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Estimating growth from length frequency distribution: comparison of ELEFAN and Bayesian approaches for red endeavour prawns (*Metapenaeus ensis*)

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Using length frequency distribution data (LFD) is cost-effective for estimating somatic growth in fish or invertebrates as length data are relatively easy to obtain. The recently developed R packages TropFishR and fishboot extend classic ELEFAN (Electronic LEngth Frequency ANalysis) programs and include more powerful optimization procedures and a bootstrap method for estimating uncertainties. Yet, the fundamental functions require users to provide search conditions (e.g. upper and lower limits for each parameter, length-class size, number of length-classes for the calculation of moving average), which can significantly affect the results. In this paper, we compare the ELEFAN approach with a Bayesian approach in analysing LFD, employing both standard and seasonal von Bertalanffy growth functions. We apply both approaches to a commercially valuable but poorly studied red endeavour prawn (*Metapenaeus ensis*) harvested in Australia's Northern Prawn Fishery. Sensitivity tests on ELEFAN confirm that any change in search settings would affect the results. Simulation studies on Bayesian growth models show that L_{inf} and K can be accurately obtained even with modal progression of only one year-class and using non-informative priors. However, age information, including the theoretical age at length zero (t_0), is difficult to estimate and requires LFD from multiple age classes and informative priors. The Bayesian models yield mean parameters of: L_{inf} = 36.56 mm (carapace length), K = 2.74 yr^{-1}, and t_0 = -0.02 yr for the males, and L_{inf} = 51.81 mm, K = 1.94 yr^{-1}, and t_0 = -0.02 yr for the females. Seasonal oscillation models fit the LFD better, but the improvement is small and the estimated season-related parameters have large variances.

Keywords: Bertalanffy, greasyback shrimp, modal progression, multi-normal mixture model, TropFishR.

Introduction

Three primary approaches have been used to estimate growth of wild fish and invertebrates (Quinn and Deriso, 1999). The most widely applied approach for fish is to use length-age measurements where age can be determined from hard body parts such as otoliths and scales. Mark–recapture technique is also a commonly used method where size increments are obtained during a known period of liberty. The third approach is to derive growth from length frequency distribution data (LFD). Although the first approach is mostly studied in fish, ageing is difficult and expensive. Estimating age from hard body parts can be uncertain due to irregular early growth patterns and structural resorption near the primordium (Campana, 2001; Kolody *et al.*, 2016). This method is unfeasible for many invertebrates as age cannot be determined from their body parts. On the other hand, mark–recapture studies can provide accurate information if carried out properly, but they are costly and labour intensive and are impracticable for invertebrates with small body. Moreover, this method requires an assumption that tagging does not affect the growth rate of the individual. If tagged individuals are captured by fishermen, the reported information can be highly inaccurate (Leroy *et al.*, 2015).

Since length can be easily measured, the third primary approach is the most cost-effective. There are two different tactics in this class of methods. For relatively long-lived species, several modes in length frequency distribution may be identified from a single sampling occasion. A growth model can then be fitted to such length data (Macdonald and Pitcher, 1979; Schnute and Fournier, 1980; Quinn and Deriso, 1999; Zhou *et al.*, 2020). Another popular technique is based on length modal progression where a series of samples (e.g. monthly) are taken from the population so the modes can be followed from one time step to the next (Pauly, 1987). The challenge of length frequency analyses is to identify sufficient modes in the length frequency distribution that can be assumed to represent true ages. The decomposition of length frequency into appropriate age classes is often statistically difficult. Typically, length modes are easier to distinguish for the younger age classes or short-lived species (Gulland and Rosenberg, 1992), but are more difficult and sometimes impossible to separate for older age classes as fish growth slows or even ceases in later life (Maunder *et al.*, 2018).

The Electronic LEngth Frequency ANalysis (ELEFAN) is perhaps the most commonly used method for modelling the modal progression from LFD. The original ELEFAN system was developed in the early 1980s (Pauly, 1987; Pauly and Morgan, 1987), and contains several computer programs (ELEFAN 0 to ELEFAN IV) to conduct stock assessment based on LFD. Amongst these programs, ELEFAN I is used to estimate growth parameters of fish or invertebrates based on modal progression. The program identifies peaks and troughs

in LFD plotted at suitable intervals (length-class size, aka bin size) by a moving average over several length classes. The plot leads to definition of peaks as those parts of LFD that are above the corresponding moving average and troughs as those parts of LFD that are below the running average. The program then calculates the maximum "sum of available peaks" (ASP) in LFD samples. A von Bertalanffy growth function (VBGF) is fitted to the available peaks in the LFD samples sequentially arranged in time. A VBGF with a parameter combination that passes through most peaks and avoiding most troughs is considered the best fit (Pauly, 1987). Earlier software for implementing ELEFAN, including the most extensively used FiSAT (Gayanilo et al., 1996), have limitations in their ability to import data and perform automated analyses. Furthermore, the earlier ELEFAN programs use the traditional search procedures, such as K-scan and response surface analysis (RSA). Recent simulations showed that K-scan has fundamental issues and produce large biases in parameter estimation (Schwamborn, 2018). RSA allows for an unconstrained, simultaneous search for possible combinations of two parameters. However, RSA cannot model seasonal growth because of multi-dimensionality with additional parameters. Another major concern with RSA is its tendency to become stuck at local maxima (Schwamborn et al., 2019).

Mildenberger et al. (2017) recently developed the TropFishR package that allows for further expansion and flexibility. More importantly, it includes two more powerful optimization procedures that search over all parameters simultaneously. The ELEFAN_SA function is based on simulated annealing (SA) and the ELEFAN_GA function is based on genetic algorithms (GA) (Taylor and Mildenberger, 2017). Simulated annealing is a probabilistic technique for approximating the global optimum of a given function. It is a metaheuristic approach used to approximate global optimization in a large search space for an optimization problem. For problems where finding an approximate global optimum is more important than finding a precise local optimum in a fixed amount of time, SA may be preferable to exact algorithms. The genetic algorithm is a metaheuristic inspired by the process of natural selection. GA is commonly used to generate high-quality solutions to optimization and search problems by relying on biologically inspired operators such as mutation, crossover, and selection.

Despite its new features, TropFishR inherits some weaknesses from original ELEFAN. ELEFAN software, including TropFishR, only produces a single set of growth parameters. These programs cannot assess the uncertainty inherent in the method or obtain confidence intervals for growth parameters within an unconstrained search space. A bootstrap-based TropFishR updated by Schwamborn et al. (2019), called "fishboot", allows for the estimation of uncertainties in the algorithms and in the LFD data. However, the fundamental functions in both packages require users to provide search conditions, including the bounds (upper and lower limits) for each parameter, the selection of the length-class size (bin size) of the length frequency data, and the number of length-classes for the calculation of moving average. It has been found that these search settings can significantly affect the results (Taylor and Mildenberger, 2017; Wang et al., 2020).

