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Reproductive biology of female blue swimmer crabs in the temperate estuaries of south-eastern Australia

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Abstract. The blue swimmer crab (BSC, *Portunus armatus*) is an economically and culturally important species distributed throughout the coastal waters of the Indo-Pacific region. Reproduction of BSC is poorly understood in south-eastern Australia, a region that is experiencing substantial tropicalisation from global warming. We examined gonadal development, egg–mass relationships, and the influence of temperature on gonadal development and egg production within five different estuaries spanning $\sim 2.5^\circ$ of latitude. A negative correlation between the gonadosomatic index (GSI, an index of gonadal development and reproductive investment) and hepatosomatic index (HSI, an index of energy storage) was observed in only the final stages of ovarian development. The weight of the egg mass increased logarithmically with body mass, accounting for up to 55% of total body mass, which was significantly larger than observed in other studies. Thermal performance curves showed a peak in individual reproductive output at a mean monthly temperature of $\sim 24^\circ\text{C}$, at which the individual egg mass weight reached a maximum and the HSI reached a minimum. Environmentally driven variation in BSC reproduction has implications for population productivity and inter-annual variation in recruitment.

Keywords: Portunidae, reproduction, egg production, fecundity, fisheries, allometry.

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Introduction

Portunidae is the family of swimming crabs, characterised by the modified pair of posterior thoracic limbs that are flattened into paddles for swimming (Stephenson and Campbell 1959). Portunid crabs constitute valuable commercial and recreational fisheries globally (West *et al.* 2015; Tweedley *et al.* 2017; Johnston *et al.* 2018) and have experienced rapid growth in harvest rates in recent decades (Food and Agriculture Organization of the United Nations 1992, 2019). Habitat loss and overexploitation increase the susceptibility of populations to climate change and associated events, such as marine heatwaves (Chandrapavan *et al.* 2019). High fishing pressure coupled with declines in recruitment arising from adverse environmental conditions have contributed to declines in several portunid fisheries globally (Tweedley *et al.* 2017), including blue swimmer crabs (*Portunus* spp. complex) in Western Australia (Johnston *et al.* 2011; Chandrapavan *et al.* 2019) and *Callinectes sapidus* in Chesapeake Bay, USA (Lipcius and Stockhausen 2002; Zohar *et al.* 2008). The *C. sapidus* fishery in Chesapeake Bay is still recovering (Huang *et al.* 2015), and only one of the major *P. armatus* fisheries in Western Australia, Shark Bay, has

rebounded to historic levels (Chandrapavan *et al.* 2019), whereas other fisheries such as Cockburn Sound are showing minimal signs of recovery (Johnston *et al.* 2021a). Measuring the links between environmental variability and recruitment will aid data-driven management of portunid fisheries (Caputi *et al.* 2014; Tweedley *et al.* 2017).

A key component of fisheries recruitment is the reproductive output of exploited populations. Gonadal development and egg production are energetically expensive processes, and are known to respond to environmental drivers (Tropea *et al.* 2015; Baliña *et al.* 2018). Gonadal development within a population is often measured using a gonadosomatic index (GSI, unit mass of gonad per unit mass of bodyweight). The GSI is a useful indicator of gonadal development, such that a high GSI indicates reproductive maturity and greater investment into reproduction (Liu *et al.* 2014). The hepatosomatic index (HSI, unit mass of hepatopancreas per unit mass of bodyweight) is a useful measure of relative energy storage, as the hepatopancreas acts as a major store of organic and inorganic reserves in crustaceans (Passano 1960; Magalhães *et al.* 2012). The egg mass index (EMI, unit mass of eggs per unit mass of

bodyweight) is a measure of relative reproductive output standardised to animal size. This may be used as a proxy for fecundity to evaluate factors affecting variability in reproductive output (Sukumaran and Neelakantan 1997; Hisam *et al.* 2018), where egg count data are not available. The relationships between the GSI, HSI and EMI can inform patterns in female reproductive condition throughout the breeding season. Therefore, quantifying these relationships alongside potential abiotic influences may aid examination of recruitment variability.

The blue swimmer crab (BSC), *Portunus armatus* (Lai *et al.* 2010), is distributed throughout the coastal and estuarine waters of tropical and temperate Australia, supporting valuable commercial and recreational fisheries (de Lestang *et al.* 2003; Johnston *et al.* 2021b). The reproductive development of BSC is strongly influenced by water temperature (de Lestang *et al.* 2003), which varies among estuaries and therefore causes significant variations in reproductive output (Shields and Wood 1993; de Lestang *et al.* 2003; Kumar *et al.* 2003; Johnson *et al.* 2010; Johnston and Yeoh 2021). Whereas BSC in tropical waters tend to exhibit little seasonality in their reproductive biology (de Lestang *et al.* 2003), the increased temperature variability in temperate estuaries may drive strong seasonal variation in reproduction (Kumar *et al.* 2003). New South Wales includes the southernmost extent of the main BSC range on the eastern Australian coast, where spawning is generally confined to summer, from November to February (Johnston *et al.* 2018). In the only comprehensive study of a BSC population in south-eastern Australia, Johnson *et al.* (2010) found substantial variation in size-at-maturity and fecundity in a NSW estuary, compared with other populations around Australia. Specifically, BSC had larger batch fecundities than did similarly sized individuals in Western Australia and larger sizes at maturity than did females in South Australia (Johnson *et al.* 2010).

