

Latitudinal and seasonal effects on growth of the Australian eastern king prawn (*Melicertus plebejus*)

Luke R. Lloyd-Jones, You-Gan Wang, Anthony J. Courtney, Andrew J. Prosser, and Steven S. Montgomery

Abstract: The growth of the Australian eastern king prawn (*Melicertus plebejus*) is understood in greater detail by quantifying the latitudinal effect. The latitudinal effect is the change in the species' growth rate during migration. Mark-recapture data ($N = 1635$, latitude 22.21°S – 34.00°S) presents northerly movement of the eastern king prawn, with New South Wales prawns showing substantial average movement of 140 km (standard deviation: 176 km) north. A generalized von Bertalanffy growth model framework is used to incorporate the latitudinal effect together with the canonical seasonal effect. Applying this method to eastern king prawn mark-recapture data guarantees consistent estimates for the latitudinal and seasonal effects. For *M. plebejus*, it was found that growth rate peaks on 25 and 29 January for males and females, respectively; is at a minimum on 27 and 31 July, respectively; and that the shape parameter, k (per year), changes by -0.0236 and -0.0556 every 1 degree of latitude south increase for males and females, respectively.

Résumé : La quantification de l'effet latitudinal permet une compréhension plus détaillée de la croissance de la crevette royale orientale australienne (*Melicertus plebejus*). L'effet latitudinal est la variation du taux de croissance de l'espèce durant la migration. Des données de marquage-recapture ($N = 1635$, latitude $22,21^{\circ}\text{S}$ – $34,00^{\circ}\text{S}$) décrivent le déplacement vers le nord de crevettes royales orientales, les crevettes de Nouvelle-Galles-du-Sud présentant un important déplacement moyen de 140 km (écart-type : 176 km) vers le nord. Un cadre reposant sur le modèle de croissance de von Bertalanffy est utilisé pour incorporer l'effet latitudinal à l'effet saisonnier canonique. L'application de cette méthode aux données de marquage-recapture pour la crevette royale orientale garantit l'estimation cohérente des effets latitudinal et saisonnier. Pour *M. plebejus*, il a été observé que le taux de croissance atteint un maximum les 25 et 29 janvier et un minimum les 27 et 31 juillet, respectivement, pour les mâles et les femelles, et que les changements du paramètre de forme, k (par année), sont de $-0,0236$ et $-0,0556$ pour chaque augmentation d'un degré de la latitude sud, respectivement, pour les mâles et les femelles.

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Introduction

The growth of fish and other aquatic fauna can be affected by many factors: environmental (food availability, temperature), anthropogenic (fishing, habitat degradation), and biological (biochemical). Assessing these influences can provide a more detailed understanding of the growth of a particular species.

The growth of organisms in subtropical and temperate waters does not necessarily proceed at the same rate throughout the year (Haddon 2011). If seasonal growth dependence is likely, it may be necessary to incorporate this into the

growth analysis (Pitcher and MacDonald 1973; Shepherd and Hearn 1983). Location of a population may also change substantially during the seasons, especially for migratory species. Therefore, a coupled growth model that incorporates the locational and seasonal changes makes sense.

Species distributed over large geographical areas exhibit body size gradients, with the majority of larger adults being recorded in colder environments (Ashton 2004; Partridge and French 1996). The geographic variation in body size is consistent with the intraspecific version of Bergmann's rule, which states that races of a species, especially endotherms, tend to be larger in colder environments to limit heat loss

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L.R. Lloyd-Jones and Y.-G. Wang,* Centre for Applications in Natural Resource Mathematics (CARM), School of Mathematics and Physics, The University of Queensland, St. Lucia, Qld 4067, Australia.

A.J. Courtney and A.J. Prosser. Queensland Department of Agriculture, Fisheries and Forestry, Ecosciences Precinct, Joe Baker Street, Dutton Park, Queensland, 4102, Australia.

S.S. Montgomery. Cronulla Fisheries Centre, 202 Nicholson Parade, Cronulla, NSW, 2230, Australia.

Corresponding author: You-Gan Wang (e-mail: you-gan.wang@uq.edu.au).

*Present address: Priestley Building 67, St. Lucia, Department of Mathematics, The University of Queensland, Brisbane, Qld, 4072, Australia.

Table 1. Summary of eastern king prawn tag and release studies in Queensland and New South Wales.

Area	Release date	No. released	No. recaptured	Percent recaptured
Fraser Island (25.7°S)	Nov. 1990	4749	984	20.7
Moreton Bay (27.3°S)	Nov. 1990	1607	109	6.8
East Moreton Island (27.3°S)	Nov. 1990, Feb. 1991	2676	206	7.7
South West Rocks (30.8°S)	Nov. 1991	2944	186	6.3
	Jan. 1992	2812	402	14
Newcastle (33.2°S)	Dec. 1991	3096	161	5.2
	Mar. 1992	3067	100	3.3
Botany Bay (34.0°S)	Feb. 1991	1221	277	22.7
	Oct. 1991	1058	556	52.6
	Feb. 1992	710	404	56.9

due to a smaller surface area to body mass ratio (Angilletta et al. 2004; Atkinson and Sibly 1997). However, it is controversial to apply this rule to ectotherms because their body temperature fluctuates rapidly with ambient temperature (Geist 1987). The thermal plasticity of body size, dubbed the temperature size rule, has been observed in bacteria, protists, plants, and animals, making it one of the most taxonomically widespread rules in biology (Angilletta et al. 2004).

One ectothermic species that is likely to experience a latitudinal change in growth is the Australian eastern king prawn (*Melicertus plebejus*, previously known as *Penaeus plebejus*). *Melicertus plebejus* inhabits coastal waters of eastern Australia and has been recorded as far north as Hayman Island (20°S), as far south as Tasmania (42°S), and at depths up to 350 m (Courtney et al. 2007). This species is the most commercially valuable prawn species in eastern Australia, with current landings (total east coast) valued at more than \$30 million (O'Neill et al. 2005; Glaister et al. 1987).

Ruello (1975) commented that *M. plebejus* migrate out of the New South Wales estuaries in the surface waters of the night ebb tides. During the darker half of the lunar cycle, they move into deeper water while moving along the coast in a north to northeast direction. Interestingly, *M. plebejus* move longer distances than most other penaeids (Ruello 1975; Somers and Kirkwood 1984; Sheridan et al. 1987). Via a tagging study, Montgomery (1990) showed that all tagged *M. plebejus* that were recaptured away from their point of release had moved north. Additionally, in a mark-recapture study of *M. plebejus*, Glaister et al. (1987) showed that prawns that moved longer distances did so in a northerly direction. Northerly movement is coupled with a movement into deeper waters as prawns from New South Wales reach the Queensland coast. According to Glaister et al. (1987), the east coast fishery of *M. plebejus* can be considered to consist of two substocks: those prawns north of 27.25°S that derive their recruitment from Moreton Bay and those prawns from 34°S to 27.25°S that recruit from Clarence River (29.43°S) south. Ruello (1975) remarked that the distribution of eastern king prawns is most likely influenced by the East Australian Current, an oceanic current system off the east coast of Australia. Knowledge of the growth of the population as they migrate is potentially important when evaluating management strategies, for example, temporal and spatial closures (Rijnsdorp and Pastoors 1995; Helser and Lai 2004). Investigating body size gradients and quantifying the change in growth at different latitudes is potentially of great interest.

Mark-recapture studies are frequently conducted to quantify growth as well as rates of movement-migration and abundance (Quinn and Deriso 1999). The von Bertalanffy growth model is often applied to mark-recapture data and is considered to model growth well (Chen et al. 1992). Determining adequate parameter estimates of the von Bertalanffy model such that growth is modelled accurately is a complex problem. This is especially evident when individual variability is considered (e.g., Wang and Thomas (1995); Wang and Die (1996); Wang and Somers (1996)). James (1991) provided a method for estimating the von Bertalanffy growth parameters via unbiased estimating equations. Wang (1999) developed a generalized von Bertalanffy growth model framework to incorporate stochastic components and explanatory variables for growth that vary with time. Xiao (1999) provided a more general framework to incorporate time-dependent factors (i.e., ambient temperature, food availability, and latitude) into growth models.

This paper derives estimating functions, based on the work of Wang (1999), that incorporate latitudinal and seasonal effects. It is hypothesized that these two factors influence the growth rate of species that migrate latitudinally over large distances. This idea is tested using eastern king prawn mark-recapture data.