Modelling growth using Bayesian techniques has been used in fisheries research (Dortel et al., 2015; Zhou et al., 2020). This approach also applies VBGF to LFD that exhibit modal progression over time. However, instead of using moving aver-

age to identify peaks and troughs, this approach identifies the modes using a multinormal mixture model and then integrates the modes and associated variances into the Bayesian model to estimate VBGF parameters. The Bayesian approach is flexible and can incorporate previous studies or expert knowledge into the modelling with varying levels of confidence. In addition, Bayesian growth models may allow estimation of age information, including theoretical age at length zero and each cohort age at sampling time.

The Northern Prawn Fishery (NPF) is Australia's most valuable prawn fishery. This fishery harvests several important commercial prawn species. Thorough studies of growth have been conducted for most species through mark–recapture experiments, including grooved tiger prawn (*Penaeus semisulcatus*) and brown tiger prawn (*P. esculentus*) (Kirkwood and Somers, 1984; Wang and Somers, 1996; Wang and Ellis, 2005; Punt et al., 2010), common banana prawn (*P. merguiensis*) (Lucas et al., 1979), red-legged banana prawn (*P. indicus*) (Loneragan et al., 2002), and blue endeavour prawn (*Metapenaeus endeavouri*) (Buckworth, 1992; Xiao, 1994; Punt et al., 2010).

The red endeavour prawn (*Metapenaeus ensis*), often called greasyback shrimp in Asian countries, is a valuable species in the NPF but relatively data-poor. There is no mark–recapture study for this species. Growth of red endeavour prawns has been studied once based on LFD collected during scientific surveys in the northeast of the Gulf of Carpentaria (Park, 1999). In Park's thesis, growth parameters were estimated using an earlier version of ELEFAN in the FiSAT computer package (Gayanilo et al., 1996). The VBGF was fitted to LFD combined over a 3-year period from March 1986 to December 1988. The study was a useful contribution to our knowledge of endeavour prawns in the NPF, but the estimated growth was considered dubious (Dichmont et al., 2008). The red endeavour prawn has a wide distribution in the Indo-Pacific Region from Japan to Australia. There have been some studies of its growth in Asia (Cheung, 1964; Waffy, 1990; Ariyama and Sano, 2015; Samphan et al., 2016). The results are variable, perhaps due to differences in sampling designs, sample sizes, modelling methods, or geographic locations.

In this paper, we compare the new ELEFAN tools (i.e. bootstrap-based ELEFAN_GA and ELEFAN_SA optimization procedures) and the Bayesian growth models (BGM) using the red endeavour prawns harvested in the NPF. We demonstrate BGM's potential capability to estimate age-related information from LFD, which is not feasible for ELEFAN. The results for *M. ensis* are not only essential for stock assessments of this species in the NPF, but also for studies in the wider Indo-Pacific region. Furthermore, the Bayesian methods could be adopted for analysing LFD for other species.

Material and methods

Study location

A series of prawn surveys were carried out each lunar month between August 1983 and March 1985 in the northwestern Gulf of Carpentaria (Somers et al., 1987) (Figure 1). A commercial trawler (Maxim) was chartered for these surveys (hence, the study is often referred to as the "Maxim surveys"). A total of 21 cruises captured commercial species of penaeids, including both blue and red endeavour prawns. Sampling gears consisted of two Florida Flyer trawl nets of headrope
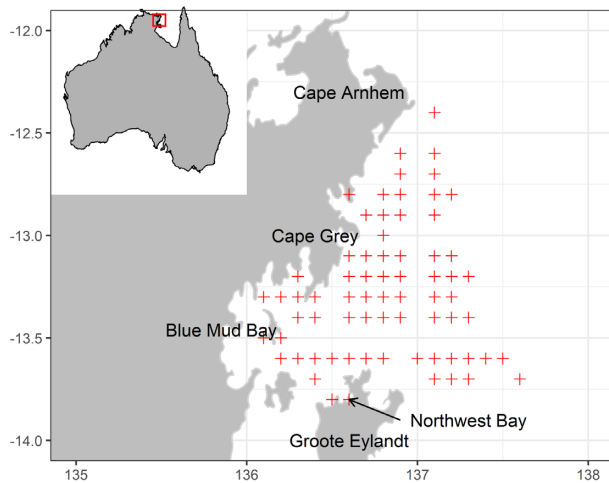
Figure 1. Maxim survey stations in the northwestern Gulf of Carpentaria.

length 11.0 m with an average internal mesh size of 46 and 38 mm at the codends. Trawl nets were typically towed for a 20 min duration. All survey trawls were carried out during the hours of darkness, from 1 h after sunset to 1 h before sunrise. The time and duration of each trawl were recorded along with the depth, latitude, and longitude of the midpoint of the trawl station. Surface temperature and salinity were measured at each of the trawl stations.

The trawl net used in the study was the gear commonly used in the commercial prawn fishery in the Gulf of Carpentaria. The large mesh size may have low efficiency for catching small prawns. An additional experiment was carried out during the cruise to investigate size selectivity. A 25-mm-stretch mesh (20 mm internal measurement) codend cover was added to the starboard trawl net. The size and abundance of prawns in the starboard codend and those in the codend cover were recorded. Based on these data, we estimated gear selectivity (the proportion of prawns encountering the gear which are retained in the catch) for carapace length CL, S_{CL}, as $S_{CL} = \frac{1}{1+e^{3.94-0.30CL}}$ (the parameter value 0.30 in mm^{-1}). The catch of prawns with carapace length CL were adjusted as $\hat{C}_{CL} = \frac{C_{CL}}{S_{CL}}$, where C_{CL} is the observed catch.

During the 21 cruises, a total of 6115 red endeavour prawns were measured and their CL ranged between 10 and 53 mm. The maximum CL was 42 mm for male and 53 mm for female. All these prawns were clean of bopyrid parasites.

Two forms of growth models

The VBGF has been widely used for modelling growth of prawns, including grooved and brown tiger prawns (Kirkwood and Somers, 1984; Somers and Kirkwood, 1991; Wang and Somers, 1996; Punt *et al.*, 2009), blue endeavour prawn (Buckworth, 1992; Watson and Turnbull, 1993; Park, 1999), red spot king prawn (*Penaeus longistylus* Kubo) (Dredge, 1990), and blue and red endeavour prawns (Park, 1999). We used two forms of VBGF, the standard formula and a modified seasonal growth model. The standard VBGF is expressed as

$$L_t = L_{\inf} \left[1 - e^{-K(t-t_0)}\right], \tag{1}$$

where $L_{\inf}$ is the asymptotic carapace length, L_t is the carapace length at age t, K is the parameter controlling the rate of

growth (also referred to as the growth constant), and t_0 is the theoretical age at zero length. This equation is often applied to size and age data and therefore also requires aging information in addition to length measurements. In this equation, K is assumed to be invariant throughout the year.

Prawn growth may experience seasonal oscillation due to environmental conditions such as seasonal changes in water temperature. By incorporating a seasonal oscillation into the standard VBGF, the seasonal growth model is (Pauly, 1987; Somers, 1988)

$$L_t = L_{\inf} \left\{1 - e^{-[K(t-t_0)+S(t)-S(t_0)]}\right\}, \tag{2}$$

where $S(t) = \frac{CK}{2\pi}\sin[2\pi(t-TS)]$ and $S(t_0) = \frac{CK}{2\pi}\sin[2\pi(t_0-TS)]$. Here, C is a constant (between 0 and 1) indicating the magnitude of the oscillation, and TS (between 0 and 1) defines the beginning of the (positive) sine wave.

