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Modelling growth of red endeavour prawns (*Metapenaeus ensis*) using new ELEFAN and Bayesian growth models

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Executive summary

Growth information is essential in many fisheries stock assessments. In the Northern Prawn Fishery (NPF), growth has been studied for several major prawn species, including grooved tiger prawns (*Penaeus semisulcatus*), brown tiger prawns (*P. esculentus*), common banana prawn (*P. merguiensis*), red-legged banana prawns (*P. indicus*), and blue endeavour prawns (*Metapenaeus endeavouri*). The red endeavour prawn (*M. ensis*) is a relatively data-poor species and its growth has been studied only once (Park, 1999). The study was a very useful contribution to our knowledge of endeavour prawns in the NPF, but the estimated parameters in Park (1999) were considered "dubious" due to a lack of rigor in data handling and the applied modelling method.

Recent requests to update the red endeavour assessment led to an investigation of previously unused data from a historical series of monthly prawn surveys carried out in the North-Western Gulf of Carpentaria between 1983 and 1985 for estimating growth. Extensive length frequency distribution data (LFD) were collected for all commercial prawn species, including red endeavour prawns. A commercial fishing vessel named "Maxim" was chartered for these surveys. Hence, the dataset was often referred to as the "Maxim surveys". Data collected during the surveys have been previously used for tiger prawn assessments, as these two species are the mainstay of the revenue of the fishery. This historical dataset had not been utilized for modelling growth of endeavour prawns. In this report, this overlooked dataset was used to estimate growth of red endeavour prawns.

We applied two major methods: (1) the classic ELEFAN (Electronical LEngth Frequency ANalysis) implemented in recently developed R packages TropFishR and fishboot, and (2) Bayesian growth models (BGM) developed in this study. We used the new algorithms, ELEFAN_GA (genetic algorithms) and ELEFAN_SA (simulated annealing) included in the two R packages. Since the von Bertalanffy growth function (VBGF) has been widely adopted for modelling prawn species, we also used this form of growth function. Furthermore, we employed two versions of VBGF, the standard 3-parameter model and a seasonal oscillation model that involves two additional parameters. Since male and female red endeavour prawns have different body sizes, all models in this study treat the two sexes separately.

The Maxim surveys provide a time series of LFD, enabling length mode progression analyses. It has been widely recognized that modelling growth from LFD cannot obtain age related information, including the theoretical age at length zero, t_0. This is because the time series of LFD includes survey timing but no actual age information. Our Bayesian growth model attempts to overcome this obstacle so that the model can estimate actual ages, including t_0. The main idea behind the BGM is to use LFD from multiple year-classes. We examined the performance of this new BGM through computer simulation. The results from the simulated synthetic LFD show that the BGM can produce reliable posteriors for VBGF parameters (including ages) when three cohorts are available. When only two cohorts are available, informative priors are needed for age-related parameters. However, it would be difficult to estimate ages when there is only one cohort. In all cases, the key growth parameters, the asymptotic length L_{inf} and the growth coefficient K, can be easily derived.

Our analysis involves a combination of 12 models: 3 methods (GA, SA, and BGM), two forms of VBGF (standard and seasonal), and two sexes. Interestingly, all models lead to comparable results, sex separated. While there are some variabilities amongst the methods and growth functions, the values are more consistent than studies on other prawn species. The seasonal oscillation models fit the LFD data better than the standard VBGF, but are statistically insignificant. For stock assessment and other applications, it is recommended the average estimates from three methods as in Table ES are used.

In the discussion, the results were compared with existing studies on modelling the growth of red endeavour prawns outside Australia and in the NPF. It is fair to state that the current analysis is the most rigorous and reliable to date. Nevertheless, there are several weaknesses in this study concerning data quality and quantities. It would be useful for future studies to simultaneously model LFD data from multiple sources under a hierarchical modelling framework.

Table ES. Recommended growth parameters (mean with sd in parenthesis) for male and female red endeavour prawns. *C* and *ts* are additional parameters from the seasonal oscillation model where *C* measures the magnitude of the oscillation and *ts* defines the beginning of the oscillation wave.

	L_{inf}	K	t_0	C	ts
Male	36.95 (0.91)	2.72 (0.37)	-0.06 (0.50)	0.48 (0.19)	0.40 (0.17)
Female	51.43 (1.80)	2.25 (0.35)	-0.02 (0.03)	0.39 (0.17)	0.66 (0.18)

Introduction

Measures of somatic growth are important for evaluating fish populations, conducting stock assessments, and making informed management decisions. In Northern Australia, thorough modelling of growth has been conducted predominantly using tag-recapture studies for grooved tiger prawns (*Penaeus semisulcatus*) and brown tiger prawns (*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 prawns (*P. indicus*) (Loneragan *et al.*, 2002), and blue endeavour prawns (*Metapenaeus endeavouri*) (Buckworth, 1992; Xiao, 1994; Punt *et al.*, 2010). The growth of red endeavour prawn (*Metapenaeus ensis*) has been studied once (Park, 1999). That study used survey data from Albatross Bay from March 1986 to March 1992. Growth parameters were estimated using an earlier version of ELEFAN (Electronical LEngth Frequency ANalysis) in the FiSAT computer package (Gayanilo *et al.*, 1996) based on monthly measurements of length frequency distribution (LFD) data. Classic and seasonal von Bertalanffy growth curves were fitted to LFD data combined over a 3-year period from March 1986 to December 1988. The study was a very 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, often called greasyback shrimp in other countries, has a wide distribution in the Indo-Pacific Region from Japan to Australia. It is a commercial species but relatively data-poor compared to other prawns such as tiger prawns and blue endeavour prawns. There have been some studies on growth of red endeavour prawns in Asia (Cheung, 1964; Waffy, 1990; Ariyama and Sano, 2015; Samphan *et al.*, 2016). The results from these studies are variable, perhaps due to differences in sampling designs, sample sizes, modelling methods, or geographic locations.

In the early 1980s, a series of monthly prawn surveys were carried out in the North-Western Gulf of Carpentaria north of Groote Eylandt. Extensive length measurements were made for all commercial prawn species, including the two endeavour prawns (Somers *et al.*, 1987). Data collected in these surveys have been previously used for tiger prawn assessments as they are the main target species in the fishery. This historical dataset has not been analysed for modelling growth of endeavour prawns. In this report, we attempt to estimate growth of red endeavour prawns from this overlooked dataset. It is the first step in an inclusive study that aims to develop and enhance stock assessments for red endeavour prawns in the NPF.

Materials and methods

Maxim surveys

A series of prawn surveys were carried out each lunar month between August 1983 and March 1985 in the North-Western Gulf of Carpentaria. A commercial trawler (F.V. Maxim) was chartered for these surveys (hence, the study is often referred to as the "Maxim surveys"). This field study was aimed at grooved and brown tiger prawns but all other prawn species in the catch were also measured and recorded. A detailed description of the surveys was documented in Somers, et al. (1987). Here we summarise some of the text from Somers, et al. (1987) and briefly describe information pertaining to red endeavour prawns.

A total of 21 cruises captured commercial species of penaeids, including both blue and red endeavour prawns. Cruises were carried out every four weeks, each lasted approximately 11 nights centred around the new moon period (i.e., beginning 5 nights before the new moon).

Sampling gears consisted of two 11.0 m (headrope length) trawl nets (Florida Flyer), with internal mesh size (actual mesh opening) averaged 46 mm and the codends 38 mm. 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 Florida Flyer net used in the study was the common gear for commercial prawn fishery in the Gulf. The large mesh size may have low efficiency for catching small prawns. An additional experiment was carried out during the duration of the cruise in December 1984 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 grooved and brown tiger prawns in the starboard codend and those in the codend cover were recorded.

For each sampling (20 min trawl), the prawns from the two nets were identified to species. Individuals were sexed and the carapace length (CL) was measured to the nearest millimetre. The moult stage for each prawn was subjectively classified, and the occurrence of bopyrid parasites was also noted.

The study area encompassed the commercial prawn fishery grounds between Groote Eylandt and Cape Arnhem in the north-western Gulf. Trawl stations were established within a grid design at intervals of approximately 6 nautical miles throughout (Figure 1). Additional stations were established in shallow inshore areas of Northwest Bay and Blue Mud Bay to collect small prawns. The shallow survey trawl-sites were located offshore from the littoral juvenile habitats of key commercial prawn species (Loneragan *et al.*, 1998). Juvenile prawns in the size range of about 2 to 10 mm CL occupy these intertidal and shallow sub-tidal habitats prior to ontogenetic emigration to deeper waters within the coastal embayment where the shallowest of the survey trawls were made. To encompass possible prawn distribution outside the fishing grounds, stations were also established along two east-west transects extended to about 50 km beyond the eastern boundary of the fishery. The stations covered a depth range of 5 to 55 m, whereas the commercial fishery is largely confined to depths between 20 and 40 m.

Data

The Maxim surveys recorded nine prawn species: *Metapenaeus endeavouri*, *M. ensis*, *Penaeus esculentus*, *P. latisulcatus*, *P. longistylus*, *P. merguiensis*, *P. monodon*, *P. semisulcatus*, and *Solenocera australiana*. During the 21 cruises over 100,000 prawns were measured, with largest numbers of grooved and brown tiger prawns recorded (Table 1). A total of 6,115 red endeavour prawns were measured and their carapace length ranged between 10 mm and 53 mm. All these prawns were free of bopyrid parasites.

Data treatment

The commercial trawl with mesh size of 46 mm and the codends 38 mm was more efficient in catching large prawns than catching small individuals. This may affect overall size composition in the catch, but had minimum effect on the mode of the length frequency distribution. Nevertheless, to avoid potential bias, we used relative gear selectivity to correct the under-representation of small prawns. Gear selectivity was estimated based on the data (Somers *et al.*, 1987) from the on-board experiment in Maxim cruises where a 25 mm stretch mesh codend was rigged to the outside of the normal codend. The selectivity for carapace length CL, S_{CL}, was estimated as (Figure 2):

$$S_{CL} = \frac{1}{1+e^{3.94+0.30CL}}. \quad (1)$$

The standard errors for the two parameters are 0.486 and 0.023 respectively. S_{CL} in equation (1) was used to adjust each prawn by measured CL, i.e., $\hat{C}_{CL} = \frac{C_{CL}}{S_{CL}}$, where C_{CL} is the observed catch of prawns with size CL, and $\hat{C}_{CL}$ is the estimated catch for this size of prawns when corrected for selectivity.

Another potential concern is the complete exclusion of prawns smaller than about 10 mm CL. A truncated size frequency distribution may be detected for young age classes, generally in March and April surveys. The missing size may bias the mode of the length frequency distribution for that age class. However, prawns < 10 mm CL are considered juvenile prawns and are common within littoral habitats adjacent to the shallow sites trawled by the F.V. Maxim (Loneragan *et al.*, 1998). Hence, large numbers of 10 mm CL prawns would not be expected to be found in deeper habitats sampled by F.V. Maxim. To correct any sampling issue due to mesh size, we assumed that LFD has a normal distribution for each age class so the missing small prawns should mirror those larger individuals in the same age group. Specifically, we first found the mode and the minimum of the LFD. We then filled in prawns smaller than the minimum (i.e., missing ones at the lower tail of the normal distribution) by the mirroring distribution of those at the upper tail of the normal distribution.

Methods for estimating growth

Two forms of growth models

The von Bertalanffy growth function (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 prawns (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

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

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):

$$L_t = L_{inf}\left\{1 - e^{-[K(t-t_0)+S(t)-S(t_0)]}\right\}, \quad (3)$$

where $S(t) = \frac{CK}{2\pi} sin[2\pi(t - ts)]$, 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.

Method 1: updated ELEFAN

The first method we used is the updated version of the ELEFAN method in R package "TropFishR" (Mildenberger *et al.*, 2017). The original ELEFAN system was developed in the early 1980s (Pauly, 1987; Pauly and Morgan, 1987), which contains several computer programs to conduct stock assessment based on length frequency data. Amongst these programs, ELEFAN I is used to estimate growth parameters of fish or invertebrates based on modal progression in the length frequency distribution (LFD). In this method, time series (e.g., month-by-month samples) of LFDs are sequentially arranged. A high-pass filter, a moving average of the LFD (e.g., 5 bins), is used to identify peaks and troughs in each and all of the time series samples. The frequencies of the LFD that reach above the moving average are detected as peaks and those that are below the moving average are detected as troughs. A VBGF is then fitted to the identified peaks, where the number of peaks that are crossed by the VBGF curve is accumulated as positive points while the troughs crossed by the curve as negative points. The program then searches for the VBGF parameters that lead to the highest positive scores and lowest negative scores.

Earlier software for implementing ELEFAN, including the most widely used FiSAT (Gayanilo *et al.*, 1996), has limitations in their ability to import data and perform automated analyses. The TropFishR package allows further expansion and flexibility. More importantly, it includes two more powerful optimisation 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 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.

In VBGF (equation 2), variable t is age. However, length frequency data often 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 in the VBGF (theoretical age at length zero). Both ELEFAN and TropFishR have the same limit (Pauly, 1987; Mildenberger *et al.*, 2017). This is because the "time" variable in the LFQ sample data 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 may be 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. The age of prawns at survey date d is: Age[d] = $d - t_{anchor} + t_0$. Because the method cannot separate t_{anchor} and t_0, actual age cannot be obtained from LFD. t_{anchor} is related to reproduction time, for example a value of 0.5 refers to July 1st, when larvae are hatched around that time with their length close to 0.

Model sensitivity to search condition

To implement ELEFAN in TropFishR (or other computer programs) the R functions require confinement in the search space for the growth parameters (we refer this to "search condition", Table 2), including ranges for all parameters in the VBGF, maximum age, and the number of LFD bins to calculate moving average. These initial settings can affect the estimates (Taylor and Mildenberger, 2017). We carried out some sensitivity tests by setting varying ranges of search condition for L_{inf} and K in both standard and seasonal growth models.

Bootstrapped ELEFAN

After exploring possible parameter space, we chose reasonable search conditions for formal growth modelling. ELEFAN software, including TropFishR, only produces a single set of VBGF parameters. These programs cannot assess the uncertainty inherent of the method, or to obtain confidence intervals for growth parameters within an unconstrained search space. Furthermore, it is possible that the ELEFAN_SA and ELEFAN_GA algorithms may be prone to the attraction effects of local maxima, where the strength of these effects will depend on the algorithm settings used. Recently, a new, robust, bootstrap-based TropFishR has been developed in R package "fishboot" (Schwamborn *et al.*, 2019) and this package was used in our analysis. In particular, we used the full bootstrap simulations (FBoot). This method considers the variability in the search algorithm as well as uncertainty in sampling the fish. In each simulation, the routine randomly resamples length data from LFDs and fits the growth model with a different random seed value. In this analysis, we carried out 100 simulations for each ELEFAN_SA and ELEFAN_GA algorithms. Statistics for each model parameter (i.e., mean, sd, min, max) were obtained from the 100 simulation outputs.