Estuaries in south-eastern Australia are warming an order of magnitude faster than predicted by current global ocean and atmospheric models, with water temperatures increasing at a rate of $0.2^{\circ}\text{C year}^{-1}$ (Scanes *et al.* 2020a). Continued warming presents a challenge to the health of estuarine ecosystems and the profitability of associated aquaculture and wild fisheries (Madeira *et al.* 2012; Food and Agriculture Organization of the United Nations 2018). Within estuaries, these changes may cause increased energetic demands and altered development in some species (Parker *et al.* 2013), reduced fecundity and egg viability (Foo and Byrne 2017) and behavioural changes (Madeira *et al.* 2012). Shifting temperature regimes vary according to the estuary geomorphology (Scanes *et al.* 2020a), which means that predicting the reproductive consequences for commercially important species may be complex. Here, we considered patterns of reproduction across estuaries in the southern part of the latitudinal range for eastern Australian BSC. Specifically, we aimed to (1) describe the interaction between the GSI (index of gonadal development and reproductive investment) and the HSI (index of energy storage) during gonadal development, (2) characterise EMI trends across south-eastern Australian BSC, and (3) assess the potential influence of temperature on gonadal development and egg mass production.

Materials and methods

Sampling locations

This research focused on BSC within the following five estuaries in south-eastern Australia: Wallis Lake ($32^{\circ}16'S$, $152^{\circ}29'E$), Port Stephens ($32^{\circ}42'S$, $152^{\circ}01'E$), Lake Macquarie ($33^{\circ}04'S$, $151^{\circ}35'E$), Botany Bay ($33^{\circ}59'S$, $151^{\circ}11'E$), and Lake Illawarra ($34^{\circ}31'S$, $150^{\circ}50'E$; Fig. 1). These estuaries exhibit distinct morphological differences (Table 1) that contribute to

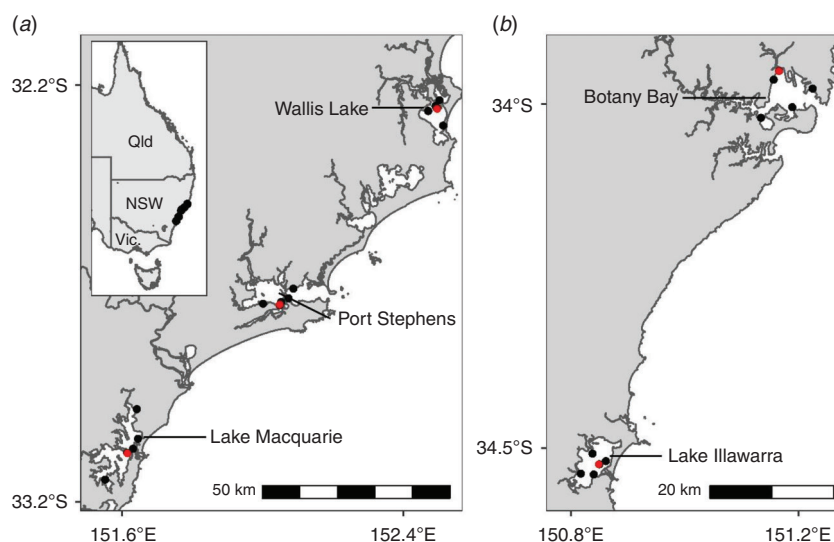


Fig. 1. Map of the five estuaries surveyed in south-eastern Australia: Wallis Lake, Port Stephens, Lake Macquarie, Botany Bay and Lake Illawarra. (a) Northern and (b) southern estuary. The inset shows the relative position of these sites on the eastern Australian coastline, with the states of Queensland (Qld), New South Wales (NSW) and Victoria (Vic.) labelled. The black points show the sampling sites. The red points show the locations of the loggers.

Table 1. Characteristics of Wallis Lake, Port Stephens, Lake Macquarie, Botany Bay and Lake Illawarra systemsData from <https://www.environment.nsw.gov.au/topics/water/estuaries/estuaries-of-nsw> (accessed 7 July 2021)

Estuary	Estuary type	Catchment area (km ²)	Estuary area (km ²)	Average depth (m)	Estuary volume (ML)
Wallis Lake	Lake	1197	98.7	2.3	217 952
Port Stephens	Drowned river valley	2967	134.4	14.1	1 741 517
Lake Macquarie	Lagoon	604	114.1	5.7	646 274
Botany Bay	Drowned river valley	1166	39.6	11.4	440 816
Lake Illawarra	Lake	238	35.8	2.1	74 275

different environmental conditions (Scanes *et al.* 2020a), allowing us to study the reproductive development of BSC under a range of temperature regimes. The majority of commercial BSC harvested within south-eastern Australia is extracted from three of these estuaries (Wallis Lake, Port Stephens and Lake Illawarra), of which 70% of total commercial landings are harvested from Wallis Lake (e.g. 99 of the 144 t harvested in NSW during 2016–2017, Johnston *et al.* 2018). Lake Macquarie and Botany Bay have no commercial harvest (Ochwada-Doyle *et al.* 2014).