Since red endeavour prawns do not change sex during their life cycle and exhibit sexual dimorphism in size, indicating distinguishable growth patterns, the two forms of VBGFs were applied to males and females separately.

Method 1: new ELEFAN tools

We explored the updated ELEFAN tools in R packages TropFishR (Mildenberger *et al.*, 2017), but focused on the functions of ELEFAN_GA_boot() and ELEFAN_SA_boot() in fishboot (Schwamborn *et al.*, 2019) for modelling growth and evaluating model uncertainties.

In the VBGF, variable t is age. However, LFD typically do not have actual age information. Instead, sampling dates are used as t. Using time instead of age has no effect on estimating parameter $L_{\inf}$ and K, but it does not allow for the estimation of parameter t_0 (theoretical age at length zero). ELEFAN implemented in TropFishR and fishboot has the same limit (Pauly, 1987; Mildenberger *et al.*, 2017). This is because the "time" variable in the LFD samples only provides the duration between samplings but does not contain actual age information. This parameter may not have an impact in the application of the growth model, as t_0 is often small for many invertebrates and bony fish. However, this parameter can make a big difference for other species such as sharks. TropFishR returns a t_0 type of parameter called t_{anchor}, which describes the fraction of the year where yearly repeating growth curves cross length equal to zero (Mildenberger *et al.*, 2017). The age of prawns at survey date d is Age[d] = $d - t_{anchor} + t_0$, which cannot be obtained due to identifiability issue. t_{anchor} is related to reproduction time in year, for example, a value of 0.5 refers to 1 July, as larvae hatch around that time with their length close to 0 mm.

We also used the full bootstrap simulations (FBoot) in fishboot to determine the variability in the search algorithm as well as uncertainty in sampling the fish (Schwamborn *et al.*, 2019). In our analysis, we carried out 100 simulations for each ELEFAN_SA and ELEFAN_GA algorithms and obtained statistics for each model's parameters.

The ELEFAN functions in TropFishR and fishboot require upper and lower limits (bounds) for the search space of the growth parameters (referred to as "search condition"), including bounds for all parameters in the VBGF, maximum age, length-class size, and length classes to calculate moving average (nMA). As these initial settings can affect the estimates (Taylor and Mildenberger, 2017), we carried out some sensitivity tests by varying the search conditions.

Method 2: Bayesian approach

The second method using Bayesian techniques involves two steps as described below. It differs from the ELEFAN method in many ways.

Mode identification

The Bayesian approach does not use moving averages to find peaks and troughs in the LFD. Instead, the first step is to fit a multi-normal mixture model (MNMM) to the LFD to determine the mean length and its variance for each age-class in each sample (survey). This step typically requires knowledge of the number of age groups in the length distribution (Schnute and Fournier, 1980; Fournier et al., 1990). This can be difficult for fish species with multiple age classes in each sample (survey), but it is relatively easy for short-lived prawn species because there is only one or two age classes in each sample. Nevertheless, it is still helpful to statistically determine the likely number of length modes. We used a multi-normal mixture model for this purpose (Macdonald and Pitcher, 1979). The MNMM assumes that the length frequency of each age group follows a normal distribution which is commonly assumed in length frequency analysis for fish (Macdonald and Pitcher, 1979; Fournier et al., 1990, 1998; Pons et al., 2019) and prawns (Kirkwood and Somers, 1984; Xu and Mohammed, 1996; Ye et al., 2003).

We used the boot.comp() function in R package mixtools (Benaglia et al., 2009) to identify the possible number of year-classes in each survey, and used the normalmixEM() function to estimate their approximate modes. We verified this set of approximate modes by comparing with LFD plots and then used the verified number of modes as the seed in the normalmixEM() function again to obtain improved estimates. The output from the MNMM include the mean length $L_{d, yc}^{MN}$ (in mm) and its standard deviation(SD) $\sigma_{d, yc}^{MN}$ for each year-class yc on survey date d.

Bayesian growth model (BGM)

In the second step, the BGM integrates MNMM output, including the uncertainty, with prior information using the Bayesian theorem to produce joint posterior distributions for all parameters (Dortel et al., 2015; Zhou et al., 2020).

To estimate growth parameters as well as age information (including t_0 and age at first and consecutive captures for each year-class), we modified equation (1) as

$$L_{d,yc} = L_{\text{inf}} \left[1 - e^{-K\left(t_{1,yc}+d-d_{1,yc}-t_0\right)} \right]. \quad (3)$$

The modal length $L_{d,yc}$ on the left-hand side is a VBGF estimated random variable. This model includes a new parameter $t_{1,yc}$, the age (in year) at first capture for year-class yc. We still used survey date d as the time variable where $d_{1,yc}$ is the first date in a series of surveys when the year-class is captured. In this equation, t_0 retains the property of that parameter in the original VBGF, i.e. it is not t_{anchor} as in TropFishR. Since $t_{1,yc}$ and $d_{1,yc}$ vary among year-classes, with multiple year-classes the LFD enables the model to identify $t_{1,yc}$ and t_0. If there is only one year-class available, it will be difficult to separate out these two confounding parameters.

The output from MNMM, i.e. $L_{d, yc}^{MN}$ and $\sigma_{d, yc}^{MN}$, were used as input into the BGM:

$$L_{d,yc}^{MN} \sim N(L_{d,yc}, \sigma_{d,yc}^{MN}) \quad (4)$$

The following prior distributions were assumed for each parameter:

$$K \sim N(2yr^{-1}, \tau = 0.0001)$$

$$L_{inf} \sim N(maxL, \tau = 0.0000001),$$

where $maxL$ is the observed sex-specific maximum carapace length.

$$t_0 \sim N(0yr, \tau = 1),$$

$$t_{1,yc} \sim N(\frac{m_{d1,yc} - 1}{12}yr, \tau = 1)$$

The mean ages at first capture $t_{1,yc}$ are based on the observation that reproductive activity (i.e. age 0) took place around the beginning of the New Year, where $m_{d1,yc}$ is the month of the first capture for year-class yc. Precision τ can be converted to SD as $SD = 1/\sqrt{\tau}$.

Similarly, the VBGF with seasonal oscillation is

$$L_{d,yc} = L_{inf} \left\{ 1 - e^{-\left[K\left(t_{1,yc}+d-d_{1,yc}-t_0\right)+S(d)-S(t_0)\right]} \right\}, \quad (5)$$

where $S(d) = \frac{CK}{2\pi} sin[2\pi(d - TS)]$. The initial priors for parameter C and TS are

$$C \sim N(0.25, \tau = 1),$$

$$TS \sim N(0.4yr, \tau = 1)$$

where more informative priors with $\tau = 10$ may be needed when data are poor (e.g. for male red endeavour prawns).