Method 2: Bayesian approach

The second method using Bayesian technique differs from the ELEFAN method in many ways. First, it does not use moving averages to find peaks and troughs in the LFD data. Instead, it fits 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). Second, it integrates MNMM output, including the uncertainty, with prior information by the Bayesian theorem to produce joint posterior distributions for all parameters (Dortel *et al.*, 2015; Zhou *et al.*, 2020).

Identifying length modes

Modelling growth based on LFD typically requires knowledge of the total number of age groups in the length distribution (Schnute and Fournier, 1980; Fournier *et al.*, 1990). This can be very difficult for fish species with multiple age classes in each dataset (survey) due to length overlap from several age classes, particularly when fish become old. However, for short-lived prawn species, it is relatively easy to identify age classes because there are only one or two age classes in each sample. Nevertheless, it is still helpful to determine the length modes statistically before applying the growth model. We used a multinormal 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 first used the boot.comp() function in R package mixtools to identify possible number of year-class 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 corrected number of modes as the seed in the normalmixEM() function again to obtain improved estimates. The output from the MNMM include the mean length $L_{d,yc}^{MN}$ and its standard deviation $\sigma_{d,yc}^{MN}$ for each year-class *yc* on survey date *d*.

Bayesian growth model (BGM)

The results of ELEFAN can be strongly affected by the prior parameter settings. Our focus of this study is to develop a Bayesian growth model that not only produces more stable results but also allow estimation of t_0 and age at first and consecutive captures for each year-class. We modified equation (2) as:

$$L_{d,yc} = L_{inf}\left[1 - e^{-K(a_{1,yc}+d-d_{1,yc}-t_0)}\right]. \quad (4)$$

This model includes a new parameter $a_{1,yc}$, the age 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 $a_{1,yc}$ and $d_{1,yc}$ vary among year-classes, the idea is to use multiple year-classes, enabling the model to identify $a_{1,yc}$ and t_0. If there is only one year-class available, it would be difficult to separate out $a_{1,yc}$ and t_0.

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

$$L_{d,yc} \sim N(L_{d,yc}^{MN}, \sigma_{d,yc}^{MN}). \quad (5)$$

The following prior distributions were assumed for the parameters:

$K \sim N(mean = 2, \tau = 0.0001)$,

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

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

$a_{1,\cdot} \sim N(mean = \mathrm{c}(0.6, 0.16, 0.2), \tau = 1)$.

The symbol "·" indicates any number of year-class. The mean ages at first capture were based on the assumption that reproductive activity (i.e., age 0) took place around the beginning of the New Year. Precision τ can be converted to standard deviation as $sd = 1/\sqrt{\tau}$.

Similarly, the VBGF with seasonal oscillation is

$$L_{d,yc} = L_{inf}\left\{1 - e^{-\left[K\left(a_{1,yc}+d-d_{1,yc}-t_0\right)+S(d)-S(t_0)\right]}\right\} \quad (6)$$

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

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

$ts \sim N(mean = 0.4, \tau = 1)$

Where more informative priors with $\tau = 10$ may be needed for the male prawns.

Model implementation

The Bayesian growth model was implemented in R (R Core Team, 2019) and JAGS (Plummer, 2003). We ran three MCMC chains, with the first 20 000 iterations discarded, and an additional 10 000 iterations used for parameter inference. Chain convergence was verified through visual inspection of the MCMC trace as well as the use of the Gelman-Robin diagnostic.

Validating BGM through simulations

It is challenging to estimate all three VBGF parameters (or 5 parameters in the seasonal oscillation model) using LFD data alone. Hence, to validate the BGM method, we carried out a simulation in which we input known parameter values similar to those of male red endeavour prawns. LFD data were generated using equation (1) with the following values:

K = 2 yr^{-1}; L_{inf} = 40 mm, t_0 = -0.04 yr, age t = 0, 1/12, 2/12, …, 18/12 (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 a sd = 2.4 based on the average sd of the LFD from the red endeavour prawns. We assumed the theoretical prawn carapace length CL = 0 was on April 1st, i.e., t_{anchor} = 3/12 = 0.25. The intention of this late reproduction time (relative to true endeavour prawns in Australia, which is around January) was to enable clearly distinguishing t_{anchor} with true t_0. Monthly surveys were conducted over the period of two years, with the first survey on January 1st. 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 covered 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 number of year-class in each survey to estimate modal mean and variance. We then used the BGM described above to estimate K, L_{inf}, t_0, and $a_{1,yc}$, as well as their variances. Three scenarios were tested: assuming the data contain three year-classes, two year-classes, and only one year-class.

We ran the Bayesian growth model with the simulated data in the similar way as for the real red endeavour prawns, i.e., three MCMC chains, with the first 20 000 iterations discarded, and an additional 10 000 iterations used for parameter inference. Chain convergence was verified through visual inspection of the MCMC trace as well as the use of the Gelman-Robin diagnostic.

It would be interesting to see how ELEFAN performs on simulated data. Therefore, we applied ELEFAN_GA_boot() to all three year-classes and ran the bootstrap 100 times.

The accuracy of BGM and ELEFAN was evaluated by relative error:

$$RE_\theta = \frac{\hat{\theta} - \theta}{\theta}\%$$

Where $\hat{\theta}$ is the estimated value for one of the VBGF parameters and θ is the known true value of the same parameter.

Results

Bootstrapped ELEFAN

Since male and female prawns have clearly distinguishable growth patterns, they were modelled separately.

Male red endeavour

The LFD clearly show one or two year-classes in most of the surveys, but they are less clear in some months (Figure 3). The estimated growth model parameters (Table 3) and their density distribution (Figure 4) were comparable between the standard VBGF and that with seasonal oscillation, and between the two alternative algorithms (GA and SA). The estimated t_{anchor} around 0.08 suggested that the peak reproduction (theoretical carapace length = 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 (0.37 by GA and 0.35 by SA) indicated that 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 is around middle May. The highest growth rate occurred at 0.25 years from that date, i.e., between August-September.

Although GA and SA methods yielded similar results, the simulated annealing method tended to produce 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 range for that parameter (e.g., L_{inf} = 37 mm is close to the mean of {30, 50} for male red endeavour in Table 2).

As expected, the estimated *K* and L_{inf} were negatively correlated with a high correlation coefficient (Figure 5). Correlations among other parameters were generally mild, although some were statistically significant.

Visually, the fitted curves to the LFD appeared to be good (Figure 6). 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 3).

Female red endeavour

The LFD modal progression of female red endeavour prawns looked similar to those of male prawns (Figure 7). One noticeable difference was the truncation of carapace length smaller than 12 mm (e.g., survey number 8, 9, and 21 in Figure 7). The estimated growth model parameters (Table 3) and their density distribution (Figure 8) were generally comparable between the standard VBGF and that with seasonal oscillation, and between the two alternative methods (GA and SA). 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, in line with that for male prawns. However, the estimated *ts* was much larger, around 0.7, indicating that the highest growth rate occurred between December-January.

The estimated K and L_{inf}, but not the other parameters, were also highly correlated for female prawns (Figure 9). Correlations among other parameters were generally mild, although some were statistically significant. Both standard and seasonal growth models using either GA or SA fitted to the LFD reasonably good (Figure 10). The deviation between the standard and seasonal models showed that female red endeavour prawns grew slower in winter and faster in summer.

Model sensitivity to search condition

We conducted various tests to evaluate sensitivity of ELEFAN_GA and ELEFAN_SA algorithms to user defined search conditions. As the condition clearly affects the results in all cases, only one example is presented here. In this case, the standard 3-parameter VBGF was implemented using ELEFAN_GA on male red endeavour LFD. The search condition was given as: L_{inf} between 40 and 50 mm, t_{anchor} between 0 and 0.5, upper K = 4, while lower K varied from 1.1 to 2.0 yr^{-1} with a step of 0.1. The test results show that as the lower K increases (i.e., search space narrows toward large K ranges), the estimated L_{inf} declines but the estimated K and t_{anchor} tend to increase (Figure 11). Although the changes are not considerable, this test reveals the importance of setting the right search condition, which isn't straightforward for every parameter.

Bayesian growth model (BGM)

Male red endeavour prawns

Unlike many fish species, the short-lived prawns typically have clearly identifiable year-classes in the LFD. The MNMM can easily estimate the parameters of the mode distribution (Figure 12). One or two modes can be identified in each survey. There were two modes from Survey No. 8 to Survey No. 13. However, low number of prawns in some surveys and length truncation due to gear selectivity or the shallow-littoral residence of small prawns (juveniles) 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 distributions (Figure 13). However, for male prawns, the theoretical age at CL = 0 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 (e.g., mean = 0 and sd = 1/sqrt(10) = 0.32). Estimating parameters C and ts in the seasonal oscillation model was also challenging for male red endeavour prawns. We tried both 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).

Correlations among the parameters were similar to the results from ELEFAN (Figure 14). Again, the K and L_{inf} were highly correlated while C, the scale of the seasonal oscillation, also had a significant inverse correlation with K and positive correlation with L_{inf}, suggesting that overestimating K or underestimating L_{inf} may lead to underestimating C.

Visually, both the standard and the seasonal growth models fitted the male LFD fairly well (Figure 15). The seasonal model seemed to cross the distribution modes closer than the standard model. The deviance information criterion (DIC) for the standard VBGF was 88.4 whereas for the seasonal model was 87.5, indicating that the more complicated model made insignificant improvements statistically.

The ages at first capture for the two cohorts $a_{1,1}$ and $a_{1,2}$, were estimated by the standard VBGF as 0.57 years old in August 1983 and 0.11 years old in March 1984. The seasonal model yielded $a_{1,1}$ and $a_{1,2}$ as 0.56 years old and 0.08 years old, respectively. The estimated mean *ts* was 0.48 (Table 4). 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

Females had a larger body size than male prawns. One or two modes can be identified in each survey. There were two modes from Survey No. 8 to Survey No. 14. There was an identifiable mode in one more survey than the males: survey 14, the week of 27 August 1984 (Figure 16). 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 (Figure 17). In addition, the estimated parameters were similar between the standard and seasonal models (Table 4).

Correlations among the parameters were generally comparable with those for male prawns (Figure 18). One noticeable difference was that parameter *C* had a weaker correlation with *K* and L_{inf}, and instead *ts* had a stronger correlation with these two key parameters.

Again, model fits for both standard and seasonal growth models did not show suspicious behaviour (Figure 19). The DIC for the standard VBGF was 115.9 whereas for the seasonal model was 112.2, meaning statistically insignificant difference.

The mean age at first capture for the two cohorts $a_{1,1}$ and $a_{1,2}$, were estimated as 0.56 years old in August 1983 and 0.08 years old in March 1984 by both standard and seasonal models. The estimated mean *ts* was 0.62 years, later than the males (Table 4). 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

We explored three scenarios: (1) all 3 year-class LFD data were available; (2) only the first and the second year-class LFD data were available; and (3) only the second year-class LFD data were available. Non-informative priors were used for parameters *K* and L_{inf} (τ = 0.0001 and τ = 0.0000001, respectively). However, since age related parameters, i.e., $a_{1,\cdot}$ and t_0, were difficult to estimate, weak priors were provided (τ = 1). Furthermore, strong informative priors (τ = 10) were also tested.

Use all 3 year-class LFD

The LFD modes of the simulated prawns were properly identified by MNMM (Figure 20). With three years of cohorts, the Bayesian growth model could accurately estimate all parameters, including age at first capture even using weak priors for these parameters (Table 5). The relative errors were low, generally within 3%, except t_0 where the true value was small (-0.04). Estimation errors (Estimate – True) were calculated for $a_{1,2}$ and $a_{1,3}$, which were -0.01 for both ages, instead of relative error because RE could not be calculated when the true value was zero.

Use 2 year-class LFD

When only two cohorts were available, the Bayesian model 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% relative error for $a_{1,1}$ and -228% for t_0. The estimation error (Estimate – True) was 0.10 for $a_{1,2}$.

Using informative priors ($\tau = 10$ or $\sigma = 0.32$) for age related parameters substantially improved the posteriors, reducing RE for $a_{1,1}$ from 30.6% to 0.3%, error for $a_{1,2}$ from 0.10 to 0, and RE for t_0 from -228% to 22.5% (Table 5).

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. However, estimating age related parameters was challenging. Reliable posterior for $a_{1,2}$ could be obtained with a strong prior (error = -0.04), but t_0 was poor (RE = 115%).

Applying ELEFAN to all 3 year-class LFD

We also evaluated the performance of ELEFAN method using simulated data. An example of using ELEFAN_GA_boot() was included in Table 5. In this case, sensible parameter search space was provided: L_{inf} from 30 to 50, K from 1 to 3, t_{anchor} from 0 to 0.5, and maximum age = 2 years. The program produced reasonably accurate estimates for K and L_{inf}, while under-estimated t_{anchor} by 21.4%.

Comparison of methods and models

In this study, we applied three methods (ELEFAN_GA_boot, ELEFAN_SA_boot, and BGM), two types of models (standard VBGF and seasonal oscillation model) to separate sexes of red endeavour prawns (a combination of 3*2*2 = 12 models). It might be demanding to assess and compare all results in Table 3 and Table 4. To assist readers understanding the differences among the models, we visually summarized the results in Figure 21 for male prawns and Figure 22 for female prawns.

Overall, results were similar across methods and models. The Bayesian approach tended to yield a slightly smaller K, which could be more reliable than the ELEFAN method because the non-informative priors had little effect on the posteriors. As the differences were not considerable, the average values from all methods and models could be used for stock assessments (Table 6). Note that the theoretical age at length 0, t_0, was averaged from BGMs only because ELEFAN method can only produce t_{anchor}.

Discussion

This report presents a comprehensive study on somatic growth of red endeavour prawns based on length frequency data. We have used the classic ELEFAN method implemented in recently developed TropFishR and fishboot packages in R. The genetic algorithm (GA) and simulated annealing (SA) are considered more robust than the traditional search procedures of response surface analysis (RSA) (which varies both *K* and L_{inf}) and *K*-Scan (which holds L_{inf} constant while varying *K*) (Mildenberger *et al.*, 2017; Taylor and Mildenberger, 2017). The bootstrap procedure further enables an assessment of uncertainty inherent of the ELEFAN method and obtaining confidence intervals for growth parameters (Schwamborn *et al.*, 2019). We have also developed a Bayesian growth model that allows estimating ages, including the theoretical age at length zero, age at first capture, and consecutive ages in each survey time step using length frequency data alone.

There are several studies on red endeavour growth 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 between March and October, 1988. The author used earlier version of 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 the FAO-ICLARM Stock Assessment Tools II (FiSAT II) (Gayanilo *et al.*, 1996). They modelled eight groups of prawns, resulting in 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 from males and females. Comparison with our results can be difficult because some of these studies used total 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 study most relevant to our analyses is the work by Park (1999) in the NPF. The growth of *M. ensis* was based on monthly research survey in Albatross Bay from 1986 to 1992. 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:

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" when growth is slowest (WP = ts – 0.25).

These estimates from Albatross Bay deviate from our results. For the males as an example, his 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. This may be in line with the peak spawning of *M. ensis* between September and December in Albatross Bay (Park, 1999).

