonally in 1997 and 1998. Females at Stage 4 began to occur in commercial catches in Spencer Gulf in August. In October, 70% of the females caught were at Stage 3 and 10% at Stage 4. In November, 40% were at Stage 3, and 40% at Stage 4. A similar pattern occurred in Gulf St Vincent.

Such morphological stages were associated with ovarian development (Figure 6). The oogonia were developed in the germinal epithelium (germarium). The oogonial cells had large nuclei and small amounts of ooplasm (Figure 6A). They underwent normal divisions and became primary oocytes, cytoplasm was transparent and nuclei remained large with uniformly distributed chromatin (Figure 6A). The ovary at Stages l and 2 contained mainly oogonia and primary oocytes. The primary oocytes started maturing with the deposition of yolk globules in the periphery of their cytoplasm (Figure 6B,C). While yolk globules were deposited cytoplasm granulated; the nucleus became solid, centrally located, and embedded in yolk droplets. In the process, many oocytes were degenerated and were reabsorbed (Figure 6D). The staining affinity of the ovary changed because of changes in its chemical constitution (Diwan & Nagabhushnam, 1975). The stain was positive to yolk globules; the maturing oocytes were stained relatively dark.

These morphological stages were also associated with ova size (Table 2). Ova of 100 μm diameter dominated Stage l, with an average diameter of 99 μm; those of 200 μm dominated Stage 2, with an average diameter of 176.2 μm; those of 250–325 μm dominated Stages 3 and 4, with an average diameter of 255 μm and 296.8 μm, respectively; those of 350–375 μm dominated in berried crabs (Stage 5), with an average diameter of 358.4 μm.

DISCUSSION

In this paper, we have examined the proportion of berried females, fecundity, gonadosomatic index and egg size by using simple generalized linear models, and ovarian cycle morphologically and histologically. Several conclusions about the reproductive biology of blue swimmer crabs off southern Australia can be drawn from this analysis.

Female blue swimmer crabs usually spawn from October to December, but occasionally to the following January. Off southern Australia, berried females are rare from April to September (Figure 2). Indeed, the (approximate) relative proportion of berried female crabs decreased from a maximum on 22 November to a minimum on 21 May, and then increased to the next maximum on 22 November. In tropical waters, by contrast, berried females often occur throughout the year and spawning is often continual (Shields & Wood, 1993). Thus, the reproductive biology of blue swimmer crabs off southern Australia differs from that in the tropics or subtropics, with spawning only occurring at certain times of the year. Such a strong seasonal pattern of spawning is closely correlated with seasonal changes in sea surface temperature and implies strong seasonal growth (Xiao, 1996, 1999; Xiao & McShane, 2000).

Spawning of female blue swimmer crabs is clearly correlated with water temperature (Stead, 1888; Rahaman, 1967; Jones, 1970; Meagher, 1971; Dhawan et al., 1976; Pillai & Nair, 1976), and can vary annually (Pillai & Nair, 1976) with changes in water temperature and other factors such

as food availability. For example, the period of spawning (as indicated by the high abundance of ovigerous females) differed slightly in Moreton Bay, Australia (Stead, 1888; Thomson, 1951; Jones, 1970). Mating does not time spawning, for it occurs throughout the year. Indeed, we have observed an insemination rate of 100% at any time of the year (Xiao et al., in preparation). A 100% insemination rate was also observed in post-moult female crabs in Moreton Bay, Australia (Sumpton et al., 1994), where the commercial fishery is based entirely on males, and females are protected by legislation. After copulation, sperm are stored in the spermathecae of females, until eggs become mature and are fertilized internally (Smith, 1982). The sperm in the spermathecae of female *Callinectes sapidus* may be viable for at least 12 months (Van Engel, 1958). Interestingly, although ovaries develop from Stage 1 to 4 throughout the year, it is only from October to the following January that ovarian development enters Stage 5 and berried females are abundant. Thus, ovarian development, maturation of eggs in the ovary and external environmental factors seem to time spawning.

Blue swimmer crabs can spawn more than once in a season, as observed in captivity[1]. Also, some berried females carried developing oocytes at Stages 2 and 3 inside the body cavity whilst also carrying an external egg mass (Figure 5G). Moreover, the fecundity of female crabs increased, somewhat gradually, from October 1998 to December 1998, and decreased 46.8% to reach its minimum in January 1999. Indeed, despite its considerable variation within a particular moult, the number of fertilized eggs in an egg-mass produced in the first batch is the largest (Campbell, 1984). Such a drastic decrease in fecundity in January 1999 might be attributed to the second batch of spawning. For a proper understanding of spawning frequency, there is a need to keep crabs in captivity and record their spawning activities.