The Bayesian growth model was implemented in R (R Core Team, 2021) and JAGS (Plummer, 2003). We ran three MCMC chains, with the first 20000 iterations discarded, and an additional 10000 iterations used for parameter inference. Chain convergence was verified through visual inspection of the MCMC traces as well as the use of the Gelman–Rubin convergence diagnostic. We used deviance information criteria (DIC) and Watanabe–Akaike information criteria (aka widely applicable information criteria, WAIC) (Gelman et al., 2014) to compare the standard and the seasonal VBGF for both male and female prawns.

Validating Bayesian growth model through simulations

It is challenging to estimate all three VBGF parameters (or five parameters in the seasonal oscillation model) using LFD alone. Hence, to validate the BGM method, we carried out a simulation with known parameter values similar to those of male red endeavour prawns as their parameters were more uncertain. Readers are advised not to be confused between the simulation exercise and the previous sections that use real data (from "Study location" to "Method 2: Bayesian approach"). LFD here were generated using equation (1) with the following values: $K = 2$ yr^{-1}; $L_{\text{inf}} = 40$ mm, $t_0 = $ -0.04 yr, age $t = 0$, 1/12, 2/12, …, 18/12 yr (i.e. monthly age from 0 to maximum 1.5 years). $N = 100$ (number of length measurements for each year-class at each sampling time). The length of these prawns followed a normal distribution with mean $L_{d,yc}$ from equation (1) and an $SD = 2.4$ based on the average SD of the LFD from the red endeavour prawns. We assumed that the theoretical prawn CL = 0 mm was on 1 April, i.e. $t_{\text{anchor}} = 3/12 = 0.25$ yr. The intention of this late reproduction time (relative to actual endeavour prawns in Australia, which is around January) was

to enable clearly distinguishing t_{anchor} with true t_0. Assumed monthly surveys were conducted over the period of two years (i.e. a total of 24 surveys), with the first survey on 1 January. Hence, three year-classes were captured: the first cohort was captured in 15 surveys (an incomplete year-class without capturing small prawns), the second cohort was captured in 16 surveys, and the third cohort was captured in 4 surveys (with only young age prawns).

We again used functions in mixtools to identify the number of year-classes in each simulated survey to estimate modal mean and variance. We then used the BGM described above to estimate VBGF parameters K, L_{inf}, t_0, and $t_{1,yc}$, as well as their variances. Three scenarios were tested: assuming the data contain three year-classes, two year-classes, and only one year-class.

Non-informative priors were used for parameters K and L_{inf} ($\tau = 0.0001$ and $\tau = 0.0000001$, respectively). However, since age related parameters, i.e. t_1, and t_0, were difficult to estimate, weak priors were provided ($\tau = 1$). Furthermore, strong informative priors ($\tau = 10$) were also tested.

Model implementation for the simulation study was the same as for the real data analysis described above. The accuracy of BGM was evaluated by relative error

$$RE_\theta = \frac{\hat{\theta} - \theta}{\theta} \%, \qquad (6)$$

where $\hat{\theta}$ is the estimated value for one of the VBGF parameters and θ is the known true value of the same parameter. In the cases when $\theta = 0$, error E was used instead: $E_\theta = \hat{\theta} - \theta$.

Results

Bootstrapped ELEFAN

Sensitivity to search condition

We conducted various tests to evaluate sensitivity of ELEFAN to user defined search conditions. As the condition clearly affected the results in all cases, only one example is presented here. In this case, the standard three-parameter VBGF was implemented using ELEFAN_GA_boot on male red endeavour prawn LFD and the evaluation focused on key parameters L_{inf} and K only. The common search condition, except those specified below, was given as: L_{inf} between 30 and 50 mm CL, t_{anchor} between 0 and 0.2 yr, K between 1 and 4 yr^{-1}, bin size = 1, MA = 5, and maxAge = 2 yr. The tests involved: (1) varying the bounds for L_{inf} where the lower L_{inf} changed from 10 mm to 40 mm CL while the upper L_{inf} was fixed at 60 mm CL; (2) varying the bounds for K where the lower K changed from 0.1 yr^{-1} to 4 yr^{-1} while the upper K was fixed at 5 yr^{-1}; (3) varying bin size from 1 to 3 mm; and (4) varying the number of bins for calculating moving average (nMA) from 5 to 9 length classes. The test results show that the mean L_{inf} and K change as any condition changes (Table 1). The table also includes relative deviations RD, similar to RE in equation (6), of the estimated mean values relative to the corresponding parameter at the first level in the same category (e.g. L_{inf} = 10 mm in the varying lower L_{inf} category). In all cases, L_{inf} was less affected by changing condition than K which can have $RD > 10\%$, likely due to the relatively wider K bounds in the search setting. Although the changes were not considerable in some cases, the test revealed the importance of setting the proper search condition, which was not straightforward for every parameter.

Table 1. Sensitivity of ELEFAN (GA_boot) to search condition.

	L_{inf}	K	RD (L_{inf})	RD (K)
Lower L_{inf} (upper L_{inf} = 60 mm)				
10	36.87	2.92		
20	36.92	2.89	0.1%	−1.0%
30	37.16	2.81	0.8%	−3.8%
40	41.88	1.75	13.6%	−40.1%
Lower K (upper K = 5)				
0.1	36.37	3.18		
1	36.15	3.29	−0.6%	3.6%
2	35.94	3.43	−1.2%	7.9%
3	35.17	3.91	−3.3%	22.9%
4	34.67	4.39	−4.7%	38.0%
Length-class size				
1	36.83	2.92		
2	36.03	3.29	−2.2%	12.8%
3	36.23	3.10	−1.6%	6.0%
nMA				
5	36.83	2.92		
7	36.56	2.99	−0.7%	2.5%
9	36.15	3.10	−1.8%	6.2%

The example applies three-parameter VBGF to male red endeavour prawn length frequency data. The relative deviation $RD = (\theta - \theta_1)/\theta_1 * 100$, where θ is either L_{inf} or K and θ_1 is the first value of the correspond parameter (i.e. on the first row of the same category).

Male red endeavour prawns

After sensitivity tests on search conditions, the following settings were chosen for male prawns: L_{inf} = {30, 50}, K = {1, 4}, t_{anchor} = {0, 0.2}, C = {0, 1}, and TS = {0, 1}. These conditions ensured the likely true parameter values to be around the intermediate boundaries and the bounds were reasonably wide. The estimated parameters and their uncertainties were comparable between the standard VBGF and that with seasonal oscillation, and between the two alternative algorithms (GA and SA) (Table 2). The estimated t_{anchor} at approximately 0.08 year suggested that the peak reproduction (theoretical CL = 0 mm) of male red endeavour prawns took place at the end of January ($0.08 * 356 = 29.2$ days from New Year's Day). The estimated TS around 0.36 indicated that male prawns started to grow faster than the average at $t_{anchor} + TS = 0.08 + 0.36 = 0.44$ years from the New Year, i.e. about 161 calendar days, which was around middle May. The highest growth rate occurred at 0.25 years from that date, i.e. between August and September.

Although GA and SA yielded similar results, the simulated annealing method produced larger uncertainties than the genetic algorithm, even though the search conditions were the same. One potential concern was the effect of the search conditions provided to the methods. For example, the estimated value for each parameter appeared to be close to the mean of the given bounds for that parameter [e.g. L_{inf} = 37 mm is close to the mean of {30, 50} for male red endeavour prawns].