Materials and methods

Data

To illustrate the method, eastern king prawn mark-recapture data were analysed. These data were obtained from mark-recapture studies undertaken in New South Wales and Queensland. Approximately 3000 recaptures were taken between 23.78°S and 34°S (Table 1). For the New South Wales data, mark-recapture experiments were done in Botany Bay (34°S) and offshore from Newcastle (30°S) and South West Rocks (32°S) in New South Wales, Australia (Table 1). Experiments offshore were done within 2.8 km of the coast off each location; each of these study areas were closed to commercial fishing for 1 month after each tagging experiment to allow tagged prawns time to disperse. For the same reason, Botany Bay was closed to fishing for 48 h after each release. Trawls of 10 min in Botany Bay and of 20 min for offshore locations were done aboard chartered commercial trawlers or the NSW Fisheries' FRV *Kapala* to collect eastern king prawns for tagging. Live prawns longer than 20 mm carapace length (CL) were sorted from the catch and placed in 450 L tanks filled with

salt water. Prawns were tagged with individually numbered yellow streamer tags and measured to the nearest whole millimetre with dial callipers between the base of the eye orbit and the posterior margin of the carapace. Tagged prawns were placed in release canisters (Emiliani 1971) submerged in 450 L tanks of salt water to await release. Prawns were inspected just prior to release, and any damaged individuals were discarded. They were released in canisters back onto the bottom in the vicinity from where they had been caught.

In 1990 and 1991, tag–release studies were undertaken in Queensland to quantify population parameters for management of the fishery. Chartered commercial trawlers and government research trawlers were used as platforms to capture, tag, and release the prawns. The duration of the trawls used to catch the prawns was relatively short to reduce stress and injury to the prawns prior to tagging (i.e., less than 20 min, equivalent to the New South Wales methods). After each trawl, live prawns larger than 20 mm CL were sorted from the catch and immediately placed in a 400 L tank with flow-through sea water. Apparently healthy individuals were identified in the tank and chosen for tagging. Just before tagging, the size and sex of the prawn were determined and recorded. An individually numbered streamer tag was inserted through the abdomen of each tagged prawn using an attached needle, between the dorsal gut and the ventral nerve chord. After the tag was inserted, the needle was torn off the tag. Tagged prawns were then placed inside an aluminium release cage, which was submerged in a second larger tank. When sufficient numbers of prawns were tagged (i.e., ≈200), the release cage was closed, removed from the tank, and lowered to the bottom using a rope. Once the cage came into contact with the bottom, a mechanical release system was activated to open the cage, allowing the tagged prawns to escape and disperse. The cage was then retrieved. As an incentive to fishers, small financial rewards were provided for each recaptured prawn. All recaptures were caught by commercial otter trawl fishers, who in addition to providing the recaptured tagged prawn, also provided information on its location and date of recapture, using prawn recapture kits that were provided to them in the days prior to release.

Following Somers and Kirkwood (1984), recaptured prawns that were at liberty less than 14 days were omitted from the analyses, leaving a total of 1559 observations. Of these 1559, 678 were male and 881 were female. This practice is carried out to ensure that the data analysed contain the best information possible. Growth before this is considered to be unrecognizable when compared with the error incurred from measurement. Theoretically, these data with very short time at liberty would provide measurement error information. However, if the growth is retarded (temporally) and recovered after 2 weeks, these data can lead to a very biased estimation (Pilling et al. 2002; Wang 1998; Hampton 1986). The raw data contains many recaptures (>500) with less than 14 days at liberty. Retaining these data may provide excess noise, making model estimation more difficult and providing biased estimates. The removed samples also contribute to latitudinal noise, making it more difficult to distinguish between small drifts and actual migration. It is noted that these removed data may contain information on measurement error, which is a trade-off from this practice.

Table 2. Summary of data for male and female eastern king prawns.

	L_1 (mm)	L_2 (mm)	$L_2 - L_1$ (mm)	T (days)
Males				
Mean	27.8	32.0	4.27	48.7
SD	3.46	4.39	3.67	47.0
Range	18.6, 39.2	20.7, 51.6	−5.4, 21.1	15, 623
Females				
Mean	29.5	35.4	5.92	48.4
SD	4.83	6.58	5.12	51.7
Range	17.5, 42.1	19.9, 57.4	−3.8, 30.8	15, 942

Before implementing the model, exploratory data analysis was carried out. Sexes were analysed separately, since von Bertalanffy growth parameters vary substantially between male and female *M. plebejus*, particularly asymptotic length (Glaister et al. 1987). If L_1 and L_2 denote the observed lengths (mm carapace) at release and recapture, respectively, and T denotes the time at liberty (days), then the data can be summarized as in Table 2. The data presents good variability with major times at liberty and large ranges of growth for many size classes (Table 2). The distribution of mark and recapture numbers is centred around the summer months, with maximum releases in November and maximum recaptures in December (Table 3). The tagging and releasing of prawns was undertaken from November to March (Table 3), as it is generally when small, recruiting eastern king prawn are present in shallow coastal waters of eastern Australia. It is noted that the recaptures are a reflection of fishing effort, with the predominance of large numbers of recaptures in peak fishing months.

The data present a substantial northerly movement by the New South Wales prawns and a significant, but reduced, northerly migration by the Queensland prawns (Table 4; Figs. 1 and 2). To standardize the movement of all animals, a linear interpolation was carried out and plotted. This was done because it is deceptive to evaluate the movement, since all plotted points have differing times at liberty (see Figs. 1d and 2d). These figures reinforce the major northerly migration undertaken by this species. All top movers (>5° movement) began migration from 34°S, with a maximum individual northerly movement of 802 km (7.22°) for males and 720 km (6.48°) for females. Given migration is present in the data, an analysis of how this change in location affects the growth of the eastern king prawn is both interesting and justified.

Growth model

The von Bertalanffy model is considered to simulate growth of aquatic species very well (Chen et al. 1992). Wang (1999) outlined a general method for incorporating covariates that contribute to the growth rate of a species into the von Bertalanffy model. Following the work of Wang (1999), we proceed to derive the coupled latitudinal and seasonal von Bertalanffy model.

The following generalized von Bertalanffy model was proposed by Wang (1999):

(1) $L'(t) = [L_\infty - L(t)]g(\theta, x_t) + \sigma(t)\varepsilon(t)$

Table 3. Distribution by number of tag–release and recapture times over 1 year for male and female eastern king prawns.

Sex and capture	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Males												
Mark	34	76	5	0	0	0	0	0	0	44	506	13
Recapture	80	45	113	19	24	9	5	0	0	1	35	348
Females												
Mark	40	106	10	0	0	0	0	0	0	81	622	22
Recapture	92	59	153	28	27	5	7	1	3	0	53	453

Table 4. Summary (number, average (km), and sample standard deviation (km)) of movement between gender and data origin for eastern king prawns.

Direction	All			Queensland						NSW					
				Male			Female			Male			Female		
	No.	Avg.	SD	No.	Avg.	SD	No.	Avg.	SD	No.	Avg.	SD	No.	Avg.	SD
North	830	37	91	318	15	9	371	15	37	58	107	148	73	144	170
South	382	6	11	107	7	14	120	7	12	62	3	2	93	2	1
No move	359	—	—	94	—	—	51	—	—	82	—	—	130	—	—
West	491	2	8	187	2	9	262	2	9	18	3	7	24	2	1
East	931	16	34	288	7	9	317	7	9	133	26	48	182	31	51
No move	149	—	—	1	—	—	6	—	—	51	—	—	90	—	—

with $\varepsilon(t)$ being a zero mean error term representing the environmental perturbation and $\sigma(t)$ accounting for the heteroscedasticity of the error process. The latitudinal and seasonal effects are incorporated into the model via a link function denoted $g(\theta, x_t)$, where θ can be a vector or a scalar. The solution to the differential eq. 1 with initial conditions $L(b_0) = l_0$ has the form

$$(2) \quad L(t) = l_0 + [L_\infty - l_0]\{1 - \exp[-z(b_0, t)]\} + w(b_0, t)$$

In eq. 2:

$$(3) \quad z(b_0, t) = \int_{b_0}^t g(\theta, x_u) du \quad \text{and}$$

$$(4) \quad w(b_0, t) = \int_{b_0}^t \{\exp[\int_{b_0}^u g(\theta, x_s) ds] \sigma(u) \varepsilon(u)\} du$$

To incorporate the latitudinal effect into our model we let

$$(5) \quad g(\theta, t) = k + \theta[d(t) - \bar{d}]$$

be the link function. In eq. 5, k represents the growth rate at latitude $d(t) = \bar{d}$, where $\bar{d}$ is suitably chosen such that it represents the data. A linear model was selected because it adequately describes the relationship between growth and latitude over the mark–recapture study area. Using a mark–recapture framework, the function $d(t)$ describes the linear interpolation between the latitude at mark d_1 and latitude at recapture d_2 after time t . Let

$$(6) \quad d(t) = d_1 + \frac{d_2 - d_1}{t_2 - t_1}(t - t_1)$$

with t_1 and t_2 being the time at mark and the time at recapture, respectively, relative to 1 January of no particular year.