The ELEFAN method may be vulnerable to various sources of uncertainty, such as gear selectivity, individual growth variability, absence of large individuals, parameter tuning, the reliability of optimization algorithms, and the selection of class interval of length frequency data (bin size) (Issac, 1990; Taylor and Mildenberger, 2017; Wang *et al.*, 2020). In addition to these concerns, it seems the LFD data from Albatross Bay surveys were combined over 6 (or 3) 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).

To interested readers, we can have a comparison of our work with blue endeavour prawns (*M. endeavouri*) in the NPF. It appears that red endeavour prawns reach a larger size but with similar growth rate. For example, the average growth parameters from summer and winter models for blue endeavour prawns are: L_{inf} = 31.655 mm and K = 3.016 yr^{-1} for males and L_{inf} = 43.495 mm and K = 1.534 yr^{-1} for females (Buckworth, 1992). A size-structured assessment model results in somewhat different values: L_{inf} = 33.26 mm and K = 2.496 yr^{-1} for the males and L_{inf} = 30.67 mm and K = 1.924 yr^{-1} for the females.

For blue endeavour prawns, estimating growth using tagging data may be more reliable than using LFD. We have also examined blue endeavour prawn LFD from the Maxim surveys. Their modes are less clear than that for the red endeavour prawns. Consequently, fitting the VBGF to such data is poorer than the results of the red endeavour prawns. We provide an example for the male blue endeavour prawns analysed by using ELEFAN_GA_boot and ELEFAN_SA_boot. The mean parameters are as follows: L_{inf} = 32.98, K = 2.15, t_{anchor} = 0.11, C = 0.45, and ts = 0.45. Although the estimated parameters do not appear to be unrealistic, we recommend that the earlier studies on blue endeavour growth based on tagging data and the size-structured assessment model should be preferred.

Although our analysis is perhaps the most comprehensive and rigorous growth modelling of red endeavour prawns, 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 eliminate the chance of catching small prawns, even though the Maxim surveys intentionally added stations in shallow inshore areas of Northwest Bay and Blue Mud Bay to collect small prawns. Apparently, prawns with carapace length smaller than 10 mm are excluded or truncated from the LFD. From an ontogenetic perspective, small red endeavour prawns ≤ 10 mm CL were not expected to be abundant within the habitats sampled by F.V. Maxim, despite some trawl sites being close inshore. Staples *et al.* (1985) found juvenile red endeavour prawns in a range of intertidal and shallow-subtidal littoral habitats in the Embley River estuary, north east GoC, along with other penaeid species. In the same estuary, Vance *et al.* (2002) identified juvenile *M. ensis* from 2 to 15 mm CL inhabiting intertidal mangrove forest/mudbanks. Ontogenetic emigration from intertidal and shallow-subtidal juvenile nursery habitats to deeper subtidal habitats has been identified as characteristic of commercial penaeid prawns throughout the Gulf of Carpentaria (Staples, 1980; Vance *et al.*, 1996; Loneragan *et al.*, 1998). Hence, many individual red endeavour prawns of about 10 mm CL would not yet have migrated from intertidal to nearshore habitats where they were available for capture during the Maxim surveys. 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 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 cover more year-classes. Further studies could simultaneously model LFD data from Albatross Bay surveys and the Maxim surveys under a hierarchical modelling framework.

The historical data used in this study were collected nearly four decades ago. One sensible concern 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. Observers onboard commercial fishing vessels measured carapace length of red endeavour prawns from 2011 to 2019 in the same region as the Maxim surveys (Northwest Gulf of Carpentaria). The largest measurements were taken in September and October. Hence, we compared these LFD with the Maxim survey samples in the same months for male and female separately. The overlayed histograms exhibit very similar distribution between the two periods (Figure 23). The only noticeable difference is a slightly larger body size for female red endeavour prawns in October 1983-1984 (mean CL 40.67mm with 39.48mm). Multiple factors may have contributed to such a 1.2mm 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 have indeed reduced over time. Nevertheless, assuming spawning time remains unchanged, the small difference in female body size would be insufficient to prevent rejecting the null hypothesis of no change in growth parameters since 1980s.

Growth information is an essential input for many stock assessments, particularly when the models operate in a fine 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 (Zhou *et al.*, 2009; Punt *et al.*, 2010). The difference in size has not been considered in the current BHPM. Incorporating the results from this report could enhance the model performance and improve the estimation of the reference points, used in the management of the stock.

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Table 1. Measurement of nine species of prawns during the Maxim surveys in the NW Gulf of Carpentaria from August 1983 to March 1985.

Species	Common name	Sample size	Min size (mm)	Max size (mm)
Metapenaeus endeavouri	Blue endeavour	12,401	10	48
Metapenaeus ensis	**Red endeavour**	**6,115**	**10**	**53**
Penaeus esculentus	Brown tiger	32,782	11	55
Penaeus latisulcatus	Western King prawn	775	15	51
Penaeus longistylus	Redspot king prawn	360	16	54
Penaeus merguiensis	Common banana	2,146	17	53
Penaeus monodon	Black tiger	19	28	79
Penaeus semisulcatus	Grooved tiger	36,912	11	58
Solenocera australiana	Coral prawn	8,645	8	48
Total		100,155	8	79

Table 2. Red endeavour prawn prior parameter ranges (search condition) provided for ELEFAN analysis in TropFishR and fishboot.

	Male		Female	
	Lower	Upper	Lower	Upper
L_{inf} (mm)	30	50	40	60
K (yr^{-1})	1	4	1	4
t_{anchor} (yr)	0	0.2	0	0.2
C	0	1	0	1
ts	0	1	0	1
Max age (yr)	2		2	

Table 3. 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 TropFishR and 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

Table 4. Parameters of the standard and seasonal oscillation VBGF for male and female red endeavour prawns estimated by Bayesian growth models.

	Standard model			Seasonal model				
	L_{inf}	*K*	t_0	L_{inf}	*K*	t_0	*C*	*ts*
Male								
mean	36.56	2.74	-0.02	37.42	2.23	-0.11	0.50	0.48
sd	0.66	0.32	0.28	1.31	0.46	0.73	0.24	0.29
median	36.51	2.73	-0.01	37.23	2.19	-0.06	0.50	0.48
L2.5%	35.39	2.15	-0.58	35.41	1.46	-1.65	0.04	0.02
U2.5%	37.98	3.40	0.51	40.54	3.24	1.15	0.94	0.97
Female								
mean	51.81	1.94	-0.04	52.01	1.91	0.00	0.47	0.62
sd	1.09	0.16	0.02	1.62	0.29	0.05	0.18	0.09
median	51.74	1.93	-0.04	51.86	1.89	0.00	0.48	0.62
L2.5%	49.86	1.64	-0.07	49.25	1.42	-0.09	0.12	0.48
U2.5%	54.11	2.26	0.00	55.60	2.55	0.09	0.80	0.77

Table 5. Performance of ELEFAN_GA and Bayesian growth model evaluated using simulation.

		TropFishR	3 ycs, weak		2 yc, strong		2 yc, weak		1 yc, strong	
Param	True	GA_boot	Mean	sd	Mean	sd	Mean	sd	Mean	sd
K	2	2.01	1.95	0.28	1.98	0.31	1.98	0.31	1.95	0.43
L_{inf}	40	40.99	40.35	1.79	40.21	1.84	40.25	1.84	40.92	3.58
$a_{1,1}$	0.33		0.33	0.15	0.33	0.10	0.43	0.15		
$a_{1,2}$	0		-0.01	0.14	0.00	0.09	0.10	0.14	-0.04	0.09
$a_{1,3}$	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	0.20								
	Relative error									
K		0.7%	-2.6%		-0.8%		-1.2%		-2.7%	
L_{inf}		2.5%	0.9%		0.5%		0.6%		2.3%	
$a_{1,1}$			0.3%		0.3%		30.6%			
$a_{1,2}$			-0.01		0.00		0.10		-0.04	
$a_{1,3}$			-0.01							
t_0			32.5%		22.5%		-228%		115%	
t_{anchor}		-21.4%								

Table 6. Estimated mean VBGF parameters from three methods (ELEFAN_GA, ELEFAN_SA, and BGM) and two models (standard and seasonal) for male and female red endeavour prawns. The theoretical age at length 0, t_0, is averaged from BGMs only because ELEFAN method cannot produce this parameter.

	L_{inf}	K	t_0	C	ts
Male					
mean	36.95	2.72	-0.06	0.48	0.40
sd	0.91	0.37	0.50	0.19	0.17
median	36.99	2.66	-0.03	0.49	0.40
L2.5%	35.24	2.11	-1.11	0.09	0.12
U2.5%	38.72	3.55	0.83	0.83	0.74
Female					
mean	51.43	2.25	-0.02	0.39	0.66
sd	1.80	0.35	0.03	0.17	0.18
median	51.19	2.24	-0.02	0.38	0.70
L2.5%	47.96	1.65	-0.08	0.10	0.20
U2.5%	55.72	3.13	0.05	0.74	0.90

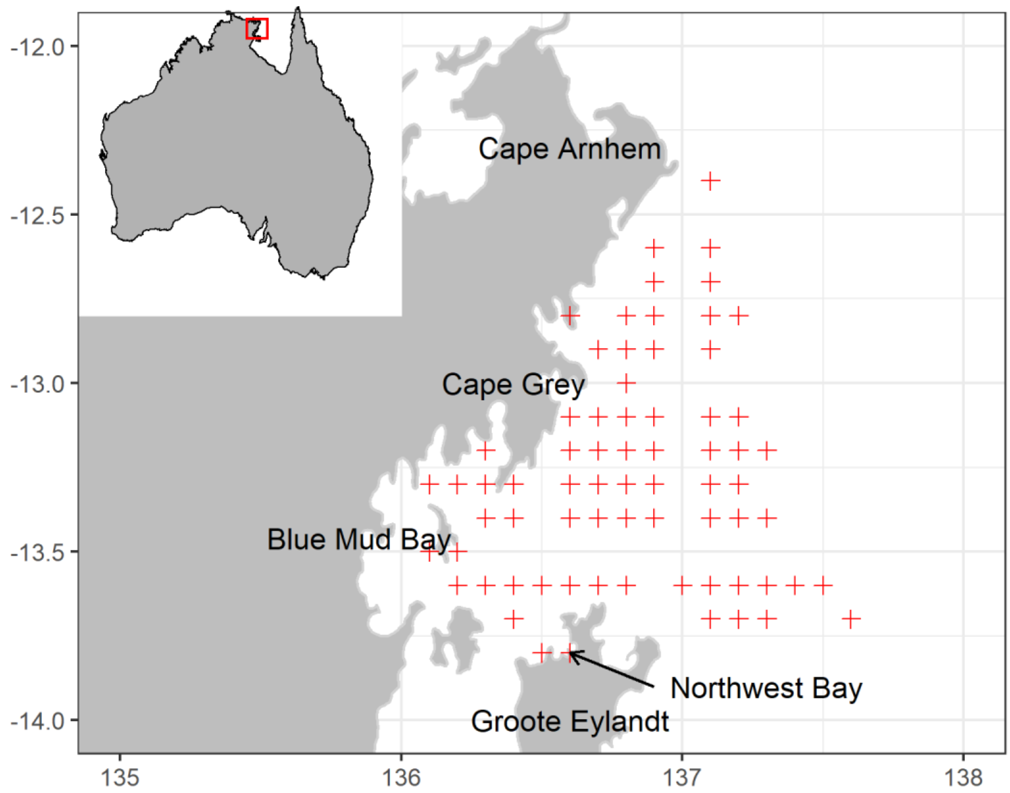

Figure 1. Maxim survey stations in the north-western Gulf of Carpentaria.

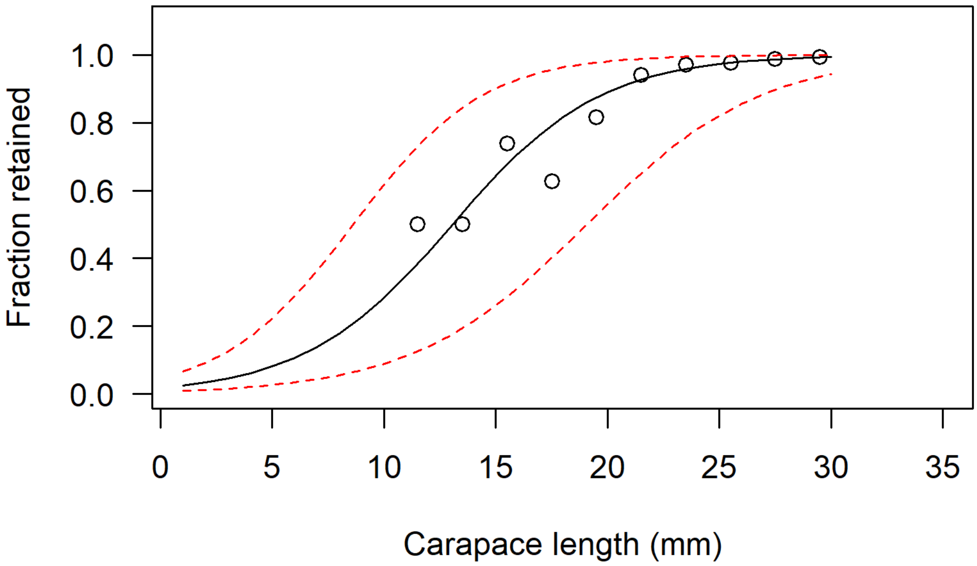

Figure 2. Prawn trawl selectivity curve based on the number of tiger prawns retained in codends with 38 mm and 20 mm internal mesh stretches. The model is S_{CL} = 1/[1+exp(3.94 – 0.30*CL)] (CL: carapace length). The red lines are 95% CI.