Sampling design and collection

Sampling was conducted at monthly intervals from October 2019 to February 2020, covering the peak spawning period (Johnson *et al.* 2010). Crabs were sampled using large-mesh (55-mm diamond mesh) crab traps (900-mm diameter by 300 mm high) in Lake Illawarra and Botany Bay and small-mesh (24-mm diamond mesh) crab traps (900 × 300 mm) in Wallis Lake, Port Stephens and Lake Macquarie. The small-mesh traps were found to be more effective at catching smaller, juvenile crabs, but did not appear to affect catch rates of larger, mature crabs (Hanamseth, Johnson, Suthers and Taylor, unpubl.data). Because juvenile (immature) crabs were excluded from our analysis, differences in gear type used among estuaries did not affect our findings. In each of the five estuaries, four sites were surveyed, with six replicate crab traps deployed per site, per sampling event. Crab traps were deployed along the sand–seagrass ecotone, 50 m apart, in water less than 4 m deep at high tide and greater than 1 m deep at low tide. Each crab trap was baited with two sea mullets (*Mugil cephalus*), cut in half and held within a bait bag clipped inside the traps. All crab traps were set overnight and retrieved the following day, with an immersion (soak-time) time between 18 and 24 h. A data logger (HOBO U24-002-C) was deployed in each estuary to provide a continuous time-series of water temperature. Although a single logger is not able to capture the entire range of temperatures within the estuaries, the logger was centrally located among our sampling locations, and located at roughly similar distances to the estuary mouth in different estuaries (to allow for comparison among estuaries).

On capture, the carapace length (CL, mm), sex and reproductive stage (immature, mature and berried) were recorded (Johnson *et al.* 2010). The reproductive stage of crabs was categorised on the basis of the carapace length (<50 mm, generally immature), shape and stiffness of the pleonal flap (angular and stiff when immature or rounded and loose when mature) and the presence of an egg mass (berried; Ryan 1967;

Ingles and Bkaum 1989; Fisher 1999). For each monthly sampling event in each estuary, 10 randomly selected mature (non-egg bearing) females were retained for examination of gonadal development. Additionally, from each monthly sampling event in each estuary, up to 10 randomly selected berried (egg bearing) females with Stage 1 eggs (Johnson *et al.* 2010) were retained for examination of gonadal development and egg mass quantification. Only fully intact females were retained because missing appendages affect GSI, HSI and EMI calculations.

Laboratory procedures

At the laboratory, retained mature crabs were weighed (nearest 0.01 g), measured (CL, to the nearest 0.1 mm) and the ovaries were staged (Liu *et al.* 2014; $n = 259$; WLL = 83; PST = 43; LMQ = 50; BGR = 37; LIL = 46). The ovaries and hepatopancreas were then dissected and weighed (wet weight) to the nearest 0.01 g to calculate GSI (Liu *et al.* 2014) and HSI (Hismayasari *et al.* 2015). The same dissection procedures as detailed above were repeated for the berried female crabs ($n = 113$; WLL = 25; PST = 18; LMQ = 38; BGR = 8; LIL = 24), but extra steps were performed to process eggs. The pleonal flap containing the fresh egg mass was removed from each crab and immersed in 400 mL of 1-M potassium hydroxide (KOH) solution for 12 h to dissolve the funiculae that hold the eggs to the setae (Johnson *et al.* 2010). Following separation, eggs were washed and strained thoroughly using a 60 µm sieve, then the total egg mass was weighed to the nearest 0.01 g. Using the total egg mass weight and total bodyweight, we then calculated the EMI (Sukumaran and Neelakantan 1997; Hisam *et al.* 2018), as follows:

$$EMI = \frac{\text{Egg mass weight} \times 100}{\text{Body weight}}$$

Statistical analysis

Analysis was conducted using the program R (ver. 3.6.3, R Foundation for Statistical Computing, Vienna, Austria) and the integrated development environment RStudio (RStudio, Inc., Boston, MA, USA, see <http://www.rstudio.com>). The GSI and HSI are ratios of organ weight to bodyweight. In this study, these proportions correlated with the size of the crab, and therefore the comparison of ratios among estuaries could be confounded by the distribution of body size. To remove the influence of total bodyweight on the relationship between GSI and HSI, linear models were fit to log-organ weight and log-bodyweight, with the slope of the resulting fit used as the exponent in the following

formulae (see Fig. S1, S2, available as Supplementary material to this paper).

$$Adj.GSI = \frac{\text{Ovary Weight}}{\text{Body Weight}^{1.292}}$$

$$Adj.HSI = \frac{\text{Hepatopancreas Weight}}{\text{Body Weight}^{0.657}}$$

Linear models were used to assess changes in the relationship between the adjusted GSI and adjusted HSI across the stages of ovarian development in mature females. This relationship was analysed by ovary stage, with Stages 2–3 and 4–5 being grouped together owing to morphological similarities and to account for potential errors in distinguishing these visually similar stages.