Visually, the fitted curves to the LFD appeared to be good (Figure 2). Adding seasonal oscillation could improve model fitting, which showed that male red endeavour prawns grew faster during later spring (August–September), consistent with the estimated t_{anchor} and TS (Table 2).

Female red endeavour prawns

We used similar search condition as those used for the males except for L_{inf} which was constrained as (40, 60). The estimated growth model parameters and their uncertainties were

Table 2. Parameters of the standard and seasonal oscillation VBGF for male and female red endeavour prawns estimated by ELEFAN using genetic algorithm (GA) and simulated annealing (SA) in fishboot.

	Standard			Seasonal oscillation				
	L_{inf}	K	t_{anchor}	L_{inf}	K	t_{anchor}	C	TS
Male GA								
Mean	36.93	2.90	0.08	37.22	2.66	0.09	0.49	0.37
SD	0.68	0.26	0.03	0.64	0.25	0.03	0.12	0.07
Median	36.88	2.85	0.08	37.38	2.63	0.09	0.51	0.37
L2.5%	35.21	2.48	0.01	36.00	2.20	0.04	0.19	0.26
U2.5%	37.81	3.54	0.13	38.47	3.22	0.15	0.68	0.50
Male SA								
Mean	36.52	3.02	0.05	37.07	2.77	0.08	0.45	0.35
SD	1.08	0.48	0.03	1.08	0.48	0.05	0.21	0.14
Median	36.75	2.87	0.04	37.22	2.68	0.06	0.46	0.35
L2.5%	34.68	2.40	0.00	34.75	2.00	0.00	0.04	0.06
U2.5%	38.05	3.96	0.13	39.46	3.94	0.19	0.87	0.75
Female GA								
Mean	50.79	2.48	0.10	50.49	2.53	0.10	0.37	0.65
SD	1.47	0.33	0.04	1.59	0.34	0.03	0.11	0.21
Median	50.60	2.50	0.09	50.47	2.53	0.09	0.36	0.68
L2.5%	47.91	1.83	0.02	46.95	1.97	0.04	0.15	0.08
U2.5%	55.12	3.27	0.18	53.99	3.36	0.15	0.57	0.97
Female SA								
Mean	51.81	2.28	0.08	51.71	2.35	0.08	0.34	0.71
SD	2.51	0.46	0.07	2.50	0.51	0.05	0.23	0.24
Median	50.99	2.30	0.06	51.49	2.30	0.07	0.30	0.80
L2.5%	47.79	1.49	0.00	45.98	1.53	0.00	0.01	0.04
U2.5%	57.72	3.55	0.20	57.78	3.80	0.19	0.86	0.96
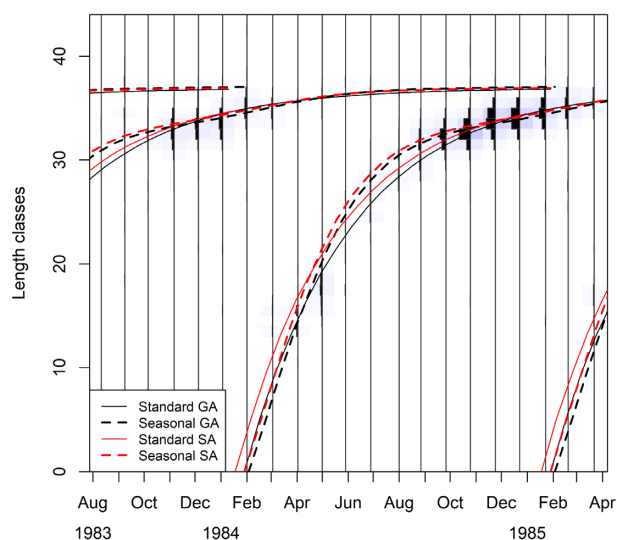
Figure 2. The standard and seasonal VBGF fitted to length frequency distribution of male *M. ensis* using ELEFAN_GA_boot() and ELEFAN_SA_boot() algorithms.
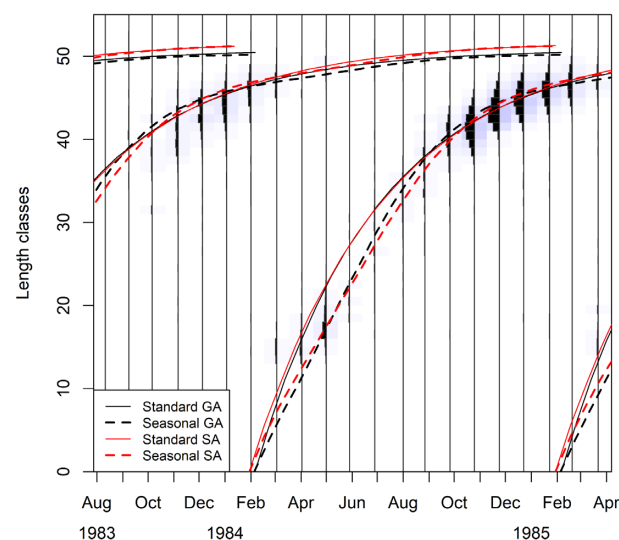
Figure 3. The standard and seasonal VBGF fitted to length frequency distribution of female *M. ensis* using ELEFAN_GA_boot() and ELEFAN_SA_boot() algorithms.

also generally comparable between the standard VBGF and that with seasonal oscillation, and between the two alternative methods (Table 2). However, the SA method tended to produce larger uncertainties than the GA. The SA method also tended to produce a slightly larger L_{inf} and larger TS but a smaller K and smaller t_{anchor} than the GA.

The estimated t_{anchor} was also about 0.08 yr, in line with that for male prawns. However, the estimated TS was much larger, around 0.7 yr, indicating that the highest growth rate occurred between December and January. Both standard and seasonal growth models using either GA or SA fitted to the

LFD reasonably well (Figure 3). The deviation between the standard and seasonal models showed that female red endeavour prawns grew slower in winter and faster in summer.

Bayesian growth model (BGM)

Male red endeavour prawns

Unlike many fish species, the short-lived red endeavour prawns typically have clearly identifiable year-classes in the LFD. The MNMM can easily estimate the parameters of the mode distribution. However, low number of prawns in some

Table 3. Posterior statistics of the standard and seasonal oscillation VBGF for male and female red endeavour prawns from Bayesian growth models.