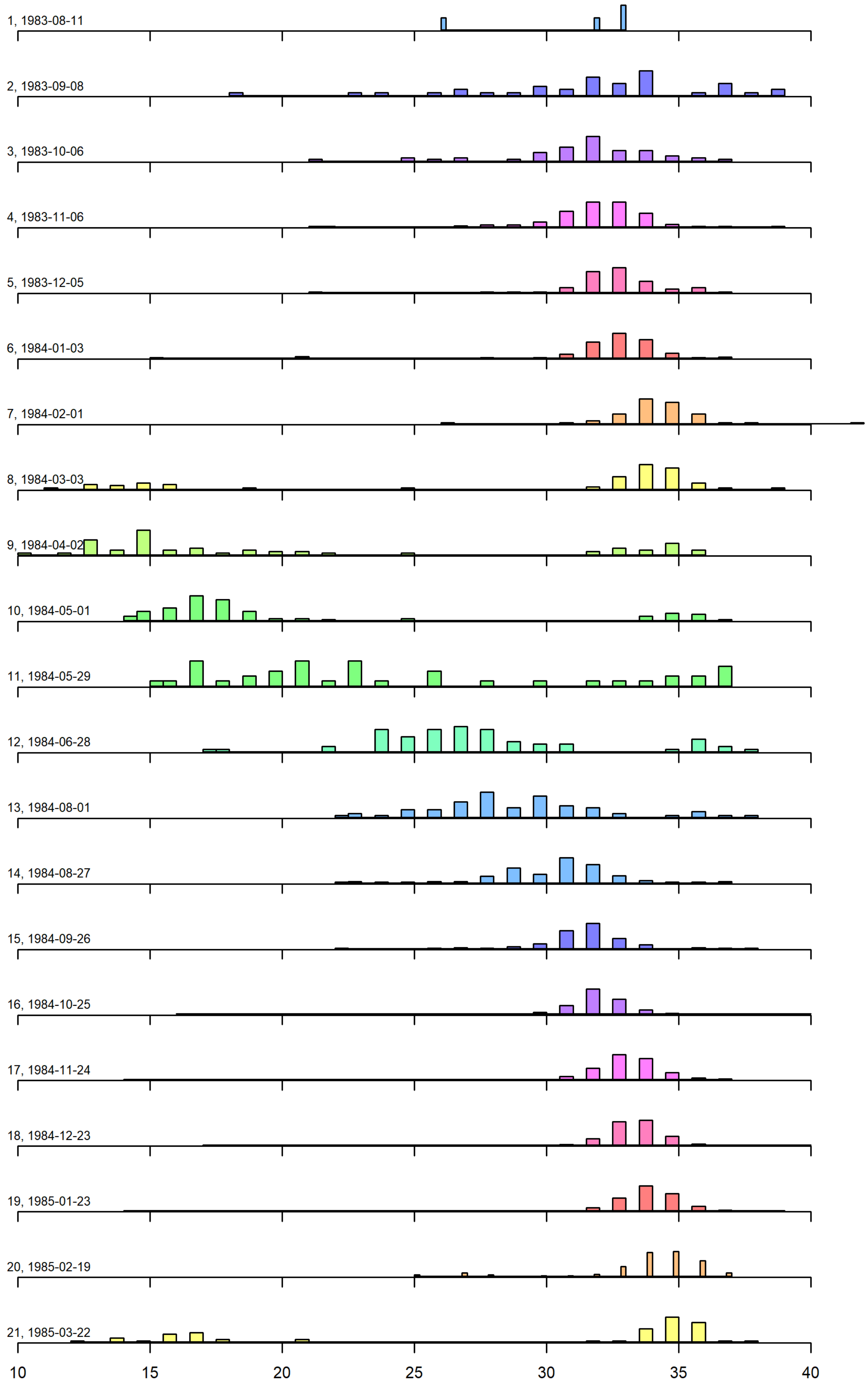

Figure 3. Length frequency distribution of male red endeavour prawns in 21 monthly surveys.

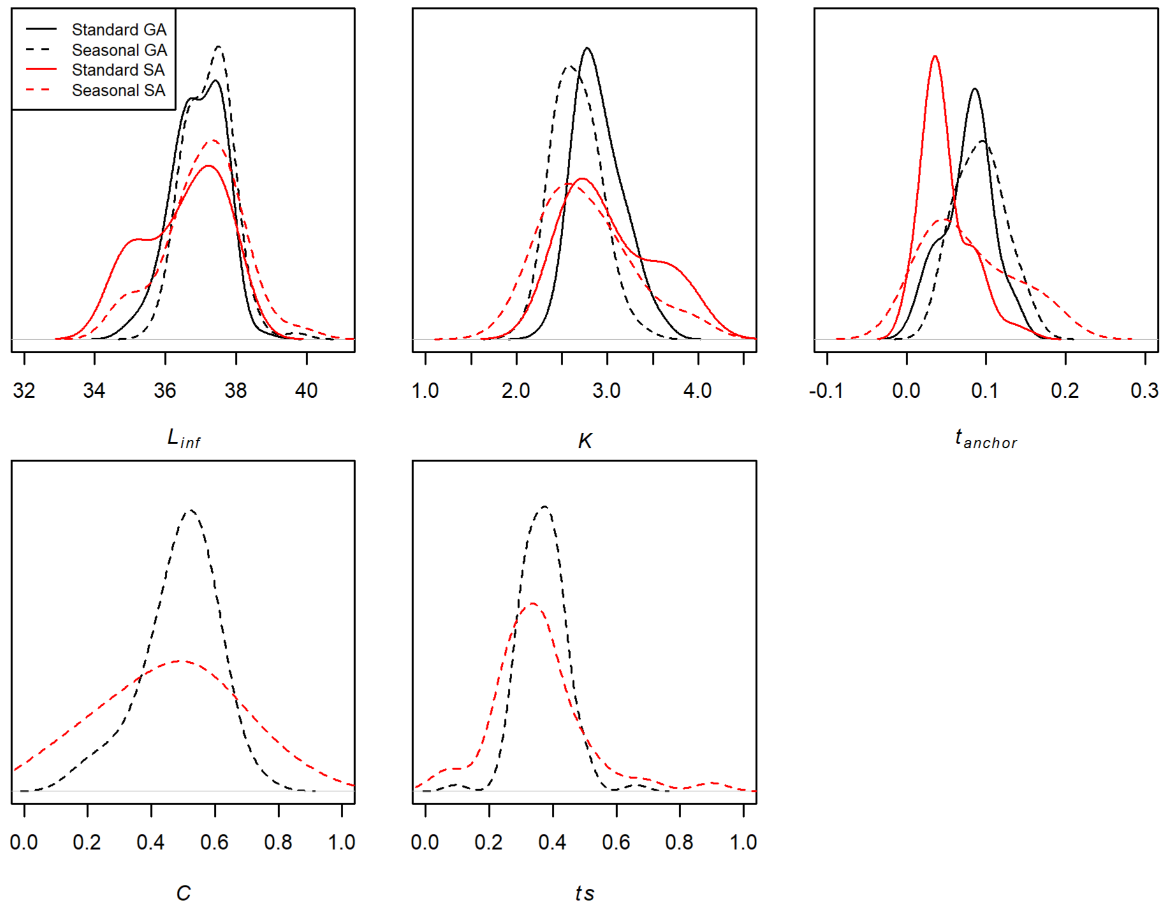

Figure 4. Density distributions of estimated parameters of the standard and seasonal VBGF for male P. ensis from 100 bootstraps of GA and SA algorithms.

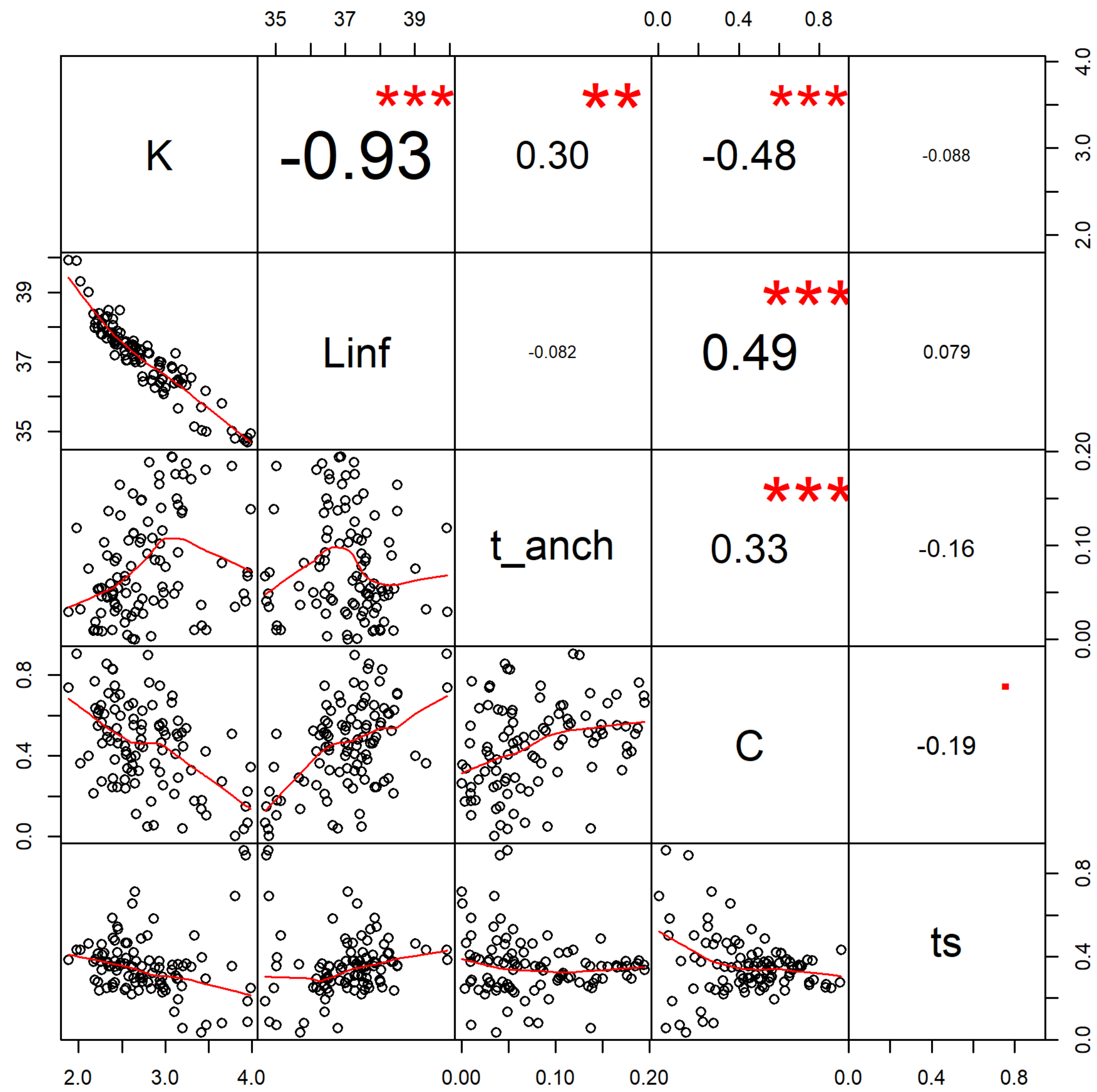

Figure 5. Correlations among the five parameters in the seasonal oscillation VBGF for male red endeavour estimated by simulated annealing ELEFAN_SA_boot(). The values on the upper triangle are Pearson correlation coefficient *r*; the stars are significant level at p = 0.1, 0.05, and 0.01 respectively.

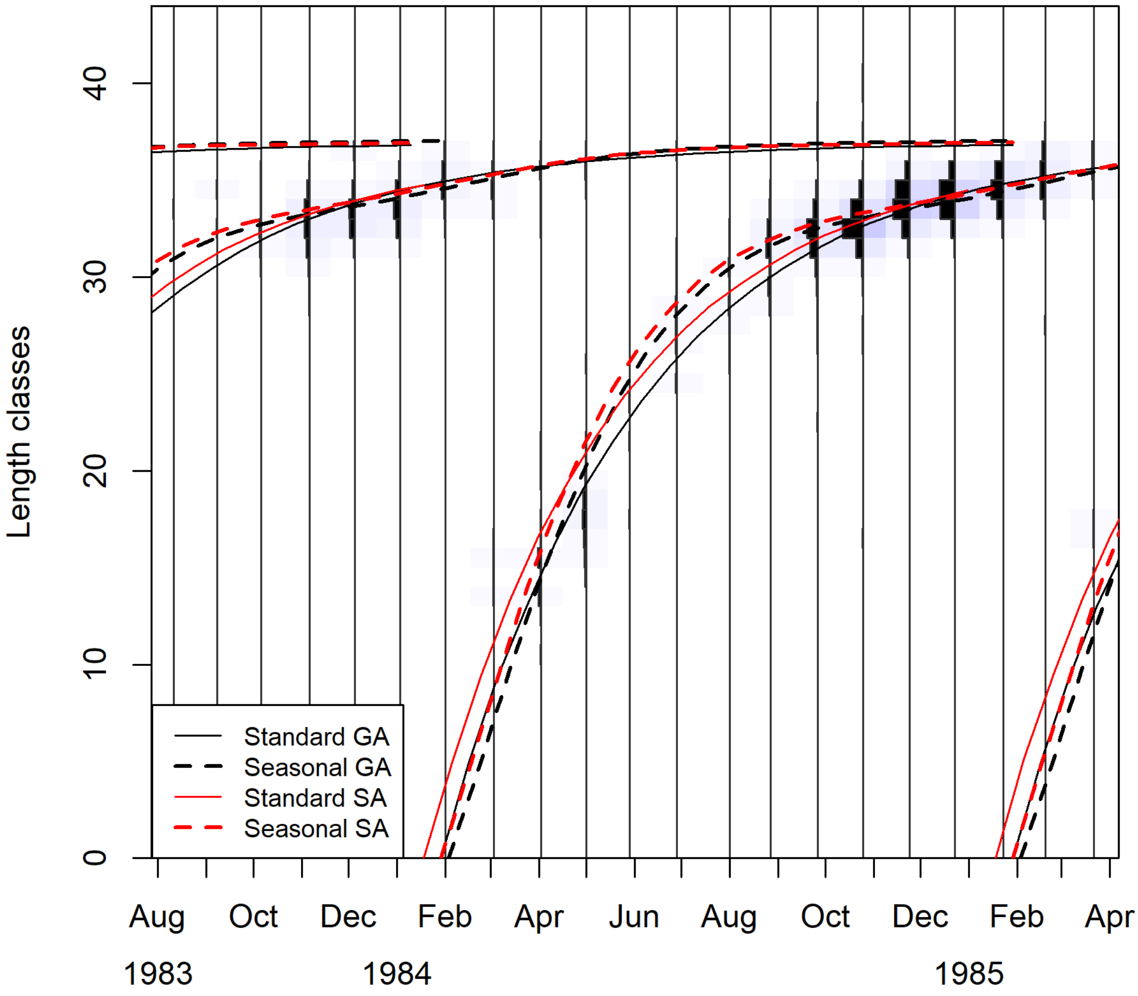

Figure 6. The standard and seasonal VBGF fitted to length frequency distribution of male *P. ensis* using ELEFAN_GA_boot() and ELEFAN_SA_boot() algorithms.