Linear models were also used to assess the relationship between crab weight and egg mass weight (for all tests, significance was based on a value of $\alpha = 0.05$). Crab weight and egg mass weight followed a logarithmic relationship, so a natural logarithm transformation was used on bodyweight in the linear model. An analysis of covariance (ANCOVA) was used to test for significant differences in this relationship among estuaries, where the weight of the egg mass was the dependent variable, total bodyweight was the covariate, and estuary was a fixed factor. A *post hoc* Tukey's test was used to test for differences across all combinations of estuaries. A two-way ANOVA was used to test for significant differences in the EMI among estuaries and sampling periods and any significant interaction between the two factors, where the EMI was the dependent variable and the estuaries and sampling period were fixed factors. *Post hoc* Tukey's tests were used to evaluate differences within fixed effects or interactions.

Generalised additive models (GAMs) were used to examine potential non-linear relationships between mean monthly temperature and the adjusted GSIs, adjusted HSIs and total egg mass weights. GAMs are a non-parametric extensions of generalised linear models (GLMs), and can be used to examine complex non-linear relationships between response variables and predictor variables by fitting complex smoothing functions to the data (Hastie and Tibshirani 1990). For each model, a smoothing function (s) was fitted to mean monthly temperature and the estuaries were included as parametric coefficients, where the intercept is denoted β_0 , as depicted in the formulae below.

$$Adj.GSI = \beta_0 + s(\text{Mean Monthly Temperature}) + \text{Estuary}$$

$$Adj.HSI = \beta_0 + s(\text{Mean Monthly Temperature}) + \text{Estuary}$$

$$\text{Egg Mass} = \beta_0 + s(\text{Mean Monthly Temperature}) + \text{Estuary}$$

Mean monthly temperatures ranged from 18.57 (Wallis Lake, October 2019) to 26.96°C (Port Stephens, February 2020). Data points were evenly distributed between 20 and 27°C; however, the single data point at 18.57°C was ~1.5°C below the next data point (20.14°C). This outlying data point introduced uncertainty and was therefore excluded, with the GAMs only modelling within the temperature range (~20–27°C).

Results

Patterns in reproductive development

Overall, 1904 adult female (1538 mature; 366 egg-bearing) BSC were caught across five estuaries during the 5-month sampling period. Of these 1904 adult females, we retained 259 mature and 122 berried female crabs for laboratory analysis. Mature females ranged in size from 51 to 93 mm CL, whereas berried females ranged in size from 57 to 89 mm CL. Only female BSC in the later stages of ovarian development (4–5) showed a significant negative linear correlation between the adjusted GSI and adjusted HSI ($F_{1,146} = 7.042$, $P = 0.009$, Table 2, Fig. 2). There was no significant interaction between the GSI and HSI in females with Stage 1 ovaries ($F_{1,45} = 2.767$, $P = 0.103$, Table 2) or Stage 2–3 ovaries ($F_{1,60} = 0.002$, $P = 0.969$, Table 2)

Egg mass weight increased logarithmically with bodyweight ($F_{1,111} = 61.430$, $P < 0.001$, Table 3). There was variability among estuaries (Fig. 3), with BSC in Lake Macquarie having the smallest coefficient and therefore the smallest increase in egg mass weight relative to bodyweight (Table 3, Tables S1, S2, available as Supplementary material to this paper). Female crabs in Wallis Lake had the largest coefficient and therefore the largest increase in egg mass with bodyweight; however, because of a lower intercept than in Botany Bay, the Wallis Lake crabs tended to have smaller egg masses than those in Botany Bay (Tables 3, S1, S2, Fig. 3). The EMI varied significantly among estuaries ($F_{4,93} = 6.477$, $P < 0.001$) and sampling periods ($F_{4,93} = 6.994$, $P < 0.001$), with a significant interaction between the two factors ($F_{11,93} = 3.575$, $P < 0.001$; Fig. 4). EMI was as large as 55% and was significantly larger in Botany Bay than in Wallis Lake ($P = 0.031$), Port Stephens ($P < 0.001$) and Lake Macquarie ($P = 0.001$; Fig. 4). Lake Illawarra had a smaller mean EMI than did Botany Bay; however, this difference was not statistically significant ($P = 0.054$).

Water temperature as a driver of variability in reproduction

The seasonal warming was evident within all five estuaries (Fig. 5), reaching a peak in the January and February sampling periods. The two more southern estuaries (Botany Bay and Lake Illawarra) never exceeded the mean monthly water temperatures of the other three more northern estuaries (Fig. 5). Generalised additive models showed that there was a non-linear relationship between mean monthly temperature and GSI, HSI and EMI (Fig. 6). The GAM for adjusted GSI explained 14.5% of the deviance in the data and showed a rapid decline in adjusted GSI above ~24°C ($n = 229$, e.d.f. = 2.812, $F = 7.390$, $P < 0.001$,

Table 2. Linear regression equations fit for the adjusted gonadosomatic index as a function of adjusted hepatosomatic index during ovarian development in mature females
Asterisks (*) denote significant probabilities

Ovary stage	Regression equation	P-value
All stages	$y = 0.25 - 2.79x$	0.015*
1	$y = 0.19 + 11.71x$	0.103
2–3	$y = 0.28 + 0.15x$	0.969
4–5	$y = 0.27 - 4.87x$	0.009*