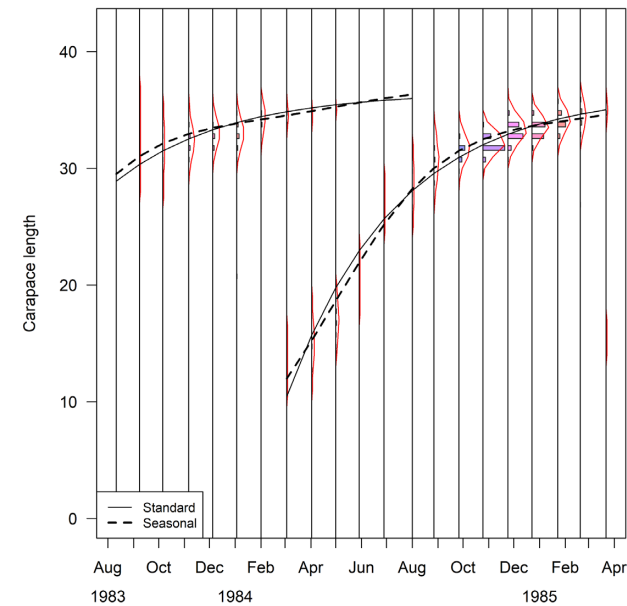|		Standard model			Seasonal model			
	L_{inf}	K	t_0	K	t_0	C	TS
Male							
Mean	36.56	2.74	− 0.02	2.23	− 0.11	0.50	0.48
SD	0.66	0.32	0.28	0.46	0.73	0.24	0.29
Median	36.51	2.73	− 0.01	2.19	− 0.06	0.50	0.48
L2.5%	35.39	2.15	− 0.58	1.46	− 1.65	0.04	0.02
U2.5%	37.98	3.40	0.51	3.24	1.15	0.94	0.97
Female							
Mean	51.81	1.94	− 0.04	1.91	0.00	0.47	0.62
SD	1.09	0.16	0.02	0.29	0.05	0.18	0.09
Median	51.74	1.93	− 0.04	1.89	0.00	0.48	0.62
L2.5%	49.86	1.64	− 0.07	1.42	− 0.09	0.12	0.48
U2.5%	54.11	2.26	0.00	2.55	0.09	0.80	0.77

Figure 4. The standard and seasonal Bayesian growth models fitted to length frequency distribution of male *M. ensis.*

surveys and length truncation due to gear selectivity may bias the estimates in some length modes.

For the standard VBGF, parameters L_{inf} and K were stable and easy to estimate, demonstrated by the non-informative priors and their narrow posterior distributions (Table 3). However, for male prawns, the theoretical age at CL = 0 mm was difficult to obtain. As noted above, the ELEFAN method cannot estimate this parameter from LFD alone. It was also challenging for the Bayesian method, which required an informative prior in this instance [mean = 0 and $SD = 1/\sqrt{10} = 0.32$]. Estimating parameters C and TS in the seasonal oscillation model was also challenging for male prawns. We tried normal, uniform, and beta distributions for these two parameters and found priors had marked influence on the posteriors. For the two fundamental growth parameters, L_{inf} and K, the seasonal oscillation model tended to produce a slightly larger L_{inf} but smaller K than the standard growth model (Table 3).

Visually, both the standard and the seasonal growth models fitted the male LFD fairly well (Figure 4). The seasonal model seemed to cross the distribution modes closer than the standard model. The standard VBGF DIC was 88.4 whereas for

the seasonal model DIC was 87.5, indicating that the more complicated model was more suitable for the LFD than the standard model. Similarly, the WAIC was 87.4 and 83.3 for the standard and the seasonal VBGF respectively, indicating improvement with two additional parameters in the seasonal model.

The ages at first capture for the two cohorts $t_{1,1}$ and $t_{1,2}$, were estimated by the standard VBGF as 0.57 yr old in August 1983 and 0.11 yr old in March 1984. The seasonal model yielded $t_{1,1}$ and $t_{1,2}$ as 0.56 yr old and 0.08 yr old, respectively. The estimated mean TS was 0.48 yr (Table 3). Together with the mean t_0 around -0.06, these values translated into prawn hatching time (age 0) around late January and the fastest growth season around late October. The oldest prawns captured in the surveys were about 18.45 months old for the 1983 cohort and 18.35 months old for the 1984 cohort.

Female red endeavour prawns
Both the standard and the seasonal Bayesian models encountered few difficulties to yield well-behaved posteriors for all parameters, including the t_0, C, and TS, that had been challenging for the male prawns (Table 3). In addition, the estimated parameters were similar between the standard and seasonal models (Table 3).

Again, both standard and seasonal growth models fitted the LFD well (Figure 5). The DIC for the standard VBGF was 115.9 whereas for the seasonal model DIC was 112.2. Similarly, the WAIC was 129.8 and 122.4 for the standard and the seasonal VBGFs, respectively, also an improvement in the seasonal model.

The mean age at first capture for the two cohorts $t_{1,1}$ and $t_{1,2}$, were estimated as 0.56 yr old in August 1983 and 0.08 yr old in March 1984 by both standard and seasonal models. The estimated mean TS was 0.62 yr, later than the males (Table 3). Together with the mean t_0 around -0.02, these values suggested that female prawn hatching time (age 0) peaked around late January and early February, and the fastest growth season was around late November and early December.

Simulation results to validate Bayesian growth model

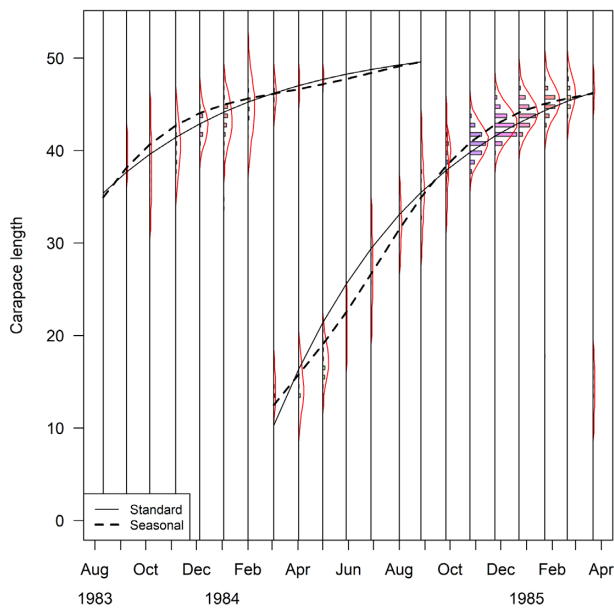We explored three scenarios of available LFD by varying number of year-classes.

Figure 5. The standard and seasonal Bayesian growth models fitted to length frequency distribution of female *M. ensis*.
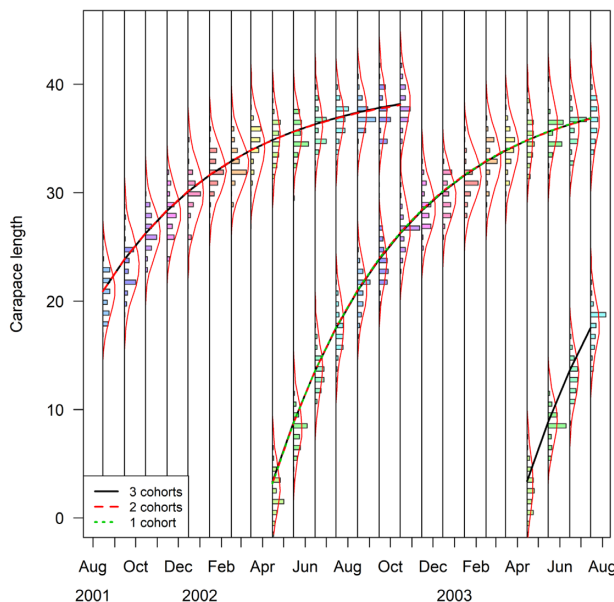

Figure 6. The standard Bayesian growth model fitted to the simulated length frequency distribution. Three scenarios are tested, assuming the data contain three, two, and only one year-class. The posterior K and L_{inf} are almost identical among the three cases, but the estimated age ($t_{1,yc}$, and t_0) differ between the three scenario due to the difference in the amount of LFD data, which does not affect the curves.