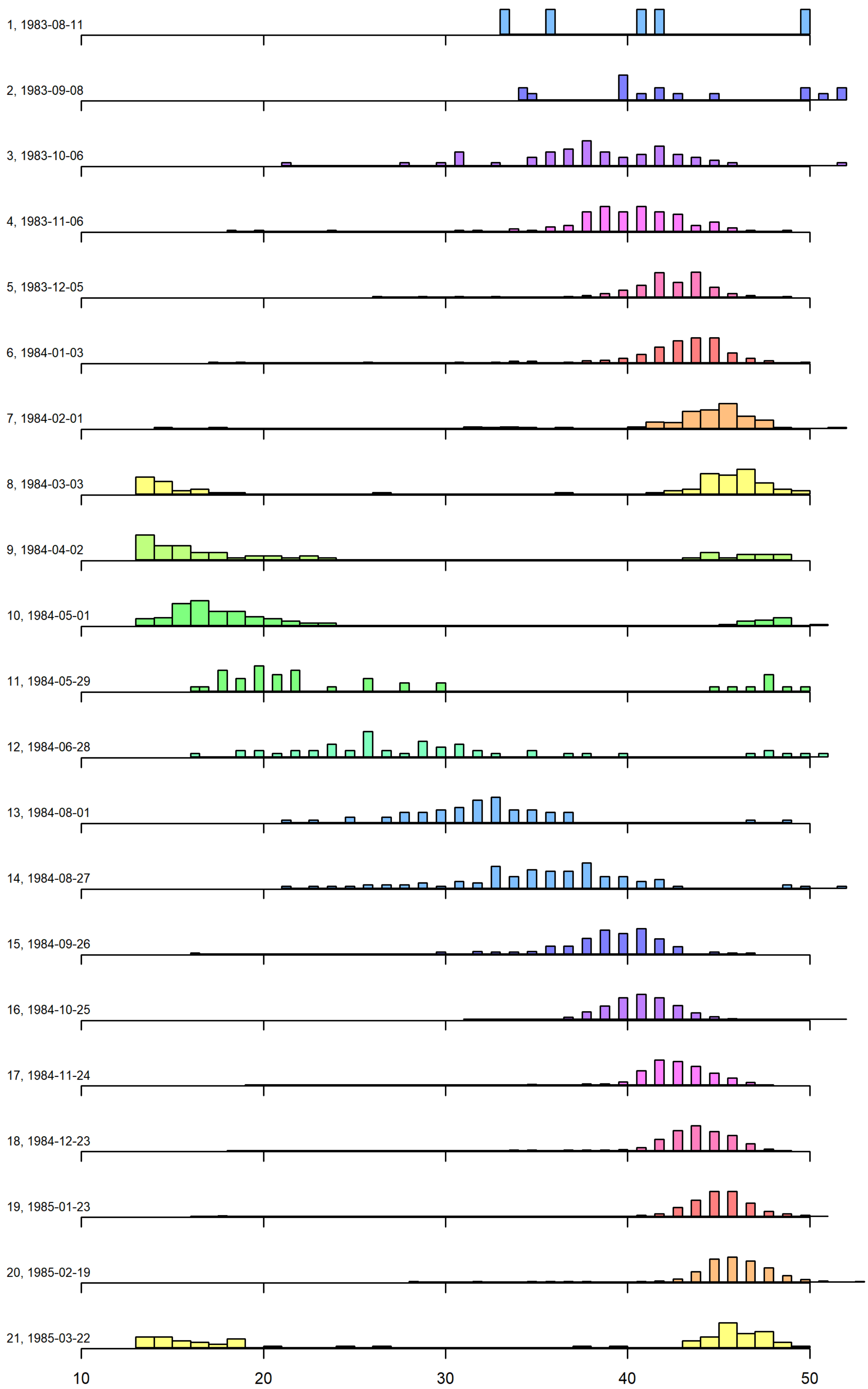

Figure 7. Length frequency distribution of female red endeavour prawns in 21 monthly surveys.

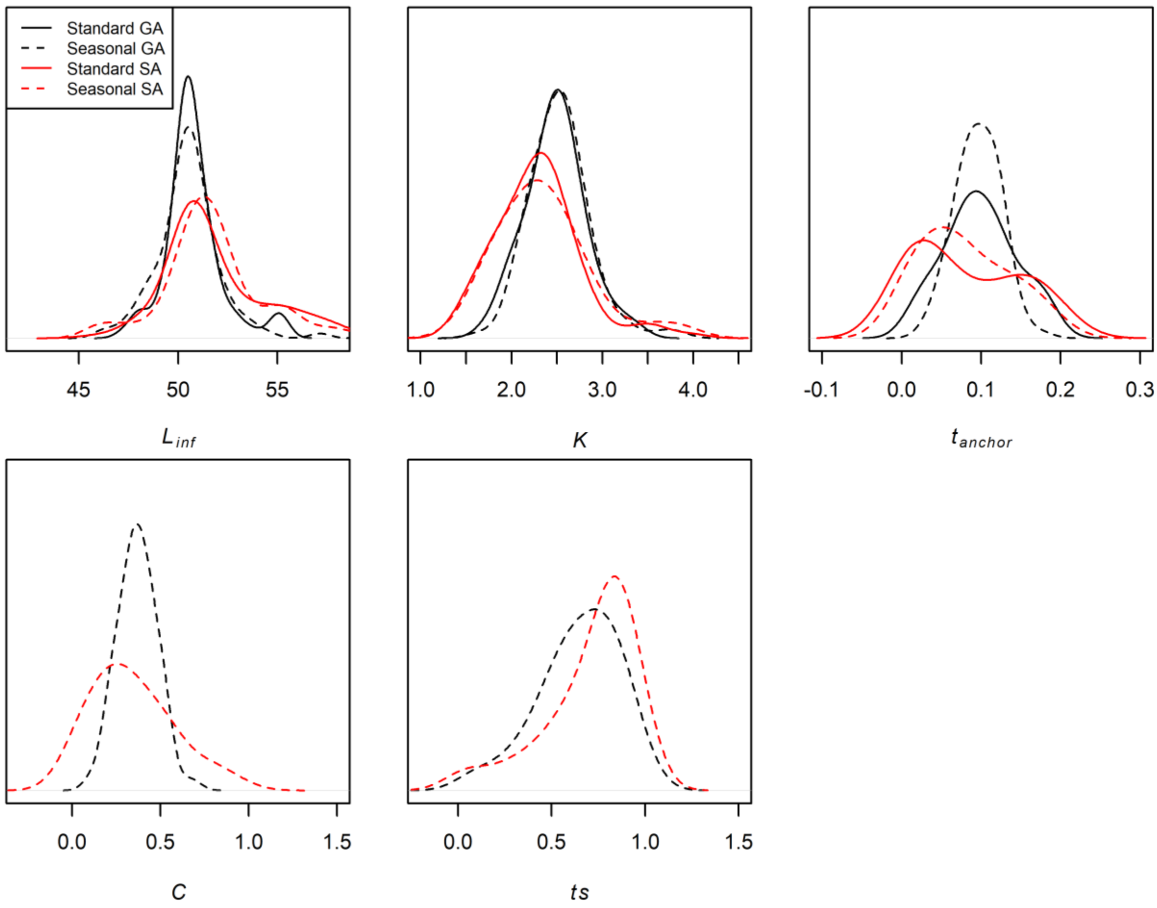

Figure 8. Density distributions of estimated parameters of the standard and seasonal VBGF for female *P. ensis* from 100 bootstraps of GA and SA algorithms.

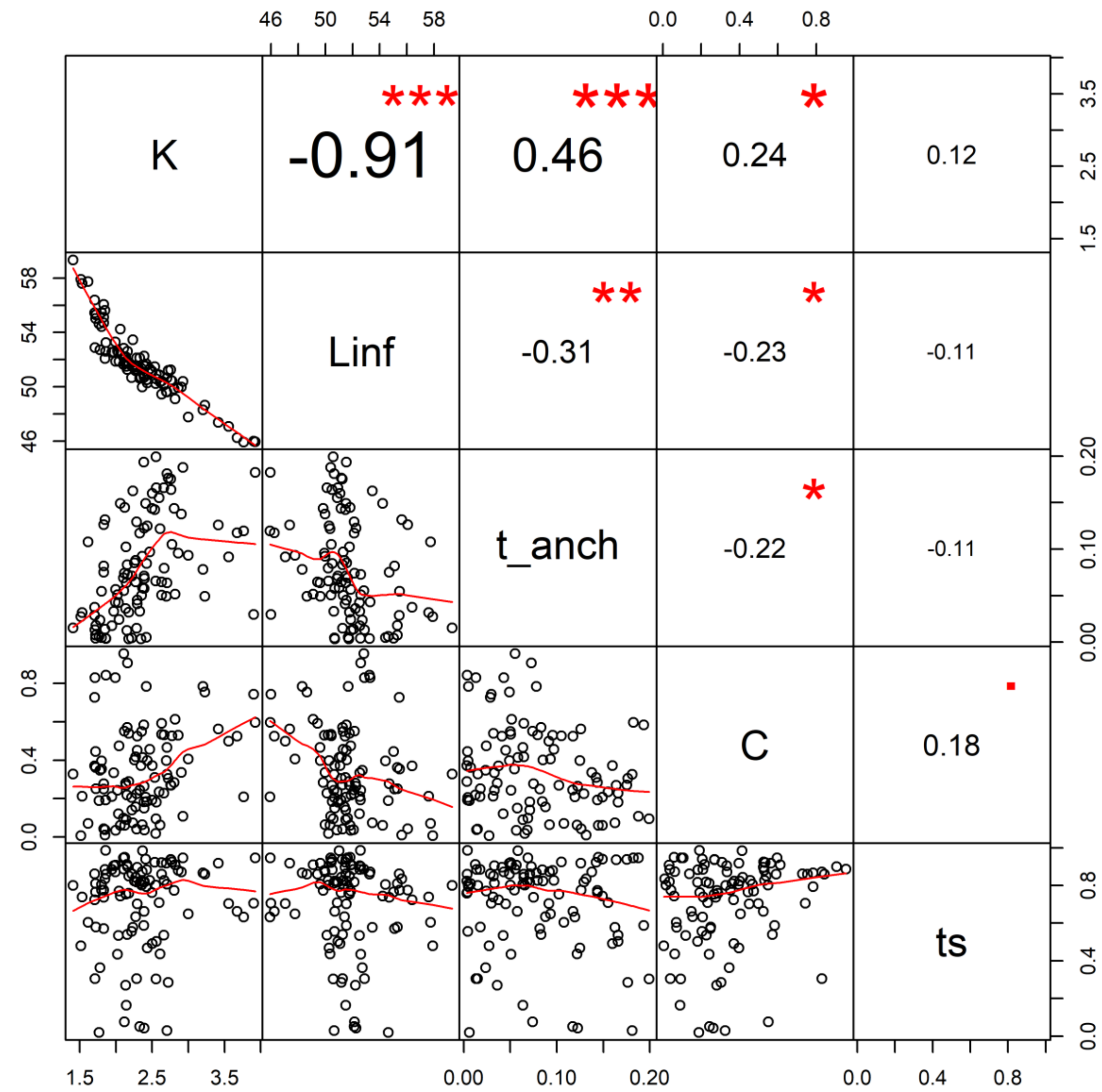

Figure 9. Correlations among the five parameters in the seasonal oscillation VBGF for female red endeavour estimated by simulated annealing ELEFAN_SA_boot(). The values on the upper triangle are Pearson correlation coefficient *r*; the stars are significant level at p = 0.1, 0.05, and 0.01 respectively.

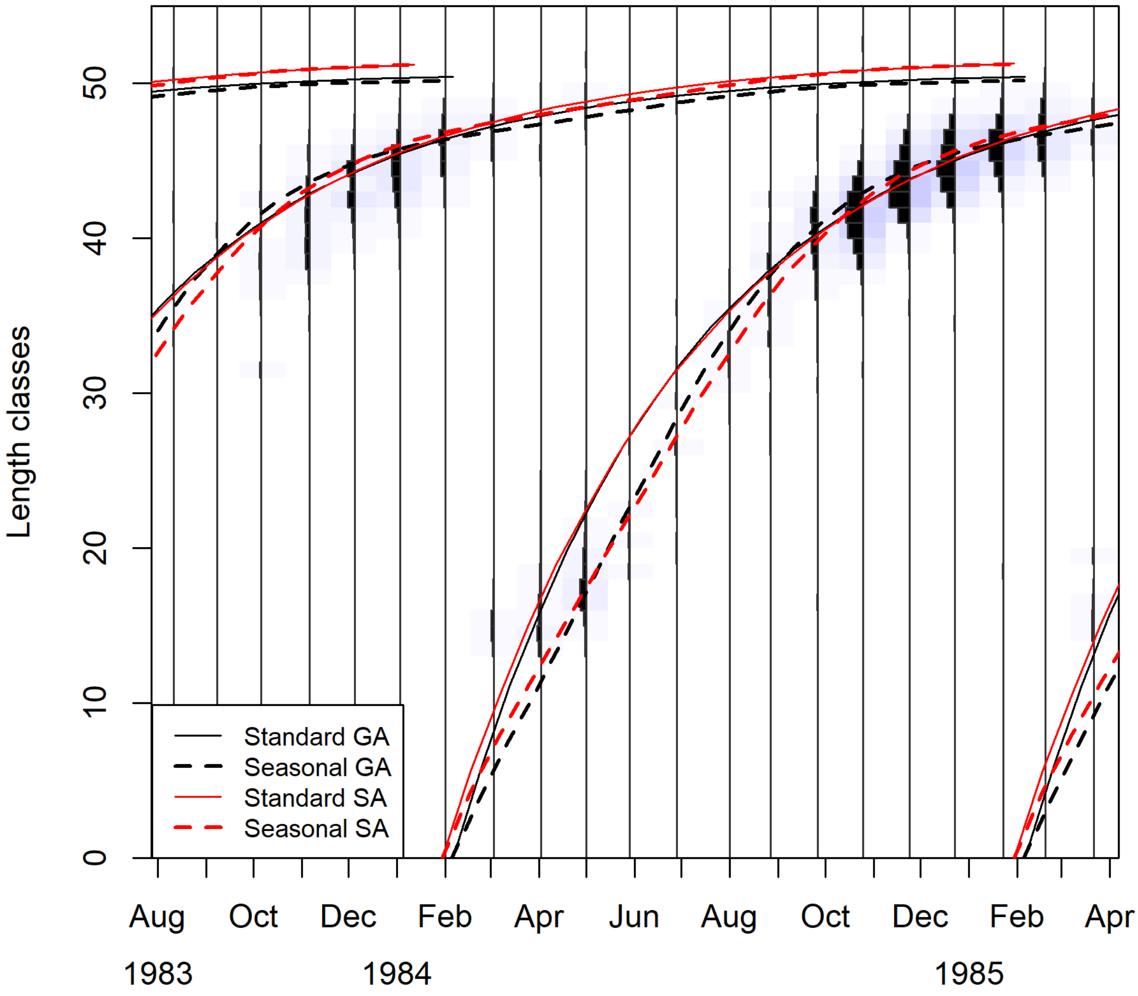

Figure 10. The standard and seasonal VBGF fitted to length frequency distribution of female **P. ensis using ELEFAN_GA_boot() and ELEFAN_SA_boot() algorithms.**

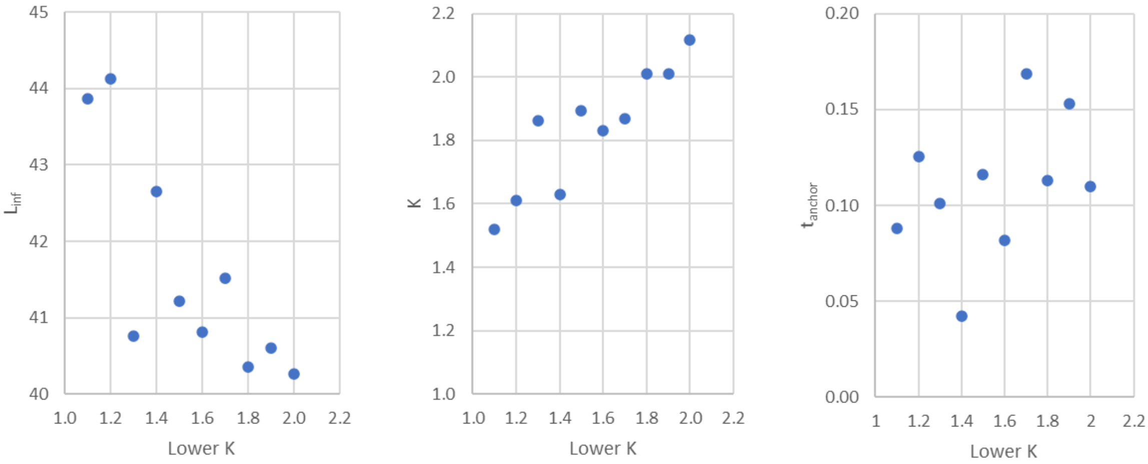

Figure 11. Effect of prior parameter range on ELEFAN estimated VBFG parameters of male red endeavour prawns. The upper *K* is set to 4 yr^{-1}, while the lower *K* varies between 1.1 and 2 yr^{-1}.