It can also be hypothesized that at different latitudes seasonality affects growth differently. To account for the seasonality, we express the final link function as a linear combination of seasonal and latitudinal effects

$$(7) \quad g(\theta, t) = k + \theta_1 \left[d_1 + \frac{d_2 - d_1}{t_2 - t_1}(t - t_1) - \bar{d} \right] + \theta_2 \cos(2\pi t) + \theta_3 \sin(2\pi t)$$

where the seasonal component of eq. 7 (eqs. 3 and 4) represent the canonical fisheries seasonal growth model (Pitcher and MacDonald 1973; Pauly and Gaschutz 1979). If a similar longitudinal expression was of interest, the following link function may describe a longitudinal effect:

$$(8) \quad g(\theta, t) = k + \theta_1 d_y(t) + \theta_2 d_x(t) + \theta_3 \cos(2\pi t) + \theta_4 \sin(2\pi t)$$

where

$$(9) \quad d_x(t) = d_{x1} + \frac{d_{x2} - d_{x1}}{t_2 - t_1}(t - t_1)$$

In eqs. 8 and 9, d_x represents the longitudinal function and d_y the latitudinal function. Please note that this link function is for use with species that have a suspected linear change in growth with respect to longitude. A longitudinal effect has not been included in this analysis; reasons for doing so are included in the Discussion.

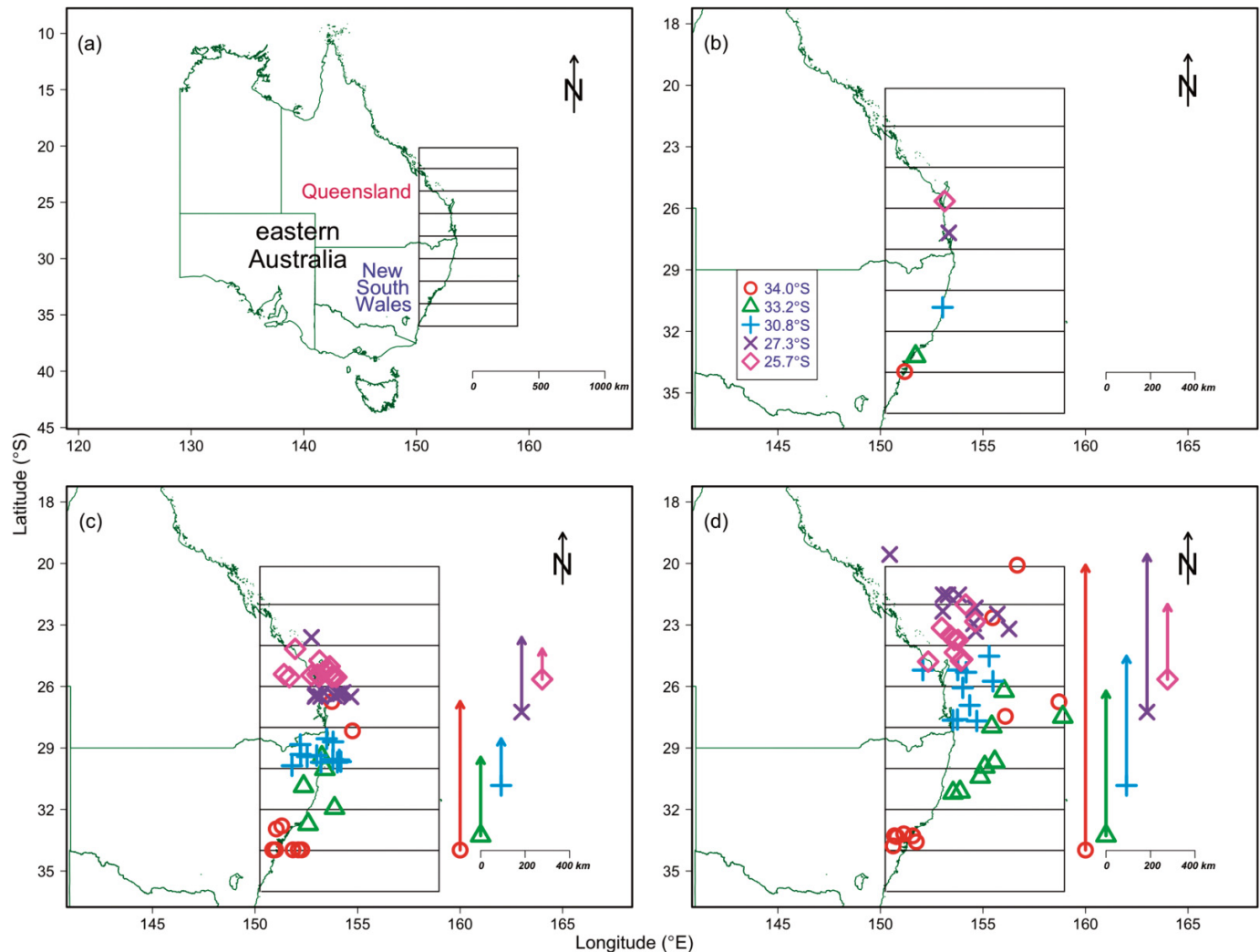
Estimation of von Bertalanffy model parameters from mark–recapture data

Having described the general von Bertalanffy growth model, it is necessary to determine an expression such that a mark–recapture study may be used. Following Wang (1999), we assume the existence of measurement error (γ_j) with each measurement of size

$$L_j = l_j + w_j + \gamma_j$$

where l_j is the expected size of the i th ($i \in (1, \dots, n)$) recaptured animal at time t_j ($j = 1, 2$) conditional on the asymptote being L_∞ . The term w_j represents process error, and for con-

Fig. 1. Male eastern king prawn mark-recapture data from the east coast of Australia: (a) position reference panel, (b) tag and release locations, (c) best recapture points based on largest movement ($>1^\circ$) with a longitudinal displacement for clarity, (d) theoretical movement (latitudinal linear interpolation) after 1 year, with a longitudinal displacement for clarity (only top 10 movers represented for clarity). Vertical lines represent the range of movement for each symbol and color type.



venience $w_j + \gamma_j$ is denoted as e_j . Process error for L_1 has no effect on the observed growth increment, whereas measurement error would have an effect. On the other hand, both process and measurement error have an effect on L_2 . Therefore, e_1 represents measurement error, while e_2 combines both process and measurement errors. The growth increment stated by Wang (1999) is

$$(10) \quad L_2 - L_1 = (L_\infty - L_1)\{1 - \exp[-z(t_1, t_2)]\} + \xi$$

where

$$(11) \quad \xi = e_2 - e_1 \exp[-z(t_1, t_2)] + (L_\infty - l_\infty)\{1 - \exp[-z(t_1, t_2)]\}$$

Equation 11 represents a random variable with mean zero (normality is not required). Note that in this paper we allow L_∞ to vary between individuals with mean l_∞ . This is done

to ensure that we take into account the variability of L_∞ between individuals. The method of James (1991), which this model is based on, guarantees that if L_∞ has variability then the estimates provided are consistent. This is a key point of difference with the method of Fabens (1965), which provides biased estimates if L_∞ is variable. Given the model is based on that of James (1991), L_∞ is allowed to vary without risk of biased estimates.