Use all three year-class LFD

The LFD modes of the simulated prawns were properly identified by MNMM (Figure 6). With three years of cohorts, the BGM could accurately estimate all parameters (except t_0) even with non-informative priors for K ($\tau = 0.0001$) and L_{inf} ($\tau = 0.0000001$) and weak priors for t_1, ($\tau = 1$) (Table 4). The relative errors were low, generally within 3%. However, estimating t_0 was challenging ($RE = 32.5\%$), where the true value was small (-0.04). Estimation error E (Estimate—True) was calculated for $t_{1,2}$ and $t_{1,3}$, which were -0.01 year for both

ages, instead of relative error because RE could not be calculated when the true value was zero.

Use two year-class LFD

When only two cohorts (one and two year-classes) were available, the BGM could still accurately estimate K and L_{inf} even with non-informative priors. However, age related parameters were less accurate when weak priors were applied, resulting in 30.6% RE for $t_{1,1}$ and -228% for t_0. The estimation error E was 0.10 year for $t_{1,2}$. Using informative priors ($\tau = 10$ or $\sigma = 0.32$) for age related parameters substantially improved the posteriors, reducing RE for $t_{1,1}$ from 30.6% to 0.3%, error for $t_{1,2}$ from 0.10 to 0, and RE for t_0 from -228% to 22.5% (Table 4).

Use only one year-class LFD

The key VBGF parameters K and L_{inf} could still be accurately estimated with non-informative priors when we only used LFD for one cohort (year-class 2) (Table 4). However, estimated age related parameters were poor. Reliable posterior for $t_{1,2}$ could be obtained with a strong prior (error = -0.04), but t_0 was very inaccurate ($RE = 115\%$).

Discussion

This paper compares the performance of two different approaches (ELEFAN and Bayesian) for studying somatic growth of red endeavour prawns based on length frequency data. We applied three methods (ELEFAN_GA_boot, ELE-FAN_SA_boot, and BGM), two types of models (standard VBGF and seasonal oscillation model) to separate sexes (a combination of $3 \times 2 \times 2 = 12$ models). ELEFAN requires users to provide search conditions for each parameter, as well as length-class size and the number of length-class for calculation of the moving average. Our sensitivity tests support the earlier findings that the search settings can significantly affect the results (Taylor and Mildenberger, 2017; Wang *et al.*, 2020). If the condition can be properly determined with some expert knowledge for interested species, ELEFAN can produce similar results as those from Bayesian approaches. For the key VBGF parameters L_{inf} and K, the Bayesian approach could be more reliable than the two ELEFAN methods because of the use of non-informative priors that had little effect on the posteriors.

Another advantage of the Bayesian growth models is their capability to estimate age information, including the theoretical age at length zero, age at first capture, and consecutive ages in each survey time step using length frequency data alone. However, informative priors may be required with limited data. Fewer data (e.g. only one or two cohorts are available) require stronger priors (smaller variance) for some parameters. For example, when the LFD include two year-classes priors on age-related parameters should be carefully constructed to provide relatively narrow distributions (e.g. variance = 0.1 for t_0 and $t_{1,yc}$). Uncertainties in the posterior distributions could hint whether stronger priors are needed and for which parameters. Fortunately, theoretical age at length zero is typically very small and the approximate spawning time is often known for most species so these informative priors can be reliably constructed. To separate parameter t_0 from age at first capture, increasing the number of year-classes in the length measurements can improve the model performance. Many fish species can live several years so length data containing

Table 4. Performance of Bayesian growth model evaluated through simulation.

Param	True	Three year-class, weak		Two year-class, strong		Two year-class, weak		One year-class, strong	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
K	2	1.95	0.28	1.98	0.31	1.98	0.31	1.95	0.43
L_{inf}	40	40.35	1.79	40.21	1.84	40.25	1.84	40.92	3.58
$t_{1,1}$	0.33	0.33	0.15	0.33	0.10	0.43	0.15		
$t_{1,2}$	0	−0.01	0.14	0.00	0.09	0.10	0.14	−0.04	0.09
$t_{1,3}$	0	−0.01	0.14						
t_0	−0.04	−0.05	0.14	−0.05	0.08	0.05	0.14	−0.09	0.08
t_{anchor}	0.25								
RE or E									
K		−2.6%		−0.8%		−1.2%		−2.7%	
L_{inf}		0.9%		0.5%		0.6%		2.3%	
$t_{1,1}$		0.3%		0.3%		30.6%			
$t_{1,2}$		−0.01		0.00		0.10		−0.04	
$t_{1,3}$		−0.01							
t_0		32.5%		22.5%		−228%		115%	
t_{anchor}									

Non-informative priors are assumed for K and L_{inf} in all scenarios while weak ($\tau = 1$) or strong ($\tau = 10$) priors are tested for $t_{1,.}$ and t_0. Relative error RE is calculated for all parameters except for $t_{1,2}$ and $t_{1,3}$ where estimation error E is used instead.

multiple year-classes would be easy to obtain. However, for short-lived invertebrates a time series of surveys extending multiple years may be required.

Aside from methodology, this study presents valuable results for studying growth of red endeavour prawns in Australia and the Indo-Pacific region. There are several studies on growth of red endeavour prawns worldwide. Simple analyses of LFD can be found in early studies, such as measuring the maximum carapace length and growth increment over a period (Cheung, 1964). Recent studies have used modelling tools. Waffy (1990) studied population dynamics of male *M. ensis* in the Gulf of Papua, Papua New Guinea. Length frequency distributions were taken from commercial fishing. The author used an earlier version of the ELEFAN software and obtained VBGF $CL_{inf} = 40.8$ mm and $K = 2.5$ yr^{-1}. Ariyama and Sano (2015) collected LFD of red endeavour prawns (called greasyback shrimp in Japan) from five areas in Osaka Bay from 1992 to 2000. They fitted the seasonally fluctuating von Bertalanffy model to female size-frequency distribution and obtained a wide range of parameters (maximum body length between 139 and 278 mm and K between 0.29 and 3.18 yr^{-1} for difference cohorts). The estimated t_0 was between 2.26 and 9.17 months, which appears to be t_{anchor} rather than theoretical age at length zero. They found that the life span was about two years and the reproductive season was mainly from June or July to September, which is summer in the northern hemisphere (opposite of reproductive timing in Australia). Samphan *et al.* (2016) studied population dynamics of red endeavour prawns in Songkhla Lake in Thailand. They obtained monthly LFD samples for a period of thirteen months from January 2010 to January 2011. Modelling growth was based on total body lengths, using program FiSAT II (Gayanilo *et al.*, 1996). They modelled eight groups of prawns, resulting in total body lengths L_{inf} ranging from 11.81 to 20.05 cm and K from 1.06 to 7.11 yr^{-1}. Unfortunately, there was no information on sex, and it appeared the analysis was based on LFD data combined for males and females. Comparison with our results can be difficult because some of these studies used total body length instead of carapace length, or their ranges were very wide. The result for male *M. ensis* in the Gulf of Papua does look close to our estimates.