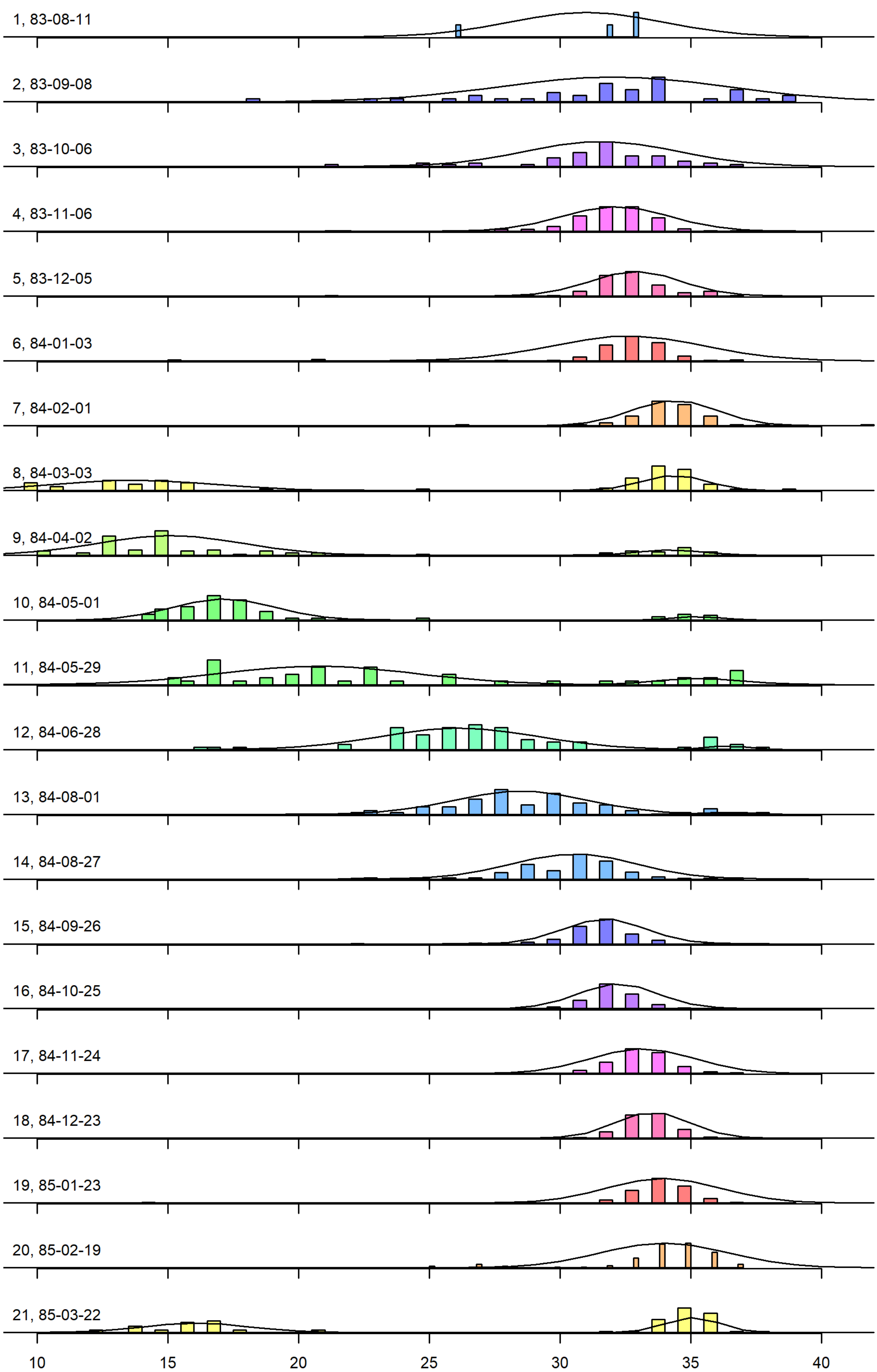

Figure 12. Male red endeavour prawn length frequency distribution modelled by a multi-normal mixture model (MNMM).

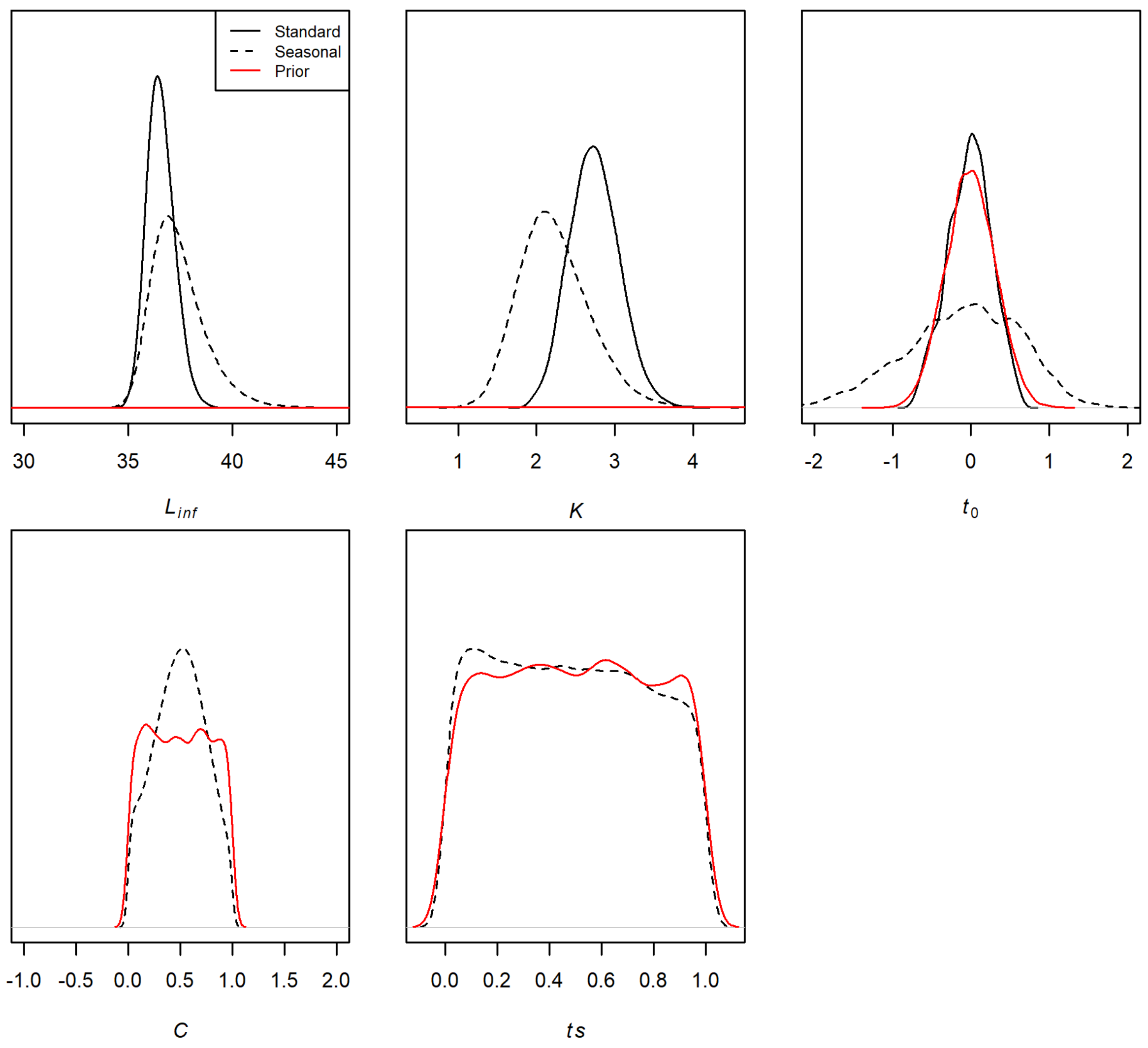

Figure 13. Density distributions of parameters for the standard and seasonal Bayesian growth models for male P. ensis.

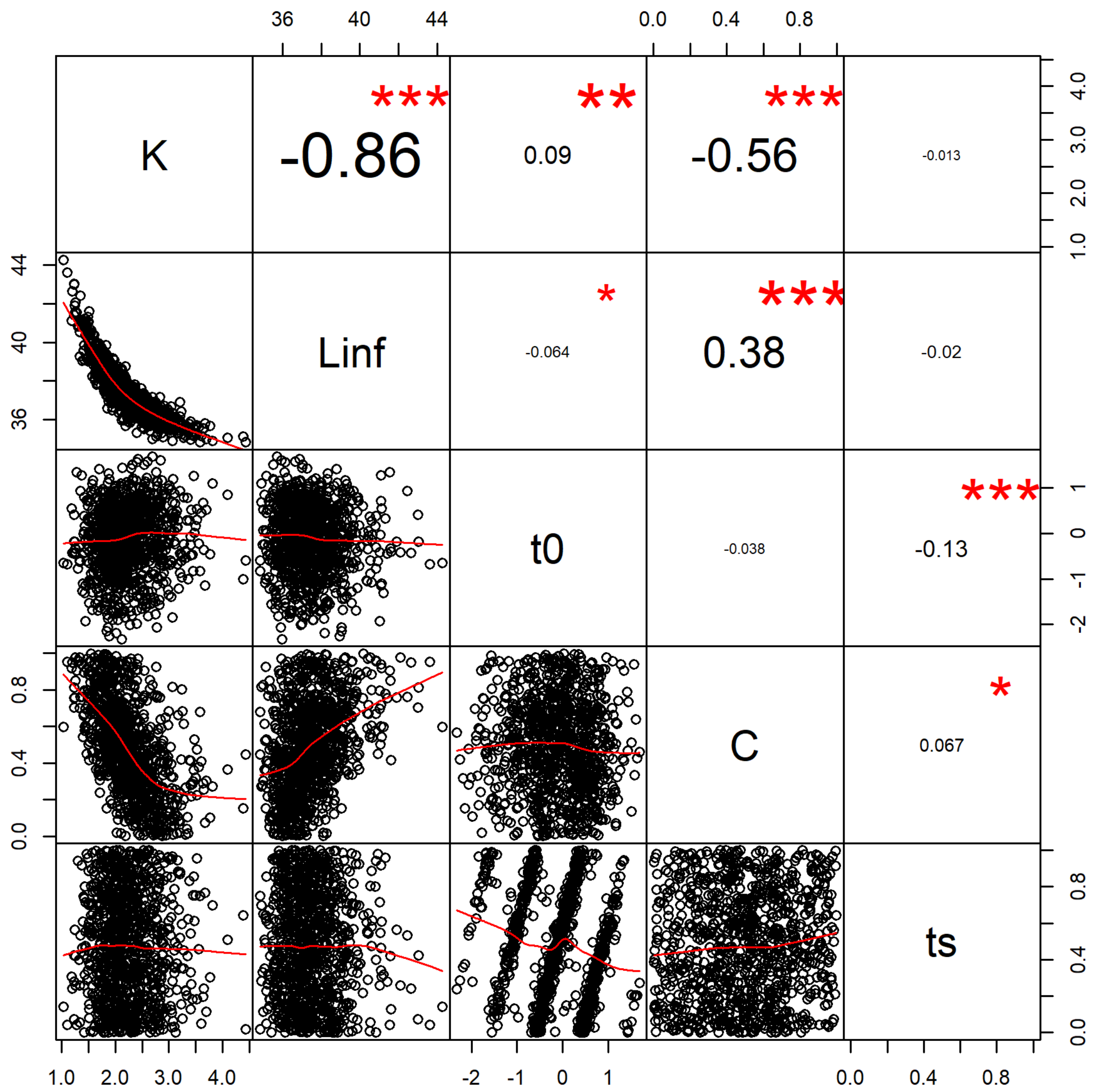

Figure 14. Correlations among the five parameters in the seasonal oscillation Bayesian growth model for male red endeavour. The values on the upper triangle are Pearson correlation coefficient *r*; the stars are significant level at p = 0.1, 0.05, and 0.01 respectively.

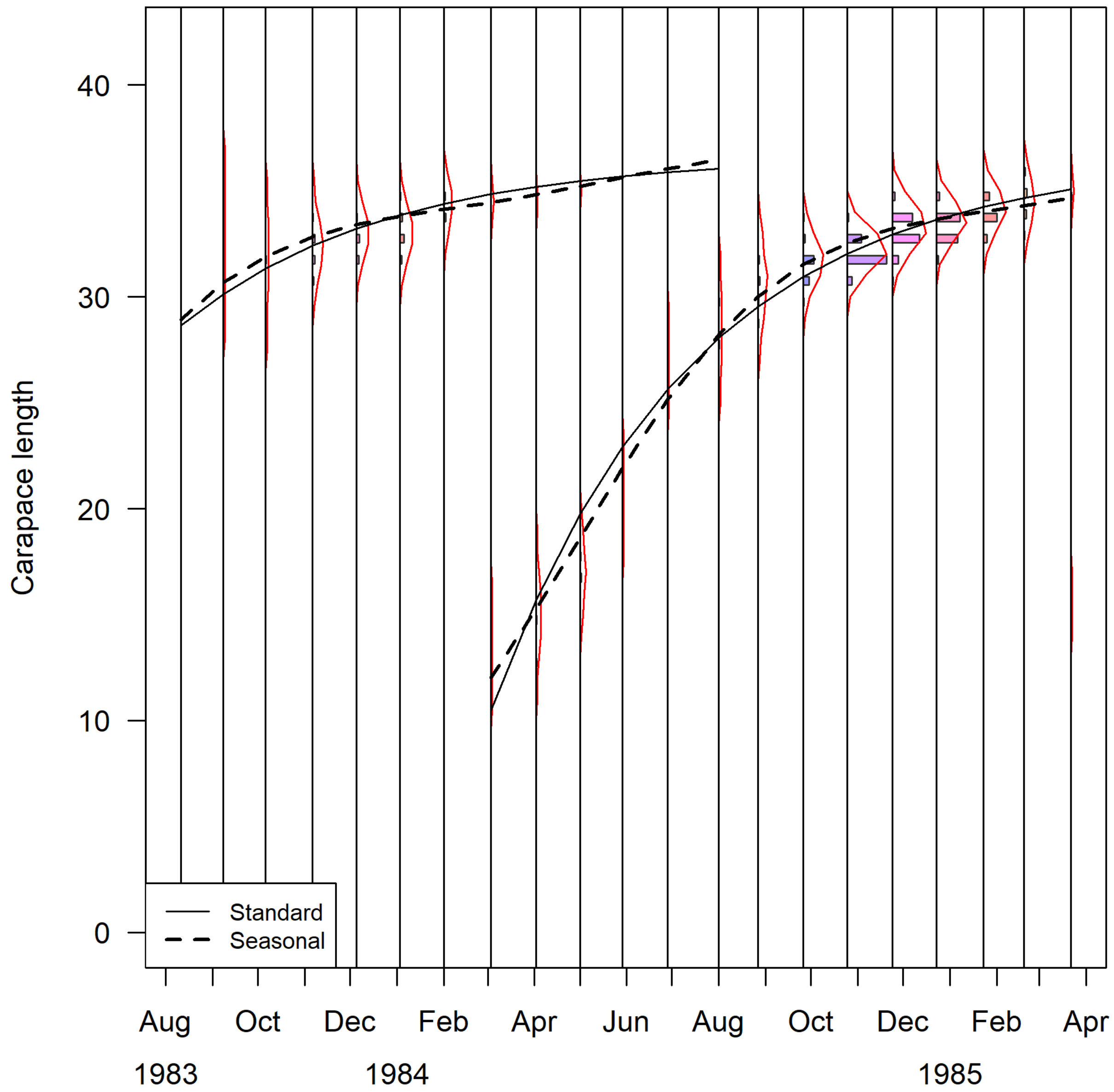

Figure 15. The standard and seasonal Bayesian growth models fitted to length frequency distribution of male *P. ensis*.