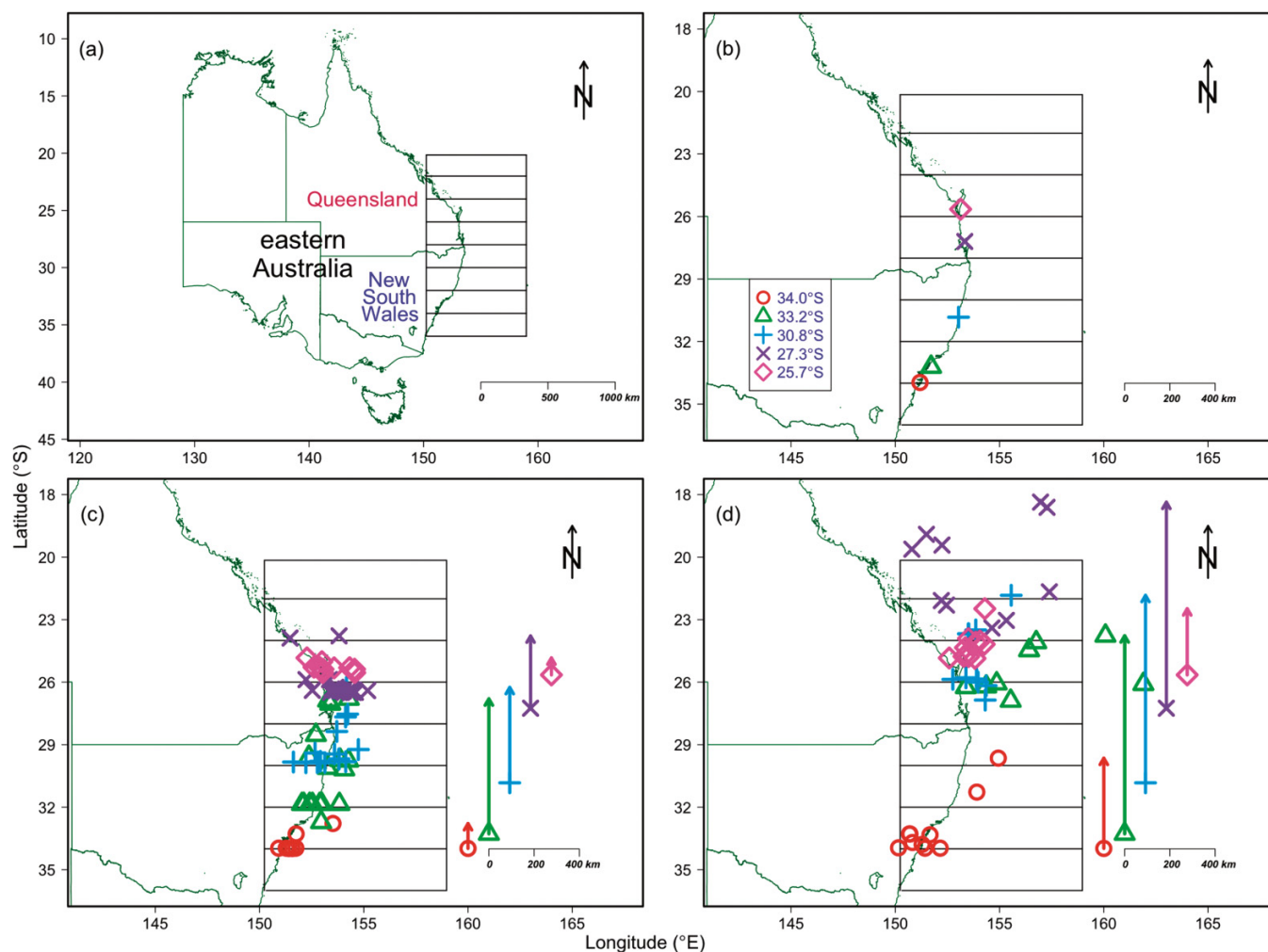
To determine the parameter estimates, the following estimating functions are used:

$$(12) \quad f_0 = \sum_i \eta_i$$

$$f_j = \sum_i \frac{\partial z(t_{1i}, t_{2i})}{\partial \theta_j} \eta_i$$

where

Fig. 2. Female eastern king prawn mark–recapture data from the east coast of Australia: (a) position reference panel, (b) tag and release locations, (c) best recapture points based on largest movement ($>1^\circ$) with a longitudinal displacement for clarity, (d) theoretical movement (latitudinal linear interpolation) after 1 year, with a longitudinal displacement for clarity (only top 10 movers represented for clarity). Vertical lines represent the range of movement for each symbol and color type.



$$(13) \quad \eta_i = (L_{2i} - L_{1i}) - (l_\infty - L_{1i})\{1 - \exp[-z(t_{1i}, t_{2i})]\}$$

In eq. 12, θ_j represents the parameters of $g(\theta, x_i)$, which includes k . These estimating functions have zero expectation and therefore produce consistent estimates. They do not require distributional assumptions and allow for extra variation attributed to growth variability, stochastic fluctuations, and unexplained sources. Estimation of the vector θ requires the minimization of the sum of the estimating functions squared. Minimization of the objective function can be done via any nonlinear optimization technique.

Once parameter estimates are found, it is important to evaluate the significance of the estimate, especially when investigating the use of a new parameter. An estimate of the asymptotic covariance matrix can be found by solving

$$\mathbf{F}^{-1} \mathbf{X} \mathbf{X}' (\mathbf{F}')^{-1}$$

where $\mathbf{F}$ is the Jacobian matrix evaluated at the estimated va-

lues, and $\mathbf{X}$ is the residual matrix (see Appendix A). Once the covariance matrix is determined, standard errors and correlations can be calculated and significance testing carried out on the parameter estimates.

Estimating latitudinal and seasonal parameters for the eastern king prawn (*M. plebejus*)

Estimation of latitudinal and seasonal parameters for the eastern king prawn requires an adaption of the general model. The growth link function $g(\theta, t)$ is given by eq. 7, which via integration (Appendix B) from t_1 to t_2 leads to

$$(14) \quad z(t_1, t_2) = kT + \theta_1 T \left(\frac{\delta d}{2} - \bar{d} \right) + \frac{\theta_2}{2\pi} [\sin(2\pi t_2) - \sin(2\pi t_1)] - \frac{\theta_3}{2\pi} [\cos(2\pi t_2) - \cos(2\pi t_1)]$$

where $T = t_2 - t_1$, and $\delta d = d_2 + d_1$. The estimating functions for the parameter set $\theta = (l_\infty, k, \theta_1, \theta_2, \theta_3)$ are

Table 5. Parameter estimates (calculated at $\bar{d} = 25^{\circ}\text{S}$ latitude) and standard errors for male and female eastern king prawns from combined seasonal and latitudinal von Bertalanffy growth model.

	k (year ⁻¹)	l_{∞} (mm)	θ_1 (k per 10°)	θ_2	θ_3
Males					
Estimate	1.43	46.7	-0.236	1.11	0.499
SE asymptote	0.340	2.43	0.283	0.360	0.278
z	4.21	19.3	-0.832	3.09	1.80
p value	0.0001	0	0.200	0.001	0.036
Females					
Estimate	1.46	61.1	-0.556	0.679	0.362
SE asymptote	0.368	5.36	0.346	0.235	0.210
z	3.97	11.4	-1.61	2.89	1.72
p value	0.0001	0	0.054	0.002	0.043

Table 6. Parameter correlation values.

Sex	$\rho_{k,l_{\infty}}$	ρ_{k,θ_1}	ρ_{k,θ_2}	ρ_{k,θ_3}	$\rho_{l_{\infty},\theta_1}$	$\rho_{l_{\infty},\theta_2}$	$\rho_{l_{\infty},\theta_3}$	ρ_{θ_1,θ_2}	ρ_{θ_1,θ_3}	ρ_{θ_2,θ_3}
Male	-0.74	-0.71	-0.046	0.17	0.66	-0.61	-0.67	-0.29	-0.43	0.87
Female	-0.93	-0.87	0.46	0.74	0.85	-0.71	-0.86	-0.65	-0.80	0.83

$$\begin{aligned} f_0 &= \sum_i \eta_i \\ f_1 &= \sum_i T_i \eta_i \\ (15) \quad f_2 &= \sum_i T_i \left(\frac{\delta d_i}{2} - \bar{d} \right) \eta_i \\ f_3 &= \sum_i [\sin(2\pi t_{i2}) - \sin(2\pi t_{i1})] \eta_i \\ f_4 &= \sum_i [\cos(2\pi t_{i2}) - \cos(2\pi t_{i1})] \eta_i \end{aligned}$$

Using these estimating functions (eq. 15), the parameters were obtained for male and female *M. plebejus* via minimizing the objective function, $F = f_0^2 + f_1^2 + f_2^2 + f_3^2 + f_4^2$, using the R programming language (<http://www.r-project.org/>). F must minimize to approximately 0 to meet the requirements of this method.

Results

Using generalized estimating equations to solve for parameter estimates from mark-recapture data provided interesting insights into the growth of the eastern king prawn. Assessing the results acquired from eq. 15, we can conclude that all parameter estimates are significant for a one-sided z test, except the male latitudinal effect. It is also noted that the female effect is weakly significant (Table 5). The condition that the residuals have expectation 0 must be met to reliably conclude that the method has worked. For both male and female data, the objective function converged in the order of 10^{-8} , which is sufficiently close to zero in our experience with James' (1991) method. The one-sided test is adequate as all estimates must be greater or less than 0 to make intuitive sense.

Correlations between all parameters are reported for both males and females (Table 6).

To make the seasonal growth parameters easier to interpret, they were converted to the canonical form (Pitcher and MacDonald 1973). The seasonal model component is often expressed as

$$(16) \quad A \sin \left[\frac{2\pi}{C}(t - \lambda) \right]$$

which is equivalent to the seasonal component in eq. 7. This is true since any linear combination of sine waves of the same period, or frequency, but with different phase shifts is also a sine wave with the same period, or frequency, but a different phase shift. This can be expressed mathematically as

$$a \sin x + b \cos x = \sqrt{a^2 + b^2} \sin(x + \phi)$$

If $a \geq 0$ then

$$\phi = \arcsin \left(\frac{b}{\sqrt{a^2 + b^2}} \right)$$

Since θ_2 and θ_3 are greater than or equal to 0, in eq. 16 $A = \sqrt{a^2 + b^2}$, $C = 1$, and $\lambda = -\frac{\phi}{2\pi}$. For males, $A_{\text{male}} = 1.22$, $\phi = 1.15$, and $\lambda_{\text{male}} = -0.183$. For females, $A_{\text{female}} = 0.770$, $\phi = 1.08$, and $\lambda_{\text{female}} = -0.172$. The parameter λ represents what direction and by how much a sine wave of this amplitude needs to be shifted, relative to the y axis, to represent the seasonal curve. The parameter A is the amplitude of the sine wave representing the seasonal variation in growth rate. Growth for *M. plebejus* peaks on the 25th and 29th of January (i.e., summer) for males and females, respectively, and reaches a minimum on the 27th and 31st of July (i.e., winter) for male and female prawns, respectively (Fig. 3).