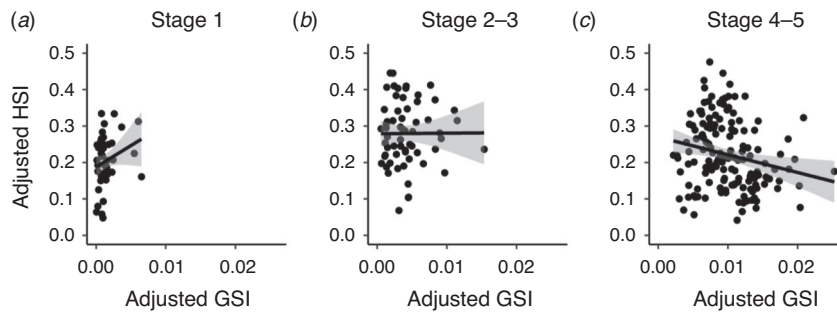


Fig. 2. Linear models illustrating the relationship between the adjusted gonadosomatic index and adjusted hepatosomatic index during ovarian development in mature females (pooled across estuaries) for (a) Stage 1 ovaries ($n = 48$), (b) Stage 2–3 ovaries ($n = 62$) and (c) Stage 4–5 ovaries ($n = 148$). The solid black line represents the linear model, and the grey area represents the confidence interval (95%).

Table 3. Linear regression equations fit for the total weight of the egg mass (g) as a function of the total bodyweight (g) of the berried crabs by estuary
Asterisks (*) denote significant probabilities

Estuary	Regression equation	P-value
All estuaries	$y = -402.28 + 87.98 \ln x$	<0.001*
Wallis Lake	$y = -539.90 + 113.39 \ln x$	<0.001*
Port Stephens	$y = -469.68 + 96.90 \ln x$	0.006*
Lake Macquarie	$y = -179.68 + 49.76 \ln x$	0.034*
Botany Bay	$y = -471.62 + 107.82 \ln x$	0.039*
Lake Illawarra	$y = -457.14 + 98.45 \ln x$	0.018*

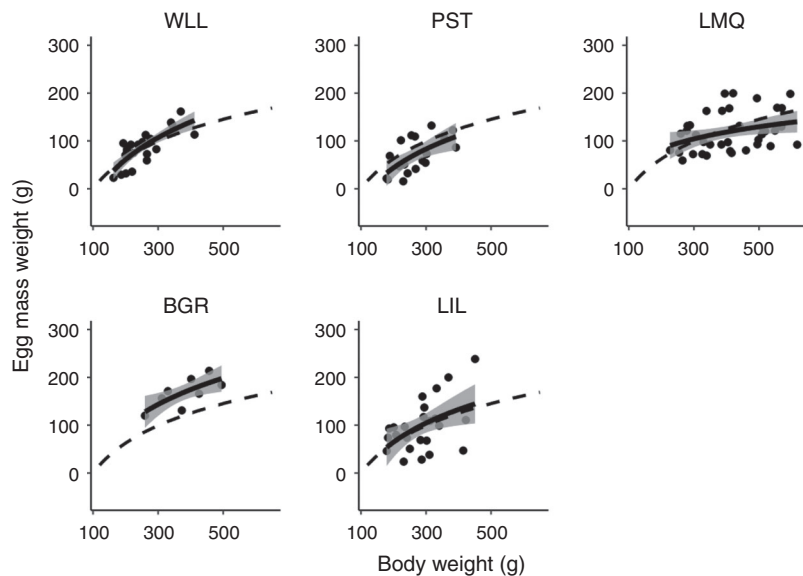


Fig. 3. Non-linear models illustrating the relationship between the total weight of the egg mass (g) and the total bodyweight (g) of berried crabs in Wallis Lake (WLL, $n = 25$), Port Stephens (PST, $n = 18$), Lake Macquarie (LMQ, $n = 38$), Botany Bay (BGR, $n = 8$) and Lake Illawarra (LIL, $n = 24$). The solid black line represents the non-linear model fit for each estuary and the grey area represents the confidence interval (95%). The dashed black line depicts a model fit for combined estuaries.