That the fecundity of a female blue swimmer crab initially increased with carapace width, maximized at a carapace width of 134 mm, and decreased thereafter (Table 1) implies that fecundity increased 83.9% for a change of carapace width from 105 to 125 mm. However, because larger eggs are potentially more viable than smaller ones in a species (Stearns, 1976), and because the egg diameter initially decreased with carapace width, minimized at a carapace width of 118 mm, and increased thereafter (Table 1), the total number of viable eggs of blue swimmer crabs would initially increase with carapace width and maximize at a carapace width of 137 mm.

A successful fitting of eqn 5 to data on the ovary weight of blue swimmer crabs as a function of time t and body weight w suggests that the commonly used gonadosomatic index (GSI) is useful but overly simplistic. Division of both sides of eqn 5 by w gives a gonadosomatic index of $\mathrm{GSI}(t; w) = f(t; w)/w = \mu\alpha(t)w(t)^{\beta-1}\varepsilon(t; w)$, which depends on time t through $\alpha(t)$ and body weight w (raised to $\frac{1}{3}$th power) at time t. It seems likely that GSIs of many other species may also depend on body weight. Ignoring this inference and other contributing variables in this species can yield substantial biases in their calculated GSIs. In our case, the larger the body weight, the more biased it is. To avoid such biases, any factors that significantly affect GSIs must be taken into account, by use of eqn 5 or more realistic models. Also, in this calculation, there is no need to calculate raw GSIs first by dividing ovary weight by body weight of an animal. This is because once a useful model for ovary weight as a function of body weight and other variables is fitted into a data set, the expected GSI can be calculated by a simple division of the expected (given the model, its parameters and data) ovary weight by body weight. Therefore, the commonly used GSI should be reformulated and generalized to reduce bias.

The reproductive cycle of the blue swimmer crab off southern Australia can be constructed. The oogonia are continuously developed in the germinal epithelium of the adult. Some oogonial cells differentiate in to primary and then secondary oocytes throughout the year. Mating also occurs throughout the year, as evidenced by our observed 100% insemination rate at any time of the year (Xiao et al., in preparation). After copulation, sperm are stored in the spermathecae of the female and may be viable for at least 12 months, until eggs are mature and fertilized internally (Van Engel, 1958). The female migrates to shallow waters (mud flats and sandy bottom) from March to September to spawn and form an external egg mass (Xiao et al., in preparation). The extruded eggs are attached to the setae on the endpod of the pleopods, undergo 'external' embryonic development, and change their colour from pale to dark yellow, to yellowish grey and grey. During this period, oogonia continue to develop in the germinal epithelium of the now externally egg-bearing female, some oogonial cells continue to develop to primary and secondary oocytes. Then, the female migrates to deep waters to hatch (release zoea) from October to the following January, and after hatching, gradually disperse back to shallow waters for feeding from January to February (Xiao et al., in preparation). Some zoeas pass through successive sub-stages to become megalopae. The larval stages mainly occur in deep waters. They undertake diel and tidal vertical migrations in the water column and are transported inshore (Sulkin, 1984), where they develop into juvenile ($<$50 mm in carapace width) crabs and forage predominantly on sand and mud flats for 8–10 months to reach a carapace width of 70–90 mm, when they develop into adults. Most adult crabs migrate to comparatively deeper waters, including sea grass beds and unvegetated habitats offshore.

Finally, this work has major implications for managing the blue swimmer crab fishery. Both the proportion and size of berried females are significant in determining the total egg production in the population and hence are important indicators for the performance of the fishery. If implemented effectively, the current management measures of a prohibition of catching berried females and a closure of fishing from December to January would have helped protect fecund females and increase egg production and hence recruitment. However, because female blue swimmer crabs in this region spawn from October, usually to December, but occasionally to next January (see above), the seasonal closure has covered only the latter half of the spawning season. Such an oversight is unfortunate, for the overall rate of fishing mortality

[1], CMFRI (Central Marine Fisheries Research Institute) unpublished data, 1998. Central Marine Fisheries Research Institute, Cochin, Kerala, India.

might have been increased by more effectively protecting fecund females, given the same level of risk of exploitation. Finally, it can be readily verified, by use of eqn 4 (for fecundity as a function of carapace widths of females) and estimates of its parameters (Table 1) that an increase in the legal minimum size of 10 mm carapace width from the current 110 to 120 mm would yield a 35.1% increase in egg production for an individual of that size range; an increase of 20 mm from 110 to 130 mm would yield a 53.8% increase in egg production for an individual of that size range. It is time to update the three management measures in the light of our findings. Specifically, we recommend maintaining the prohibition of catching berried females, extending the seasonal closure from October to January, and maintaining current legal minimum size.

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