Fig. 3. Estimated seasonal growth curves for male (solid line) and female (dashed line) eastern king prawns at 25°S latitude. Estimates for growth parameters are calculated from eq. 15.

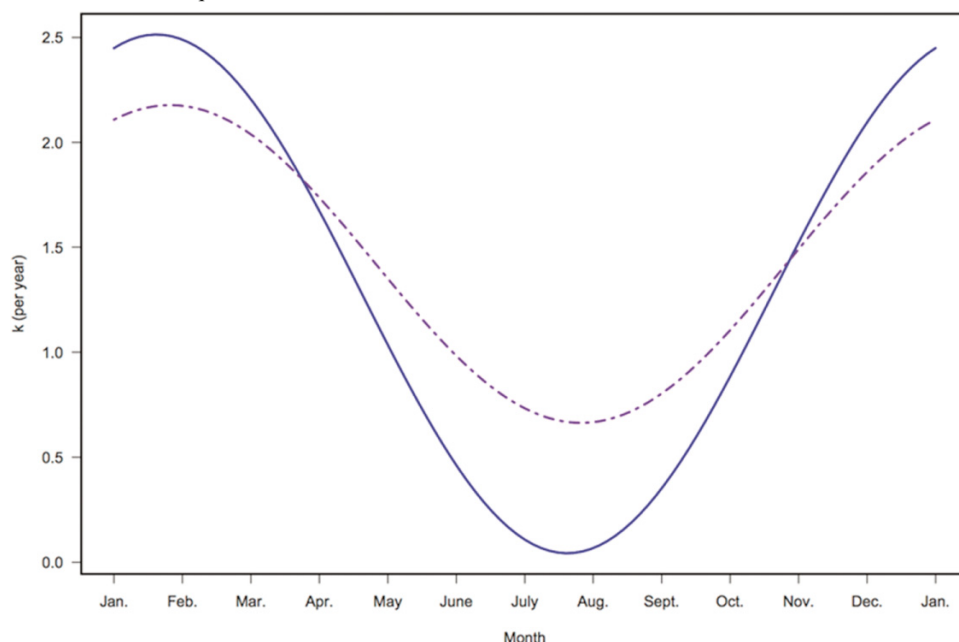
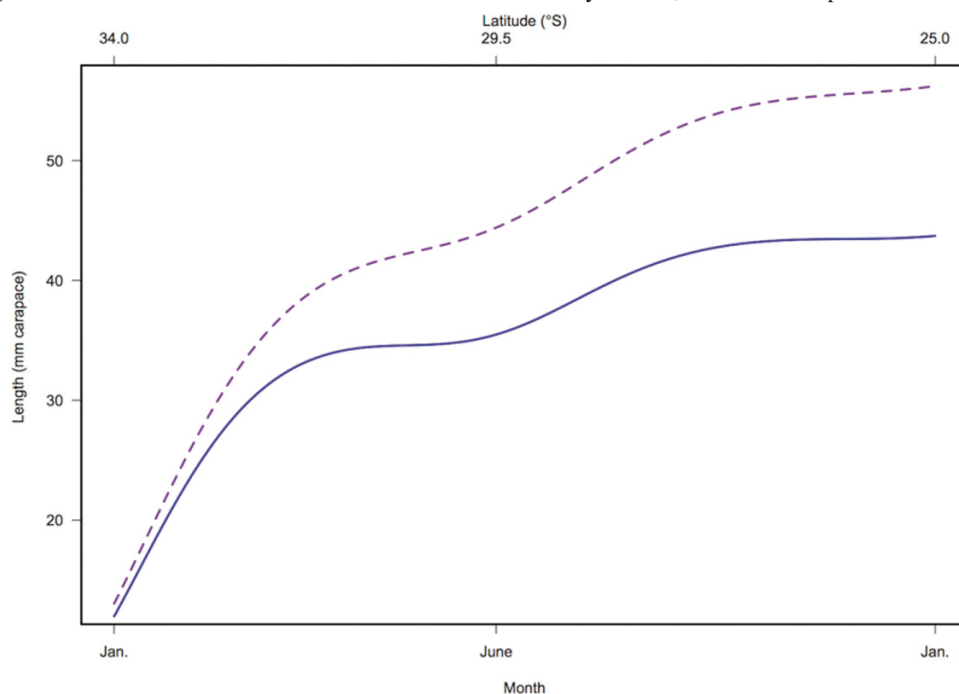


Fig. 4. Theoretical von Bertalanffy growth curves for male (solid line) and female (dashed line) eastern king prawns, incorporating a seasonal and latitudinal change. Movement is shown between 34°S and 25°S over 330 days with $l_0 = 17$ mm carapace.



The two growth link functions at $\bar{d} = 25^\circ\text{S}$ for males and females are

$$(17) \quad g(\theta, t) = 1.43 - 0.0236[d(t) - 25] + 1.11 \cos(2\pi t) + 0.499 \sin(2\pi t) \quad (\text{male})$$

$$(18) \quad g(\theta, t) = 1.46 - 0.0556[d(t) - 25] + 0.679 \cos(2\pi t) + 0.362 \sin(2\pi t) \quad (\text{female})$$

Equations 17 and 18 can be used to investigate the growth at

a particular latitude (fixed $d(t)$) or for a hypothesized latitudinal movement of *M. plebejus* (Fig. 3). To illustrate a further use for these functions (eqs. 17 and 18), we followed the mean of a female *M. plebejus* population from their nursery grounds in New South Wales (34°S) to Fraser Island (25°S), a migration taking approximately 330 days. The migration interval is the approximate average time taken by those animals that showed the greatest migration ($>5^\circ$ movement). The curves assume that migration begins in January, which is not the case for all animals. Assuming this interpolation is ade-

quate, a mean initial CL of 17 mm (with some distribution) was chosen. The *M. plebejus* population follows a linear northerly route, growing with a von Bertalanffy growth curve of the following nature:

$$l_j = l_0 + (l_\infty - l_0)\{1 - \exp[-z(t_1, t_2)]\}$$

arriving off the coast of Fraser Island with a mean length of 56.2 mm CL. The mean of the *M. plebejus* population followed a von Bertalanffy growth curve, growing more rapidly in the months between November and April, with a dramatic slowing of growth in opposing months (Fig. 4). It is noted that a similar calculation can be done for that of the male population.

Discussion

The concept of accounting for extra information via generalized estimating equations was applied to eastern king prawn data. The method quantified how growth changes with respect to latitudinal and seasonal change for different sexes. The inclusion of the latitudinal effect is of particular application to fisheries that require knowledge of growth over a range of latitudes. The eastern king prawn fishery, which extends over much of the Australian eastern continental shelf, is one such fishery. However, breeding habits, food sources, preferred habitat, and many other factors could play a role in a species' growth rate. Influences such as these may be explored further with this method.

However, studies have shown that ectotherms such as the Australian eastern king prawn usually grow to bigger final sizes when reared in cooler conditions (Atkinson and Sibly 1997; Brunel and Dickey-Collas 2010; Bělehrádek and Mann 1935). Life history analysis suggests that it is adaptive for adults to be smaller if reared in conditions that slow down juvenile growth. However, it is usually observed that adults grow to be larger if growth is limited by temperature (Atkinson and Sibly 1997). This idea is closely linked with the negative correlation between the mean von Bertalanffy growth parameters l_∞ and k .

Helser and Lai (2004) presented a Bayesian hierarchical method that also allowed the calculation of correlations with a latitudinal interaction. They noticed that l_∞ and $\ln k$ decline with increasing northerly latitudes. Pilling et al. (2002) pointed out that in practice few studies present direct evidence that these parameters are actually negatively correlated. Although there are exceptions (Hart and Chute 2009), the literature generally suggests that these values lie between -0.8 and -0.9 . The current study has shown that for the eastern king prawn, k decreases with an increase in latitude, as seen in the study of Helser and Lai (2004). Incorporating knowledge of how l_∞ varies with latitude would be an interesting extension of this method.

The reasons for the temperature size rule remain enigmatic, but the link between fecundity and body size is an underpinning factor. Reproductive events are generally less frequent in colder environments; therefore, natural selection could favour a larger body size to enhance fecundity at each reproductive episode. Furthermore, a larger asymptotic size could enable individuals to produce larger offspring or to provide better parental care (Angilletta et al. 2004). These ideas may be relevant to eastern king prawns. For example, the relationship between fecundity and size (Courtney et al.