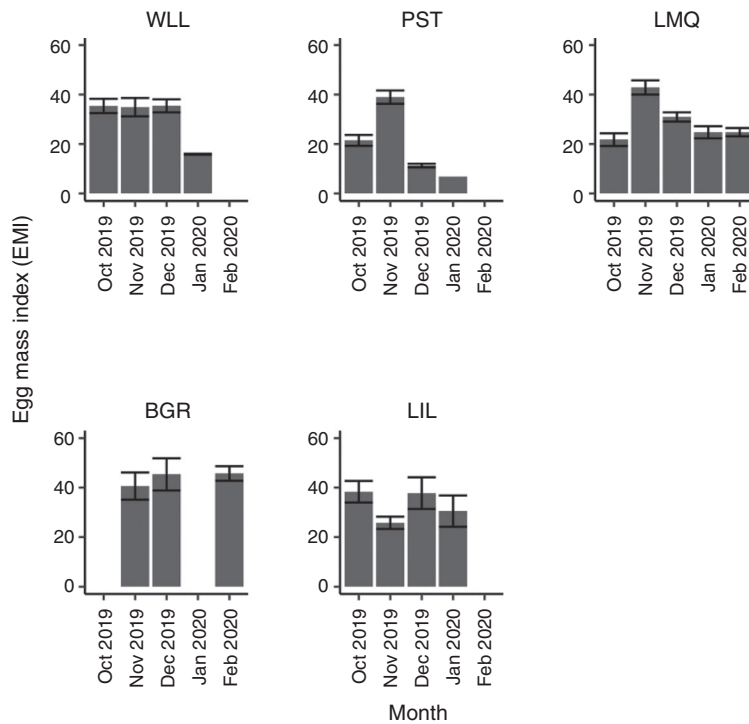


Fig. 4. Bar charts showing egg mass index (EMI) in Wallis Lake (WLL), Port Stephens (PST), Lake Macquarie (LMQ), Botany Bay (BGR) and Lake Illawarra (LIL) for each month with the sampling period (October 2019 – February 2020). The top of grey box indicates the mean, and the error bars indicate the standard error.

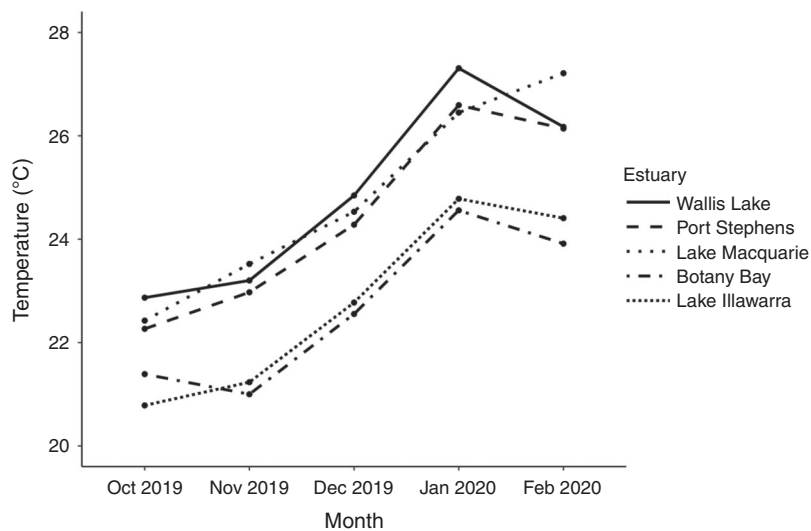


Fig. 5. Mean monthly water temperatures in Wallis Lake, Port Stephens Estuary, Lake Macquarie, Botany Bay and Lake Illawarra between October 2019 and February 2020. The water temperature in these estuaries peaked in the January and February sampling periods, with mean monthly temperatures as follows: Wallis Lake = 27.3°C, Port Stephens = 26.6°C, Lake Macquarie = 27.2°C, Botany Bay = 24.6°C and Lake Illawarra = 24.8°C. The data were gathered using HOBO U24-002-C data loggers deployed at a depth of 1 m throughout the sampling period. Water temperatures in Lake Macquarie are influenced by the release of hot water by the Mannering Park Power Station and Eraring power station, two coal-fired power stations situated on the shores of the estuary (Taylor *et al.* 2017).

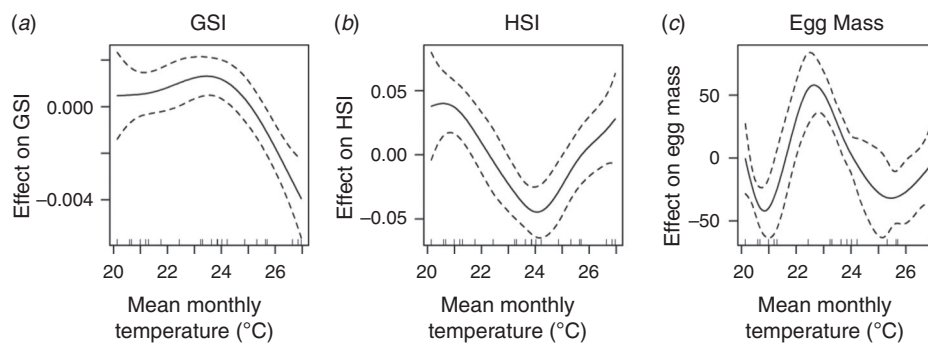


Fig. 6. Thermal performance curves from generalised additive models fit for the (a) gonadosomatic index, (b) hepatosomatic index and (c) total egg mass on mean monthly temperature in each estuary for the month before capture. The solid line depicts the fit of the model to the data and the dashed lines represent the confidence interval (95%). The ticks on the x -axis indicate the mean monthly temperatures of each sampling effort.

Fig. 6); the GAM for adjusted HSI explained 13.3% of the deviance in the data and appeared to reach a minimum at $\sim 24^{\circ}\text{C}$ ($n = 228$, e.d.f = 3.675, $F = 6.26$, $P < 0.001$, Fig. 6). The GAM for EMI explained 66% of the deviance in the data, with a maxima occurring at $\sim 23^{\circ}\text{C}$ ($n = 80$, e.d.f = 5.662, $F = 9.892$, $P < 0.001$, Fig. 6).