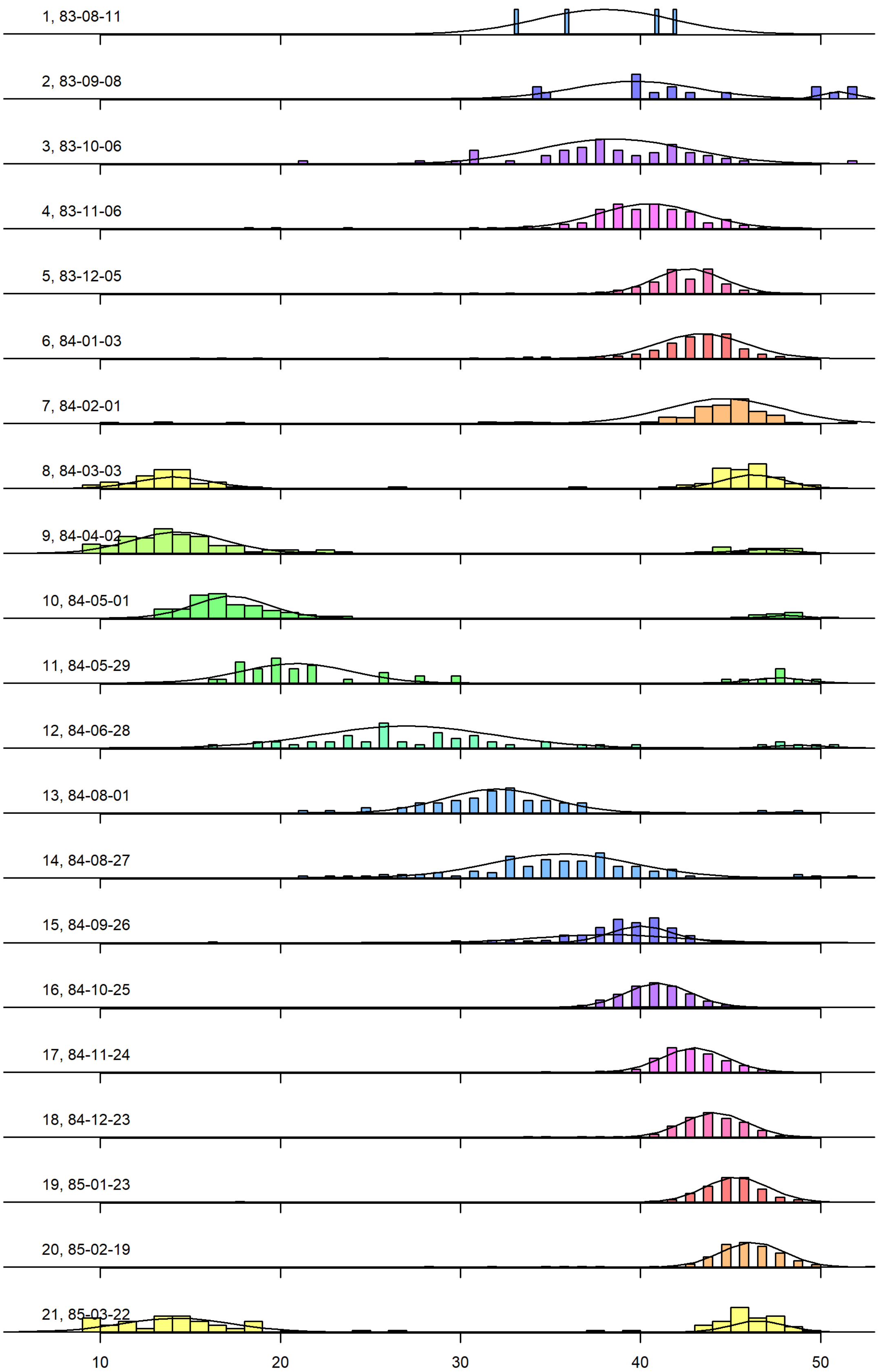

Figure 16. Female red endeavour prawn length frequency distribution modelled by a multi-normal mixture model (MNMM).

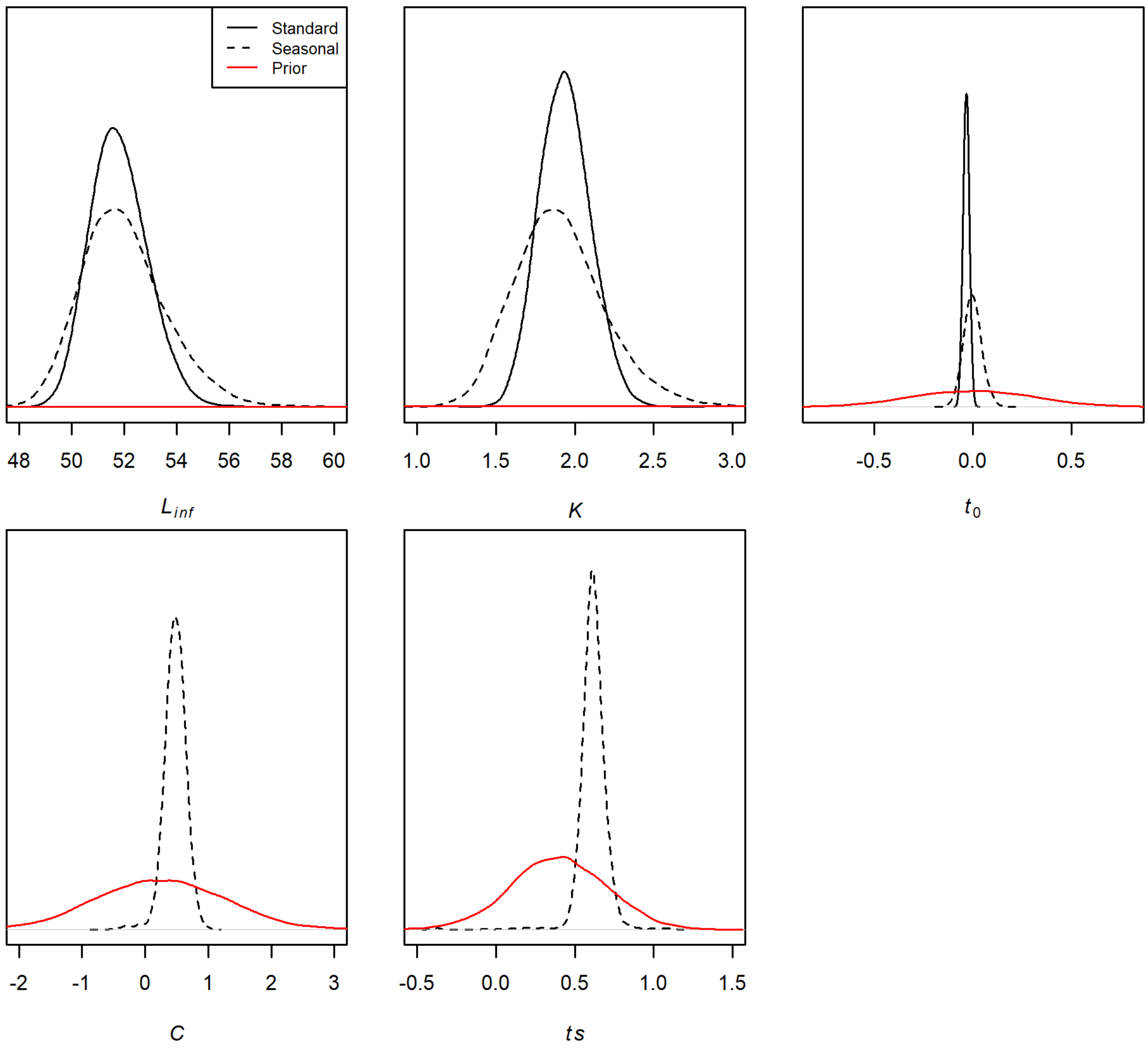

Figure 17. Density distributions of parameters for the standard and seasonal Bayesian growth models for female *P. ensis*.

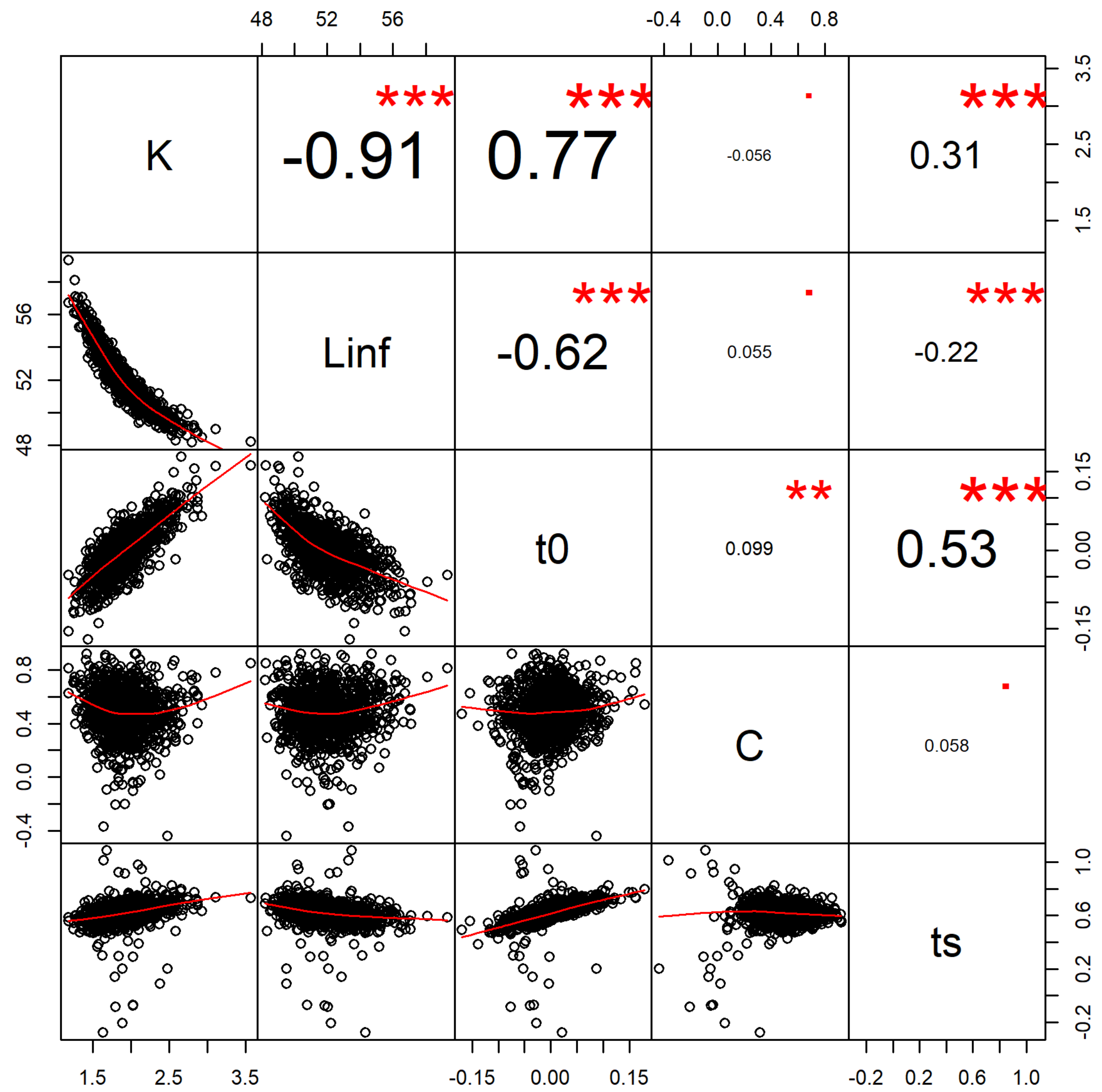

Figure 18. Correlations among the five parameters in the seasonal oscillation Bayesian growth model for female red endeavour. The values on the upper triangle are Pearson correlation coefficient *r*; the stars are significant level at *p* = 0.1, 0.05, and 0.01 respectively.