1995) indicates that the larger sizes attained by female eastern king prawns in lower latitudes results in higher egg production compared with their counterparts found further south. Furthermore, the proportion of females with mature and ripe stage ovaries declines with increasing latitude (Montgomery et al. 2007). The higher growth rate associated with migrating northwards appears to be associated with increased reproductive output. Hence, the northerly migration undertaken by eastern king prawns may be a driving force for natural selection, which results in reproductive benefit for this species.

Yamahira and Conover (2002) demonstrated genetically based latitudinal variation in reaction norms for growth in response to temperature. The predominant form of latitudinal adaptation both within and among species was shown to be a countergradient response to length of the growing season. Northern forms (Northern Hemisphere) accelerate growth more rapidly with temperature than do those from the south. This is most likely caused by an adaptation to the length of the growing season. Short growing seasons and long winters in the north favour genotypes with the capacity for rapid summer growth (Yamahira and Conover 2002). The seasonal analysis for eastern king prawns shows that males and females have large differences. Male growth is more variable ($A_{\text{male}} = 1.22$) than female growth ($A_{\text{female}} = 0.770$) and begins earlier ($\lambda_{\text{male}} = -0.183$) than for females ($\lambda_{\text{female}} = -0.172$).

Incorporating the effect of latitude into the von Bertalanffy growth model via an application of the work of Wang (1999) has created some key points of difference to the current literature. Using the von Bertalanffy model preserves the biological basis for growth prediction. Using estimating functions allows for simple implementation from small mark-recapture data sets and guarantees asymptotically consistent and unbiased estimates for both growth and additional covariate parameters. The estimating functions do not require distributional assumptions, take into account varying L_∞ , and allow other stochastic or unexplained error sources. Once the parameters are estimated, the link function determines the growth allowing for extra analyses to be done, as demonstrated herein. This allows for seasonal curves to be calculated at any latitude, which is particularly useful when stock assessment takes migration into consideration. In this method, growth is not averaged over space or time, as in methods such as Fabens (1965) or even that of James (1991), resulting in more accurate estimates. These analyses must be carried out tentatively, as there are underlying assumptions about what the estimates mean. For example, we assumed that the growth function represents the mean of the population rather than that of an individual.

The importance of a statistically insignificant latitudinal effect for males is dubious. The fact that the parameter is not significant does not mean there is no latitudinal effect. The nonsignificance may be due to the effect being smaller than that of females, therefore placing greater emphasis on variance estimation. For males, the coefficient of variation was estimated from less information-rich data compared with females, with a mean change in latitude of 0.134° for males compared with 0.156° for females, approximately 16% more information. There are also approximately 23% more recaptures for females compared with males. Recent unpublished mark-recapture results on *M. plebejus* from its most northern

distribution indicate sexual differences, with females moving longer average distances, at higher speeds, higher recapture rates, and shorter periods-at-liberty than males. One hypothesis for this is that females are required to develop ovaries, which leads to greater ingestion of food and lipoproteins, making them more vulnerable to capture. Another hypothesis is that males have higher rates of natural mortality than females, thus dying at a younger age, and therefore resulting in fewer recaptures. In Queensland, females dominate the greater depths (i.e., >150 m), and it may be that males, being smaller, are just not designed for the greater depth habitats, possibly because of the higher pressures. This may inhibit their migration–movement to greater depths.

It is well known in prawn biology and prawn fisheries that prawns move from shallow to deep water as they grow (Glaister et al. 1987; Ruello 1975). There are also some reports that some species actually move back into shallow waters to overwinter in rivers (i.e., banana prawns, *Penaeus merguensis*) or actually move into shallower waters after spawning (Crococ and Kerr 1983). However, the overwhelming data indicate “shallow to deep” overall movement. It is hypothesized that eastern king prawns are trying to follow depth contours, rather than trying to migrate eastward. The complex shape of the eastern Australian continental shelf strongly affects the longitudinal movement of the prawns.

To explain the longitudinal movement, one needs an understanding of the continental shelf and the shelf edge or “shoulder”. From southern (33°S) to northern (28°S) New South Wales, the continental shelf is quite narrow and is most narrow around Byron Bay (≈29°S), where the shelf is about ≈70 km wide. The shelf edge runs parallel to the coast in a northeasterly direction. Thus, as the New South Wales prawns migrate north along depth contours, they move in a northeasterly direction. Once north of Byron Bay (29°S), the continental shelf shoulder runs north–south to Fraser Island (25°S), then north of Fraser Island (25°S) to Lady Elliot and Musgrave Islands (23°S), where the shelf shoulder turns and runs northwest. Hence, it is found that a higher proportion of Queensland tagged prawns move westward. Given this, the longitudinal change present, which is predominantly eastward, is likely to be heavily influenced by (i) the prawns choosing to follow depth contours as they grow and move northwards and (ii) the shape of the eastern Australian continental shelf and the shelf edge. Therefore, an attempt to quantify this movement into deeper water is difficult to model with longitude alone. This and the relatively small change in longitude present in the data are the primary reasons why longitude was left out of the final model for the eastern king prawn.

Knowledge of the true movement from New South Wales with respect to path taken, time to migrate along this path, reasons for migration (ocean currents), effects of additional covariates, and implications for fishery management need to be better understood to make full use of the results and model. We have some insight into the true movement of *M. plebejus*, which is south to north. However, knowledge of the true path taken (perhaps parabolic) could prove the linear interpolation to be a gross assumption. It is clear, however, that the general movement is north, with less northerly movement for Queensland prawns. The introduction of additional covariates such as depth would be an excellent extension of

this method, but it is noted that a large, well-planned data set would be required to detect the influences of these covariates. The inclusion of temperature as a covariate would be a natural extension of this method, but determining how it shall be included will depend heavily on the data and species being studied.

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References

- Angilletta, M.J., Jr, Steury, T.D., and Sears, M.W. 2004. Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. *Integr. Comp. Biol.* **44**(6): 498–509. doi:10.1093/icb/44.6.498. PMID:21676736.
- Ashton, K.G. 2004. Sensitivity of intraspecific latitudinal clines of body size for tetrapods to sampling, latitude and body size. *Integr. Comp. Biol.* **44**(6): 403–412. doi:10.1093/icb/44.6.403. PMID:21676726.
- Atkinson, D., and Sibly, R.M. 1997. Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends Ecol. Evol.* **12**(6): 235–239. doi:10.1016/S0169-5347(97)01058-6. PMID:21238056.
- Bělehrádek, J., and Mann, S.E. 1935. Temperature and living matter: with 70 illustrations. Vol. 8. Gebrüder Borntraeger, Berlin, Germany.
- Brunel, T., and Dickey-Collas, M. 2010. Effects of temperature and population density on von Bertalanffy growth parameters in Atlantic herring: a macro-ecological analysis. *Mar. Ecol. Prog. Ser.* **405**: 15–28. doi:10.3354/meps08491.
- Chen, Y., Jackson, D.A., and Harvey, H.H. 1992. A comparison of von Bertalanffy and polynomial functions in modelling fish growth data. *Can. J. Fish. Aquat. Sci.* **49**(6): 1228–1235. doi:10.1139/f92-138.
- Courtney, A.J., Montgomery, S.S., Die, D.J., Andrew, N.L., Cosgrove, M.G., and Blount, C. 1995. Maturation in the female eastern king prawn *Penaeus plebejus* from coastal waters of eastern Australia, and considerations for quantifying egg production in penaeid prawns. *Mar. Biol. (Berl.)*, **122**(4): 547–556. doi:10.1007/BF00350677.
- Courtney, A.J., Haddy, J.A., Campbell, M.J., Roy, D.P., Tonks, M.L., Gaddes, S.W., Chilcott, K.E., O'Neill, M.F., Brown, I.W., McLennan, M., Jebreen, E.J., van der Geest, C., Rose, C., Kistle, S., Turnbull, C.T., Kyne, P.M., Bennett, M.B., and Taylor, J. 2007. Bycatch weight, composition and preliminary estimates of the impact of bycatch reduction devices in Queensland's trawl fishery. Fisheries Research and Development Corporation (FRDC), Brisbane, Qld.
- Crococ, P.J., and Kerr, J.D. 1983. Maturation and spawning of the banana prawn *Penaeus merguensis* de Man (Crustacea: Penaeidae) in the Gulf of Carpentaria, Australia. *J. Exp. Mar. Biol. Ecol.* **69**(1): 37–59. doi:10.1016/0022-0981(83)90171-5.
- Emiliani, D.A. 1971. Equipment for holding and releasing penaeid shrimp during marking experiments. *Fish Bull.* **69**(1): 247–250.
- Fabens, A.J. 1965. Properties and fitting of the von Bertalanffy growth curve. *Growth*, **29**(3): 265–289. PMID:5865688.
- Geist, V. 1987. Bergmann's rule is invalid. *Can. J. Zool.* **65**(4): 1035–1038. doi:10.1139/z87-164.
- Glaister, J.P., Lau, T., and McDonall, V.C. 1987. Growth and migration of tagged eastern Australian king prawns, *Penaeus plebejus* Hess. *Mar. Freshw. Res.* **38**(2): 225–241. doi:10.1071/MF9870225.