Discussion

Our data showed that gonadal development was related to the mobilisation of reserves from the hepatopancreas during the final stages of ovarian development in BSC. We found that the weight of the egg mass increased logarithmically with total bodyweight and was strongly influenced by water temperature. In the cooler waters of Botany Bay, there was a stronger relationship between size and egg mass weight, with larger females producing proportionally larger egg masses. We observed a peak in gonadal development and egg production at $\sim 24^{\circ}\text{C}$, with a decline in reproductive development either side of this optimum temperature.

Relationship between the GSI and HSI

The hepatopancreas is the largest store of energy reserves in crustaceans and is crucial in the absorption, storage and metabolism of nutrients for physiological processes (Wang *et al.* 2014). The significant negative relationship between the adjusted GSI and HSI in the final stages of ovarian development (Fig. 2) reflects the high energy demands of this process (Wang *et al.* 2014). Only in the final stages of ovarian development are the reserves of the hepatopancreas significantly drawn on, and therefore ovarian development through Stages 1–3 is presumably directly sustained by foraging. During the final stage of ovarian development, the reproductive output of a female crab is therefore likely to be determined by the quantity of reserves mobilised from the hepatopancreas to the ovaries. Increased stress as a result of fluctuations in temperature may increase energetic demand from other physiological processes, limiting the resources available for ovarian development and egg production (Tropea *et al.* 2015; Baliña *et al.* 2018). In crustaceans such as *Neocaridina davidi* and *N. heteropoda*, ovarian maturation and spawning were found to be inhibited because of stress at high temperatures (33 and 32°C respectively), because of reduced mobilisation of

biochemical reserves to the ovaries (Tropea *et al.* 2015; Baliña *et al.* 2018). Temperature is evidently a key driver of variability in gonadal development and energy expenditure in crustaceans (Tropea *et al.* 2015; Baliña *et al.* 2018), with suboptimal environmental conditions potentially reducing investment into reproduction, as depicted in Fig. 6 and discussed below.

Relationship between crab size and egg mass weight

Crabs in Botany Bay showed a larger increase in egg mass weight per unit of total bodyweight than did crabs in other estuaries (Fig. 3). Botany Bay is a drowned river valley, with a deep, wide entrance facilitating oceanic exchange with the Tasman Sea (Kingsford and Suthers 1994), which maintains cooler average temperatures than do the other estuaries (Fig. 5). In Western Australia, batch fecundity has been shown to increase with latitude from the subtropical estuaries (Shark Bay) towards the temperate estuaries (Geographe Bay; Johnston and Yeoh 2021). Warmer environments may facilitate the production of smaller and more frequent egg batches (Johnston and Yeoh 2021), a reproductive strategy that may reduce the risk of overall recruitment failure by spawning over a longer timeframe (McEvoy and McEvoy 1992). This may explain why BSC in tropical and subtropical environments can achieve rapid batch production and year-round spawning (up to 3 batches per year; de Lestang *et al.* 2003), whereas BSC in temperate environments are constrained in the production of fewer batches, and a shorter spawning season in which to produce them (up to 3 batches, but only in larger individuals, during the period October–January; Kumar *et al.* 2000; Kumar *et al.* 2003).

The egg mass index was as high as 55% in the berried females and was, on average, 34% in females with 70–80 mm CL (equivalent to ~ 144 –189-mm carapace width), indicating significant reproductive investment. By contrast, *Portunus pelagicus* in the tropical waters of southern Thailand had a maximum EMI of only 29% (Hisam *et al.* 2018). Another study of *Portunus sanguinolentus* and *P. pelagicus* in the south-western coast of India found that the EMI peaked at an average of 15% in females with 100–110-mm carapace width and at an average of 12% in females between 130- and 140-mm carapace width respectively (Sukumaran and Neelakantan 1997). *Portunus pelagicus* in south-eastern India showed similarly low EMIs

to these, with a maximum average of ~17% in females with 120–129-mm carapace width (Josileen 2013). With a much larger EMI, BSC in temperate south-eastern Australia appear to be investing more resources per brood than do portunid crabs in other more tropical environments (Sukumaran and Neelakantan 1997; Josileen 2013; Hisam *et al.* 2018). Such a difference in reproductive strategy, likely owing to cooler water, would lead to the production of fewer, but larger, egg masses by larger females in temperate environments (de Lestang *et al.* 2003; Hines *et al.* 2010; Johnston and Yeoh 2021).

Water temperature as a driver of variability in reproduction

Temperature variability can significantly affect individual reproduction (de Lestang *et al.* 2003) and contribute to year-on-year variation in recruitment and fisheries productivity (Johnston *et al.* 2011). Gonadal development and egg production are energetically expensive for ectotherms, and the GSI may be used as an index of thermal performance (Payne *et al.* 2016). The total egg mass weight produced by crabs within a single batch peaked during months with a mean temperature between ~23 and 24°C (Fig. 6). Conditions above 24°C approach a critical temperature for BSC, at which their reproductive functions begin to slow and lose efficiency, as indicated by the rapid decline in GSI above 24°C (Fig. 6; Shelford 1931; Frederick and Pörtner 2000; Jost *et al.* 2012). Concurrently, the adjusted HSI, as an indicator of the energy reserves within the female crab, reached a minimum within the same temperature range (Fig. 6), indicating that under these optimal conditions, the crabs were drawing more resources from the hepatopancreas to maximise reproductive output.