The most relevant study is the work by Park (1999) in the NPF. The growth of *M. ensis* was based on monthly research survey in Albatross Bay (the northeast of Gulf of Carpentaria which is opposite side of the Gulf from our study) from 1986 to 1992. The ELEFAN program in FiSAT was applied to model separated growth of males and females using both standard and seasonal VBGF. The estimated model parameters were as follows (carapace length L_{inf} in mm and K in yr^{-1}):

Male : Standard : $L_{inf} = 39$, $K = 1.5$;
  Seasonal : $L_{inf} = 38$, $K = 1.6$, $C = 0.4$, $WP = 0.6$;
Female : Standard : $L_{inf} = 45$, $K = 2.5$;
  Seasonal : $L_{inf} = 46.6$, $K = 1.9$, $C = 0.5$, $WP = 0.7$.

Here WP is the "winter point" (in fraction of year) when growth is slowest ($WP = TS − 0.25$).

These estimates from Albatross Bay deviate from our results. For the males as an example, Park's (1999) estimated L_{inf} is slightly larger than our estimate while K is smaller than ours. The hypothetical age at length zero was assumed to be 0 (in fact this should be t_{anchor} as ELEFAN cannot estimate t_0). Hence, the estimate TS of 0.85 is larger than our estimates. For the females, his L_{inf} is smaller than ours but the average K from the standard and seasonal models is comparable with ours. Again, TS is larger, indicating the fast growth season is around March. In addition to known ELEFAN's vulnerabilities (Issac, 1990; Taylor and Mildenberger, 2017; Wang *et al.*, 2020), the LFD from Albatross Bay surveys were combined over three years into a single year monthly dataset. Such a treatment not only masks the variation between year-classes but also reduces the quantity of data (the number of year-class).

Figures 2–5 show that the growth models with seasonal oscillation appear to fit the LFD better than the standard VBGF. Both DIC and WAIC calculated in the Bayesian models also support the visual observation. The estimated faster growth season in late spring and summer than in winter generally agrees with environmental condition and prawn biology (Somers and Kirkwood, 1991). However, the difference between the standard and seasonal growth models is small as measured by DIC. WAIC is more sensitive (males: 87.4 and 83.3 and females: 129.8 and 122.4 for the standard and seasonal VBGF respectively). The two season-related parameters

(*C* and *TS*) are more difficult to estimate and result in higher uncertainties than growth parameters L_{inf} and *K*. Less variable environmental condition than that in the subtropical and temperate zones [e.g. the mean surface water temperature varied between 23 and 31°C during the Maxim surveys (Somers *et al.*, 1987)] may have enabled continuous somatic growth for prawn species (Buckworth, 1992). Therefore, the results of either the standard or the seasonal oscillation model can be adopted depending on the purpose of their application. For example, the seasonal model may be preferred in stock-assessment with a short time step while the standard model be used in multispecies assessments that only use the standard growth model for all prawn species (Punt *et al.*, 2010).

Our analysis is perhaps the most comprehensive and rigorous growth modelling of red endeavour prawns so far, but there are a few possible weaknesses. First, the sample size is not ideally large. There are insufficient length measurements of large and old prawns. On the other hand, gear selectivity and possibly survey sites eliminated the chance of catching small prawns. Prawns with carapace length smaller than 10 mm are excluded or truncated from the LFD. The length frequency modes of these size groups cannot be detected in the LFD or their shapes may have been distorted. The quality of the data can potentially affect the accuracy of the model output. Moreover, only two year-classes are available from the 21 consecutive surveys. It would be very helpful, particularly for the Bayesian method, if the surveys covered more year-classes.

Although the data collected in the "Maxim surveys" over three decades ago have been used multiple times to study other prawn species, this study is the first time to use the historical data to model the growth of red endeavour prawns. The results can certainly be useful for stock-assessment as stock-assessment models require various types of historical data. However, if fisheries assessment focuses on recent years, one sensible question is whether the biology of the prawns has changed over time. Extensive evidences show that temperature and fishing can cause changes in fish life-history (Baudron *et al.*, 2014; Shan *et al.*, 2017; Audzijonyte *et al.*, 2020; Liu *et al.*, 2021). To address this potential issue, we obtained length frequency data collected in the Scientific Observer program (there has been no monthly survey in the past three decades). Observers onboard commercial fishing vessels measured carapace length of red endeavour prawns from 2011 to 2019 during the fishing season (August to November) in the same region (Northwest Gulf of Carpentaria). The largest measurements were taken in September and October. Hence, we compared these LFD with the data used in this study in the same months for males and females separately. The overlayed histograms exhibit very similar distribution between the two periods (results not shown). The mean carapace lengths between the two periods are nearly identically for males in both months and for females in September. The only noticeable difference is a slightly larger body size for females in October 1983–1984 (mean CL 40.67 mm) vs that of 2011–2019 (39.48 mm). Multiple factors may have contributed to such a 1.2 mm difference, including sampling error, less perfect location and timing between the two periods, although we cannot exclude the possibility that body size of female prawns in October have indeed reduced over time. Nevertheless, assuming spawning time remains unchanged, the small difference in female body size in October would be insufficient to reject the null hypothesis of no change in growth parameters since the 1980s.

Growth information is an essential input for many stock assessments, particularly when the models operate on a finer time step, such as monthly or weekly dynamics (Dichmont *et al.*, 2003, 2008; Punt *et al.*, 2010; Plagányi *et al.*, 2020). For age-aggregated population dynamics models that apply an annual time step, growth information can enhance the assessment when fishing season has changed over time. Since stock assessment models heavily rely on catch data, when fish size in the catch changes during the history of the fishery due to changes in management, catch at different life stages will affect the population dynamics differently. Ignoring size and age difference could bias the subsequential model parameters. For example, the average size of endeavour prawns in the early years tended to be smaller because they were taken earlier in the season. Currently, the Bayesian hierarchical production model (BHPM) is the primary tool for endeavour prawns in the multispecies bio-economic model which is applied every second year to estimate management reference points and provide recommendation on annual total allowable effort (Zhou *et al.*, 2009; Punt *et al.*, 2010). The difference in size has not been considered in the current BHPM, and therefore incorporating the results from this research could enhance the model performance and improve the estimation of the reference points, used in the management of the stock.

Author contributions

SZ led the project, including design, methodology, analysis, and drafting and revising the manuscript. TH aided interpretation of the results. YL performed some modelling and analyses. MM, TV, and RD collected and curated the data. All authors contributed to drafting and revising the manuscript.

Conflict of interest

The authors have no conflicts of interest to declare.

Data availability statement

The data underlying this article were provided by CSIRO by permission. Data will be shared on request to the corresponding author with permission of CSIRO.

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