- Haddon, M. 2011. Modelling and quantitative methods in fisheries. 2nd ed. CRC Press–Chapman and Hall Group, Boca Raton, Fla.
- Hampton, J. 1986. Effect of tagging on the condition of southern bluefin tuna, *Thunnus maccoyii* (Castlenau). Mar. Freshw. Res. **37**(6): 699–705. doi:10.1071/MF9860699.
- Hart, D.R., and Chute, A.S. 2009. Estimating von Bertalanffy growth parameters from growth increment data using a linear mixed-effects model, with an application to the sea scallop *Placopecten magellanicus*. ICES J. Mar. Sci. **66**(10): 2165–2175. doi:10.1093/icesjms/fsp188.
- Helser, T.E., and Lai, H.-L. 2004. A Bayesian hierarchical meta-analysis of fish growth: with an example for North American largemouth bass, *Micropterus salmoides*. Ecol. Model. **178**(3–4): 399–416. doi:10.1016/j.ecolmodel.2004.02.013.
- James, I.R. 1991. Estimation of von Bertalanffy growth curve parameters from recapture data. Biometrics, **47**(4): 1519–1530. doi:10.2307/2532403.
- Montgomery, S.S. 1990. Movements of juvenile eastern king prawns, *Penaeus plebejus*, and identification of stock along the east coast of Australia. Fish. Res. **9**(3): 189–208. doi:10.1016/S0165-7836(05)80001-3.
- Montgomery, S.S., Courtney, A.J., Blount, C., Stewart, J., Die, D.J., Cosgrove, M., and O'Neill, M.F. 2007. Patterns in the distribution and abundance of female eastern king prawns, *Melicertus plebejus* (Hess, 1865), capable of spawning and reproductive potential in waters off eastern Australia. Fish. Res. **88**(1–3): 80–87. doi:10.1016/j.fishres.2007.08.002.
- O'Neill, M.F., Courtney, A.J., Good, N.M., Turnbull, C.T., Yeomans, K.M., Staunton-Smith, J., and Shootingstar, C. 2005. Reference point management and the role of catch-per-unit effort in prawn and scallop fisheries. Tech. Rep. Fisheries Research and Development Corporation (FRDC), Brisbane, Qld.
- Partridge, L., and French, V. 1996. Thermal evolution of ectotherm body size: why get big in the cold? In Animals and temperature: phenotypic and evolutionary adaptation. Society for Experimental Biology Semnar Series No. 59. Edited by I.A. Johnson and A.F. Bennett. Cambridge University Press, UK. pp. 265–292. doi:10.1017/CBO9780511721854.012.
- Pauly, D., and Gaschutz, G. 1979. A simple method for fitting oscillating length growth data, with a program for pocket calculators. ICES CM, **6**: 24–26.
- Pilling, G.M., Kirkwood, G.P., and Walker, S.G. 2002. An improved method for estimating individual growth variability in fish, and the correlation between von Bertalanffy growth parameters. Can. J. Fish. Aquat. Sci. **59**(3): 424–432. doi:10.1139/f02-022.
- Pitcher, T.J., and MacDonald, P.D.M. 1973. Two models for seasonal growth in fishes. J. Appl. Ecol. **10**(2): 599–606. doi:10.2307/2402304.
- Quinn, T.J., and Deriso, R.B. 1999. Quantitative fish dynamics (biological resource management). Oxford University Press, New York.
- Rijnsdorp, A.D., and Pastoors, M.A. 1995. Modelling the spatial dynamics and fisheries of North Sea plaice (*Pleuronectes platessa* L.) based on tagging data. ICES J. Mar. Sci. **52**(6): 963–980. doi:10.1006/jmsc.1995.0092.
- Ruello, N.V. 1975. Geographical distribution, growth and breeding migration of the eastern Australian king prawn *Penaeus plebejus* Hess. Mar. Freshw. Res. **26**(3): 343–354. doi:10.1071/MF9750343.
- Shepherd, S.A., and Hearn, W.S. 1983. Studies on Southern Australian abalone (genus *Haliotis*). IV. Growth of *H. laevigata* and *H. ruber*. Mar. Freshw. Res. **34**(3): 461–475. doi:10.1071/MF9830461.
- Sheridan, P.F., Patella, F.J., Jr, Baxter, N., and Emiliani, D.A. 1987. Movements of brown shrimp, *Penaeus aztecus*, and pink shrimp, *P. duorarum*, relative to the US–Mexico border in the western Gulf of Mexico. Mar. Fish. Rev. **49**: 14–19.
- Somers, I.F., and Kirkwood, G.P. 1984. Movements of tagged tiger prawns, *Penaeus* spp., in the western Gulf of Carpentaria. Mar. Freshw. Res. **35**(6): 713–723. doi:10.1071/MF9840713.
- Wang, Y. 1998. Theory and methods: growth curves with explanatory variables and estimation of the effect of tagging. Australian and New Zealand Journal of Statistics, **40**(3): 299–304. doi:10.1111/1467-842X.00034.
- Wang, Y.G. 1999. Estimating equations for parameters in stochastic growth models from tag–recapture data. Biometrics, **55**(3): 900–903. doi:10.1111/j.0006-341X.1999.00900.x. PMID:11315025.
- Wang, Y.G., and Die, D. 1996. Stock–recruitment relationships of the tiger prawns (*Penaeus esculentus* and *Penaeus semisulcatus*) in the Australian northern prawn fishery. Mar. Freshw. Res. **47**(1): 87–95. doi:10.1071/MF9960087.
- Wang, Y.G., and Somers, I.F. 1996. A simple method for estimating growth parameters from multiple length–frequency data in presence of continuous recruitment. Fish. Res. **28**(1): 45–56. doi:10.1016/0165-7836(96)00484-5.
- Wang, Y.G., and Thomas, M.R. 1995. Accounting for individual variability in the von Bertalanffy growth model. Can. J. Fish. Aquat. Sci. **52**(7): 1368–1375. doi:10.1139/f95-132.
- Xiao, Y. 1999. General age- and time-dependent growth models for animals. Fish Bull. **97**(3): 690–701.
- Yamahira, K., and Conover, D.O. 2002. Intra- vs. interspecific latitudinal variation in growth: adaptation to temperature or seasonality? Ecology, **83**(5): 1252–1262. doi:10.1890/0012-9658(2002)083[1252:IVILVI]2.0.CO;2.

Appendix A. Asymptotic variance

To simplify the calculation, we represent the estimating functions in matrix form.

Let

$$\begin{aligned}\mathbf{S} &= \left(\frac{\delta d_i}{2} - \bar{d}, \dots, \frac{\delta d_n}{2} - \bar{d} \right) \\ \mathbf{Q} &= \left\{ \frac{1}{2\pi} [\sin(2\pi t_{i2}) - \sin(2\pi t_{i1})], \dots, \frac{1}{2\pi} [\sin(2\pi t_{n2}) - \sin(2\pi t_{n1})] \right\} \\ \mathbf{R} &= \left\{ \frac{-1}{2\pi} [\cos(2\pi t_{i2}) - \cos(2\pi t_{i1})], \dots, \frac{-1}{2\pi} [\cos(2\pi t_{n2}) - \cos(2\pi t_{n1})] \right\} \\ \mathbf{T} &= (T_1, \dots, T_n) \\ \boldsymbol{\theta} &= (k, \theta_1, \theta_2, \theta_3) \\ \boldsymbol{\beta} &= (\mathbf{T}, \mathbf{ST}, \mathbf{Q}, \mathbf{R})\end{aligned}$$

where $\mathbf{ST}$ represents component-wise multiplication, and $\boldsymbol{\beta}$ is an $n \times 4$ matrix. We can now represent $\boldsymbol{\eta}$ more succinctly:

$$\boldsymbol{\eta} = (\mathbf{L}_\infty - \mathbf{L}_1)[1 - \exp(-\boldsymbol{\theta}\boldsymbol{\beta}')] - \Delta\mathbf{L}$$

where $\Delta\mathbf{L} = \mathbf{L}_2 - \mathbf{L}_1$. Now the estimating functions can be represented in the following way. Let

$$\begin{aligned}\mathbf{C} &= [(1, 1, 1, \dots, 1), \mathbf{T}, \mathbf{ST}, 2\pi\mathbf{Q}, -2\pi\mathbf{R}]' \\ \mathbf{f} &= \boldsymbol{\eta}\mathbf{C}\end{aligned}$$