In their study of climate change within south-eastern Australian estuaries, Scanes *et al.* (2020a) observed an average warming of 2.16°C across a 12-year period (0.2°C year⁻¹). The average summer temperature during this period (2007–2018) was 24.8°C in Wallis Lake, 23.5°C in Port Stephens, 25.2°C in Lake Macquarie and 23.3°C in Lake Illawarra; there were no data for Botany Bay from this study (Scanes *et al.* 2020b). The estuaries in the present study currently maintain average summer temperatures close to the observed optimal temperature range for BSC reproduction; however, as the warming trend observed in Scanes *et al.* (2020a) continues, average temperatures in the spawning season may exceed the optimal range and begin to impede reproduction. Incorporating temperature-based reproduction modelling into fisheries assessment may aid in the prediction of variation in fisheries productivity, which can subsequently support adaptation of management arrangements (e.g. de Lestang *et al.* 2010). An extreme heatwave event in Western Australia during 2011 led to major reductions in recruitment within several invertebrate fisheries, including BSC, and highlighted the susceptibility of coastal invertebrate stocks to extreme environmental events (Caputi *et al.* 2016; Chandrapavan *et al.* 2019). This event also highlighted the importance of early detection of changes in the temperature–reproduction–recruitment dynamic, to allow for management to protect vulnerable spawning stock (Caputi *et al.* 2016; Chandrapavan *et al.* 2019).

Potential impacts of tropicalisation

Anthropogenic climate change is driving global ocean warming, with accelerated warming in temperate regions with

poleward-flowing western boundary currents (Wu *et al.* 2012; Vergés *et al.* 2014). The accelerated warming and ‘tropicalisation’ of temperate marine environments is particularly rapid in estuaries on the south-eastern Australian coastline (Scanes *et al.* 2020a). It is still uncertain how tropicalisation may affect the reproduction of BSC, and subsequently influence fisheries productivity in south-eastern Australia. The study of latitudinal clines in population size structure, EMI, and batch fecundity may represent a useful proxy for the effect of changing temperatures, and aid prediction of potential climate impacts in the future. In a study examining the effects of climate change on *C. sapidus* in Chesapeake Bay, a temperate estuary in the USA, Hines *et al.* (2010) predicted that warming waters may promote rapid growth and brood production in smaller females, with increased juvenile mortality and a reduced size at maturity. Although warming in temperate waters was predicted to potentially increase the reproductive output of this population, it was noted that the complex interactive effects of multiple stressors associated with climate change, alongside exploitation, make it difficult to accurately predict and act on future circumstances (Hines *et al.* 2010). In Western Australia, the reproductive biology in *P. armatus* was found to exhibit high plasticity in response to spatial and temporal variations in temperature (Johnston and Yeoh 2021). For example, size at maturity decreased with latitude (Johnston and Yeoh 2021), whereas batch fecundity was found to increase with latitude. Considering the findings of our study alongside other recent reports on the effect of temperature on reproduction (e.g. Johnston and Yeoh 2021), tropicalisation of temperate estuaries within south-eastern Australia may lead to a shift towards the production of smaller batches, more frequently throughout a longer spawning season, by females with a larger size at maturity.

Study limitations

It is prudent to consider several additional factors that may affect the relationships reported in our study. The use of baited traps has been shown to introduce a bias towards large, sexually mature crabs, potentially causing the over-representation of mature females in each size class and an underestimation of the size at maturity of female crabs (Smith *et al.* 2004); sampling methods such as seine-netting and otter trawling may provide more representative size structures for BSC (Smith *et al.* 2004). It is also important to acknowledge that this study was conducted only over a 5-month period (October 2019 to February 2020), with no replication across successive years. Year-round sampling over multiple successive years would allow us to better understand the influence of temperature on year-to-year recruitment and fisheries productivity, as well as the broader impact of climate change and tropicalisation on BSC reproduction. Finally, our study compared only gonad development (ovary weight), energy reserves (hepatopancreas weight) and egg mass weight (as a proxy for egg production) relative to total body mass, whereas fecundity (the number of offspring produced) is also commonly used as a measure of reproductive output. Future studies examining fecundity (i.e. egg production) across similar scales will further strengthen our understanding of the impacts of temperature, climate change, and tropicalisation on BSC reproduction.

Conclusions

In conclusion, we found the most fecund females in Botany Bay, the estuary with the largest exposure to the ocean and the lowest summer water temperature (Fig. 5). Thermal performance curves showed a peak in individual reproductive output at a mean monthly temperature of ~24°C. Above 24°C, the GSI (an index of gonadal development) began to decline. Temperature is a clear driver of spatial and temporal variation in reproduction in female BSC. Further investigation that examines similar relationships over broader temporal scales will improve our understanding of how environmental variability and coastal warming influence reproduction, recruitment and fisheries productivity in south-eastern Australia. Modelling of environment–reproduction–recruitment relationships will also support fisheries management practices, to ensure that harvest levels remain sustainable alongside the influence of environmental change.

Data availability

Data will be made available on reasonable request.

Conflicts of interest

The authors declare that they have no conflicts of interest.

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