To complete the asymptotic variance calculation, we need the design matrix $\mathbf{D}_g$. Let

$$X_i = \eta_i \begin{pmatrix} 1 \\ T_i \\ S_i T_i \\ Q_i \\ R_i \end{pmatrix}$$

$$\mathbf{D}_g = \sum_i X_i X_i^T = \begin{pmatrix} \mathbf{1} \\ \mathbf{T} \\ \mathbf{ST} \\ \mathbf{Q} \\ \mathbf{R} \end{pmatrix} \boldsymbol{\eta}\boldsymbol{\eta}' (\mathbf{1} \mathbf{T} \mathbf{ST} \mathbf{Q} \mathbf{R}) = \sum_i \eta_i^2 \begin{pmatrix} 1 & T_i & S_i T_i & Q_i & R_i \\ T_i & T_i^2 & S_i T_i^2 & Q_i T_i & R_i T_i \\ S_i T_i & S_i T_i^2 & S_i^2 T_i^2 & S_i T_i Q_i & S_i T_i R_i \\ Q_i & Q_i T_i & Q_i S_i T_i & Q_i^2 & Q_i R_i \\ R_i & R_i T_i & R_i S_i T_i & R_i Q_i & R_i^2 \end{pmatrix}$$

and $\mathbf{F}$ the Jacobian

$$\mathbf{F} = \begin{pmatrix} \frac{\partial f_0}{\partial k} & \frac{\partial f_0}{\partial l_\infty} & \frac{\partial f_0}{\partial \theta_1} & \frac{\partial f_0}{\partial \theta_2} & \frac{\partial f_0}{\partial \theta_3} \\ \frac{\partial f_1}{\partial k} & \frac{\partial f_1}{\partial l_\infty} & \frac{\partial f_1}{\partial \theta_1} & \frac{\partial f_1}{\partial \theta_2} & \frac{\partial f_1}{\partial \theta_3} \\ \frac{\partial f_2}{\partial k} & \frac{\partial f_2}{\partial l_\infty} & \frac{\partial f_2}{\partial \theta_1} & \frac{\partial f_2}{\partial \theta_2} & \frac{\partial f_2}{\partial \theta_3} \\ \frac{\partial f_3}{\partial k} & \frac{\partial f_3}{\partial l_\infty} & \frac{\partial f_3}{\partial \theta_1} & \frac{\partial f_3}{\partial \theta_2} & \frac{\partial f_3}{\partial \theta_3} \\ \frac{\partial f_4}{\partial k} & \frac{\partial f_4}{\partial l_\infty} & \frac{\partial f_4}{\partial \theta_1} & \frac{\partial f_4}{\partial \theta_2} & \frac{\partial f_4}{\partial \theta_3} \end{pmatrix} = \begin{pmatrix} \mathbf{1} \\ \mathbf{T} \\ \mathbf{ST} \\ \mathbf{Q} \\ \mathbf{R} \end{pmatrix} \nabla \mathbf{f}_0$$

Let

$$\begin{aligned}
 z &= kT_i + \theta_1 T_i S_i + \theta_2 Q_i - \theta_3 R_i \\
 f_0 &= \sum_i \eta_i = \sum_i (l_\infty - L_{1i}) [1 - \exp(-z_i)] - (L_{2i} - L_{1i}) \\
 f_1 &= \sum_i \eta_i T_i = \sum_i T_i \{ (l_\infty - L_{1i}) [1 - \exp(-z_i)] - (L_{2i} - L_{1i}) \} \\
 f_2 &= \sum_i \eta_i S_i T_i = \sum_i S_i T_i \{ (l_\infty - L_{1i}) [1 - \exp(-z_i)] - (L_{2i} - L_{1i}) \} \\
 f_3 &= \sum_i Q_i = \{ (l_\infty - L_{1i}) [1 - \exp(-z_i)] - (L_{2i} - L_{1i}) \} \\
 f_4 &= \sum_i R_i = \{ (l_\infty - L_{1i}) [1 - \exp(-z_i)] - (L_{2i} - L_{1i}) \}
 \end{aligned}$$

Letting $L_{2i} - L_{1i} = A$ and $B = l_\infty - L_{1i}$, the derivatives with respect to the parameter set form the gradient of f_0 . The derivatives are as follows:

$$\begin{aligned}
 \frac{\partial f_0}{\partial k} &= \sum_i \frac{\partial}{\partial k} B - B \exp[-(kT_i + \theta_1 T_i S_i + \theta_2 Q_i - \theta_3 R_i)] - A = \sum_i T_i B \exp[-(kT_i + \theta_1 T_i S_i + \theta_2 Q_i - \theta_3 R_i)] \\
 \frac{\partial f_0}{\partial l_\infty} &= \sum_i \frac{\partial}{\partial l_\infty} l_\infty - L_{1i} - (l_\infty - L_{1i}) \exp[-(kT_i + \theta_1 T_i S_i + \theta_2 Q_i - \theta_3 R_i)] - A = \sum_i 1 - \exp[-(kT_i + \theta_1 T_i S_i + \theta_2 Q_i - \theta_3 R_i)] \\
 \frac{\partial f_0}{\partial \theta_1} &= \sum_i \frac{\partial}{\partial \theta} B - B \exp[-(kT_i + \theta_1 T_i S_i + \theta_2 Q_i - \theta_3 R_i)] - A = \sum_i B T_i S_i \exp[-(kT_i + \theta_1 T_i S_i + \theta_2 Q_i - \theta_3 R_i)] \\
 \frac{\partial f_0}{\partial \theta_2} &= \sum_i \frac{\partial}{\partial \theta} B - B \exp[-(kT_i + \theta_1 T_i S_i + \theta_2 Q_i - \theta_3 R_i)] - A = \sum_i B Q_i \exp[-(kT_i + \theta_1 T_i S_i + \theta_2 Q_i - \theta_3 R_i)] \\
 \frac{\partial f_0}{\partial \theta_3} &= \sum_i \frac{\partial}{\partial \theta} B - B \exp[-(kT_i + \theta_1 T_i S_i + \theta_2 Q_i - \theta_3 R_i)] - A = \sum_i B R_i \exp[-(kT_i + \theta_1 T_i S_i + \theta_2 Q_i - \theta_3 R_i)]
 \end{aligned}$$

The other rows of the Jacobian matrix are scalars of these derivatives by T_i , $S_i T_i$, Q_i , and R_i , respectively. The standard errors for the latitudinal effect can be found by solving the following equation. According to Maritz (1995), the covariance matrix is estimated by

$$\mathbf{C} = \mathbf{F}^{-1} \mathbf{D}_g (\mathbf{F}')^{-1}$$

and the standard errors equal $\sqrt{\text{diag}(\mathbf{C})}$. The correlations are the standard Pearson correlations that can be calculated from the covariance matrix.

Reference

Maritz, J. 1995. Distribution-free statistical methods. Chapman & Hall-CRC, London, England.

Appendix B. Derivation of $d(t)$

The proposed link function to characterize the latitudinal effect is

$$g(\theta, t) = k + \theta[d(t) - \bar{d}]$$

where k is the proposed maximum at $\bar{d}$, and $d(t)$ is the latitude at some time t . Lai and Kimura (2002) transformed latitudes d_1 and d_2 in the link function into Euclidian distances departing from the reference latitude $\bar{d}$. They did this to account for spatial variability in survey sampling for sea scallops. The latitude at some time t will be the linear interpolation of the form

$$d(t) = d_1 + \frac{d_2 - d_1}{t_2 - t_1}(t - t_1)$$

To implement a similar method to Wang (1999), we need to integrate over the time at liberty to obtain $z(t_1, t_2)$ (eq. 14). The constant $\bar{d}$ is also added to correct for the range in which the latitude in the data set is defined. Letting $d_2 - d_1 = \Delta d$ and adding the seasonal components to the model the integral becomes

$$\begin{aligned} z(t_1, t_2) &= \int_{t_1}^{t_2} k + \theta_1 \left[d_1 + \frac{\Delta d}{t_2 - t_1} (t - t_1) - \bar{d} \right] + \theta_2 \cos(2\pi t) + \theta_3 \sin(2\pi t) dt \\ &= \left[kt + \theta_1 d_1 t + \theta_1 \frac{\Delta d}{t_2 - t_1} \frac{t^2}{2} - \theta_1 \frac{\Delta d}{t_2 - t_1} t t_1 - t \bar{d} + \frac{\theta_2}{2\pi} \sin(2\pi t) - \frac{\theta_3}{2\pi} \cos(2\pi t) \right]_{t_1}^{t_2} \\ &= k(t_2 - t_1) + \theta_1(t_2 - t_1) \left(\frac{d_1 + d_2}{2} - \bar{d} \right) + \frac{\theta_2}{2\pi} [\sin(2\pi t_2) - \sin(2\pi t_1)] - \frac{\theta_3}{2\pi} [\cos(2\pi t_2) - \cos(2\pi t_1)] \end{aligned}$$

Reference

- Lai, H.-L., and Kimura, D.K. 2002. Analyzing survey experiments having spatial variability with an application to a sea scallop fishing experiment. *Fish. Res.* **56**(3): 239–259. doi:10.1016/S0165-7836(01)00323-X.