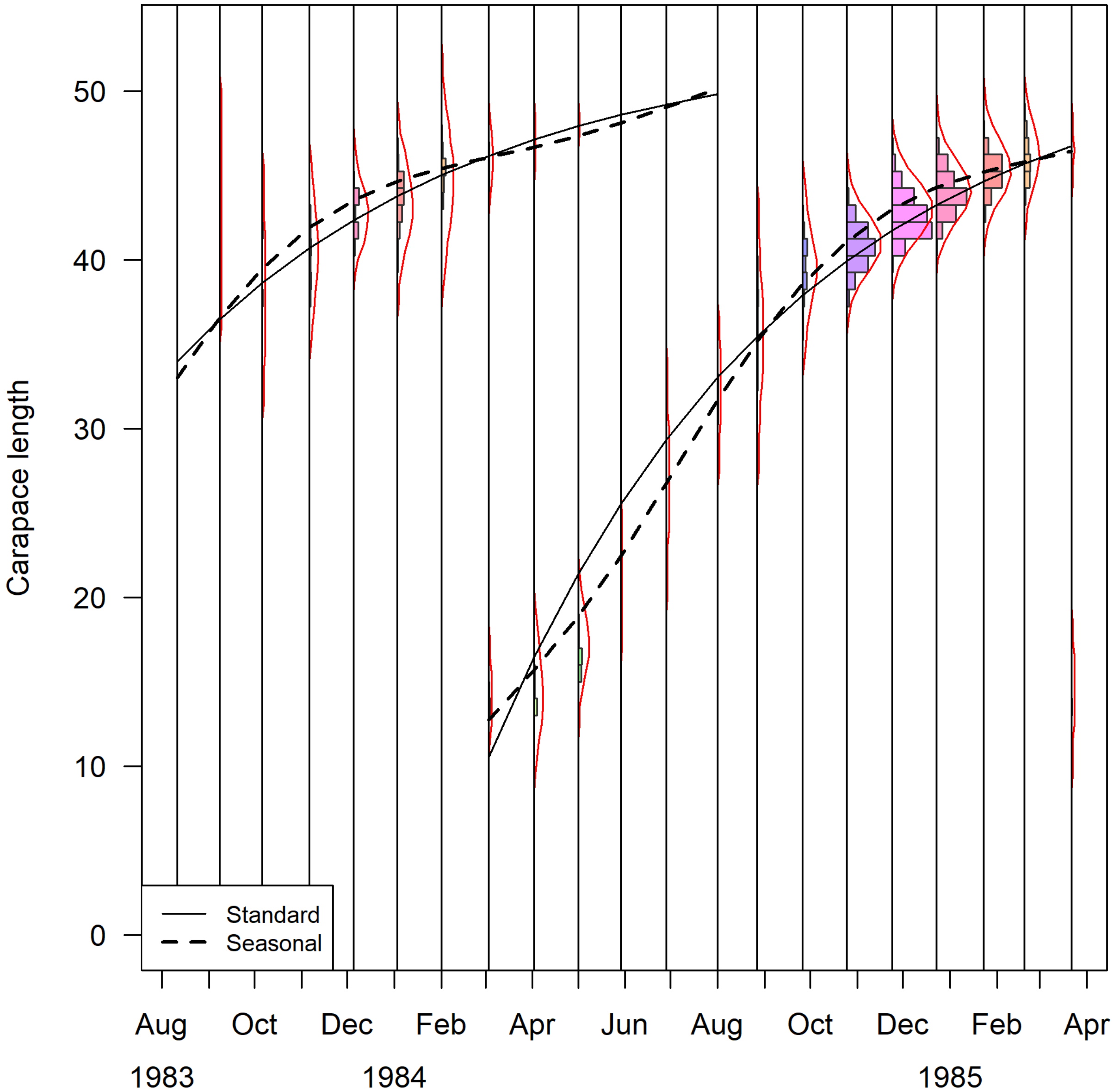

Figure 19. The standard and seasonal Bayesian growth models fitted to length frequency distribution of female *P. ensis*.

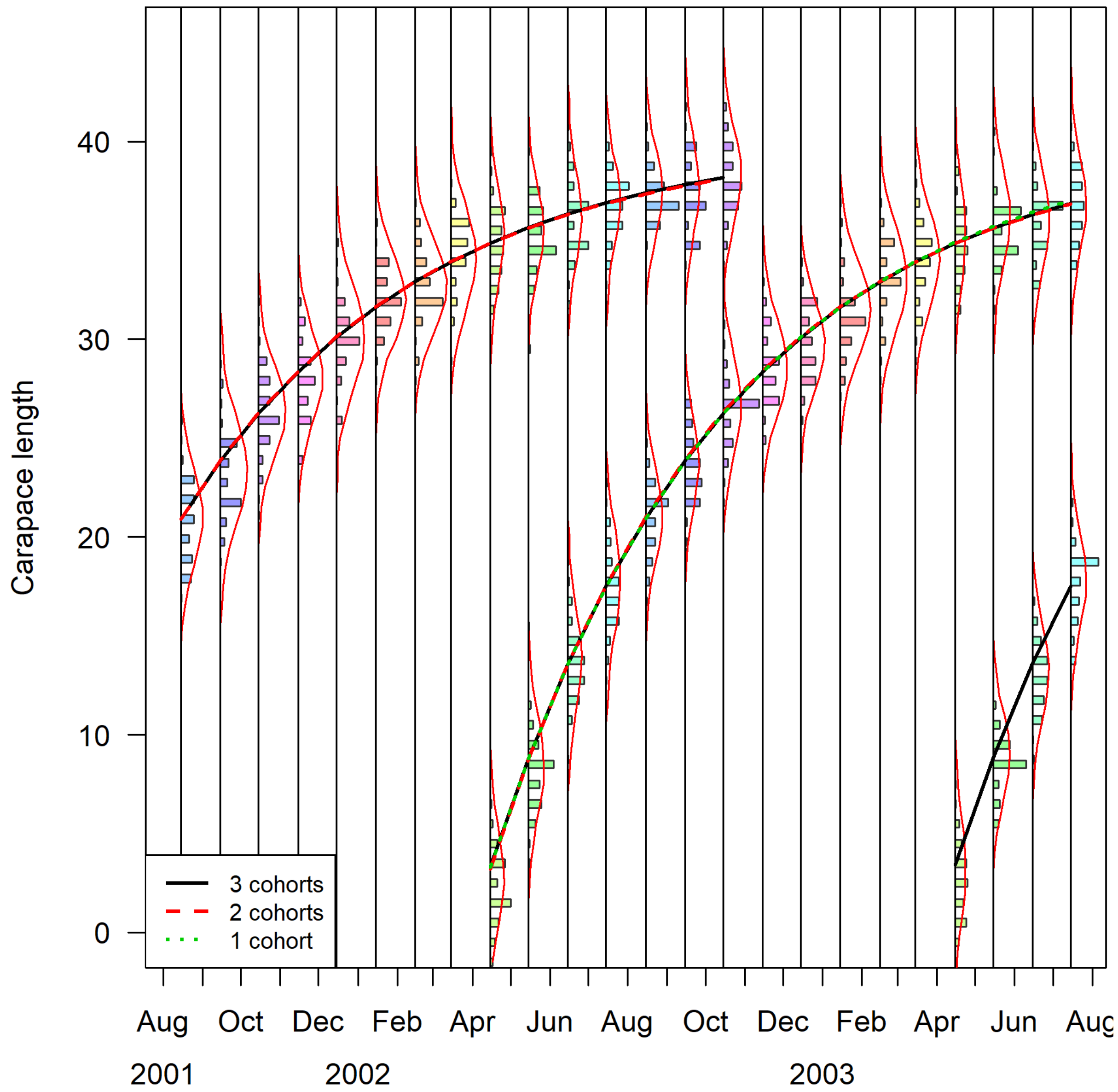

Figure 20. The standard Bayesian growth model fitted to the simulated length frequency distribution. Three scenarios are tested, assuming the data contain 3, 2, and only 1 year-class. The posterior K and L_{inf} are almost identical among the three cases, but the estimated age ($a_{1,yc}$, and t_0) differ between the three scenario due to the difference in the amount of LFD data, which does not affect the curves.

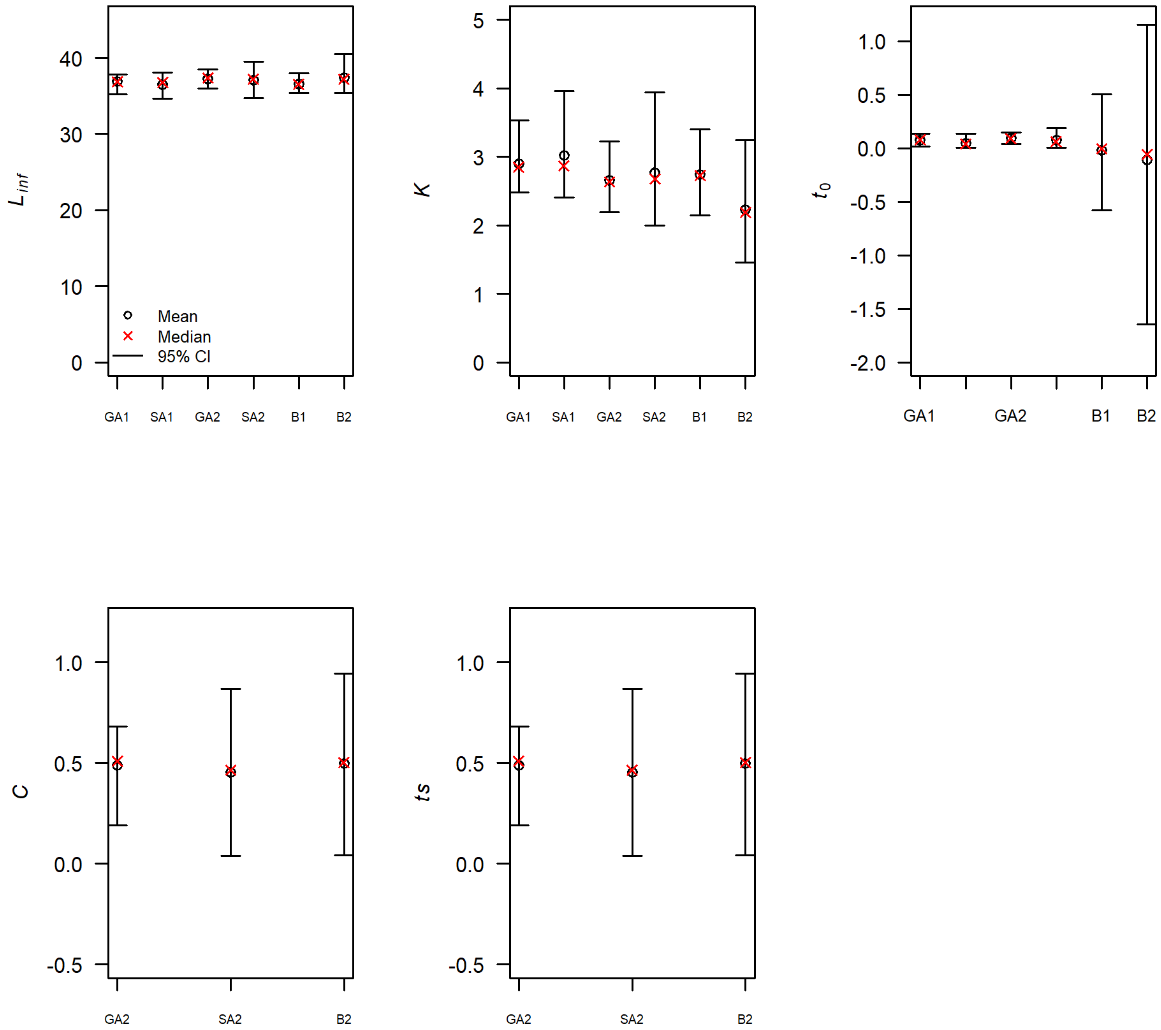

Figure 21. Comparison of male red endeavour prawn VBGF parameters estimated by ELEFAN_GA_boot (GA) and ELEFAN_SA_boot, and Bayesian model (B). The number following the method is: 1 = standard VBGF, 2 = seasonal oscillation growth model. Note that t_0 is t_{anchor} for GA and SA methods.

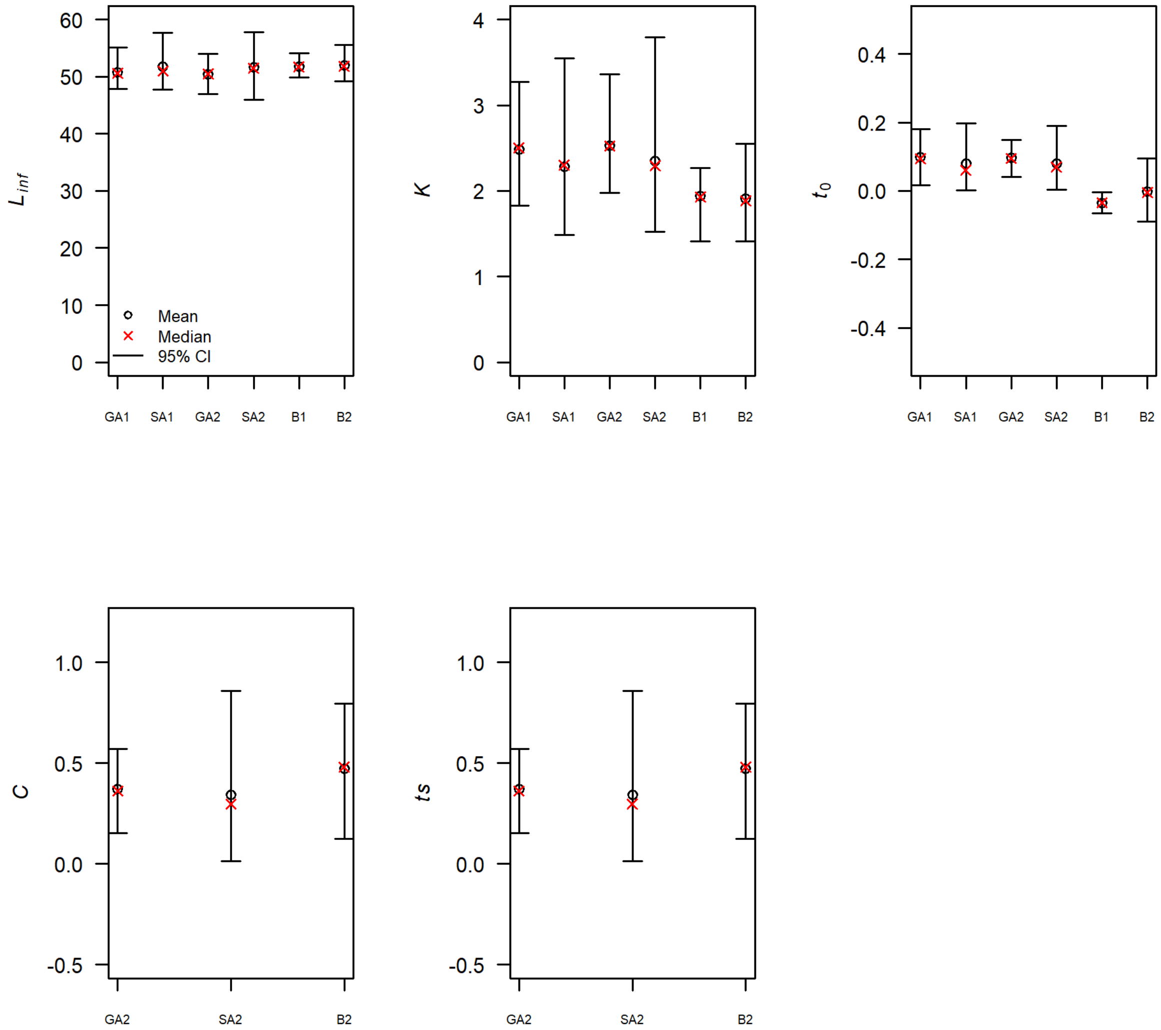

Figure 22. Comparison of female red endeavour prawn VBGF parameters estimated by ELEFAN_GA_boot (GA) and ELEFAN_SA_boot, and Bayesian model (B). The number following the method is: 1 = standard VBGF, 2 = seasonal oscillation growth model. Note that t_0 is t_{anchor} for GA and SA methods.

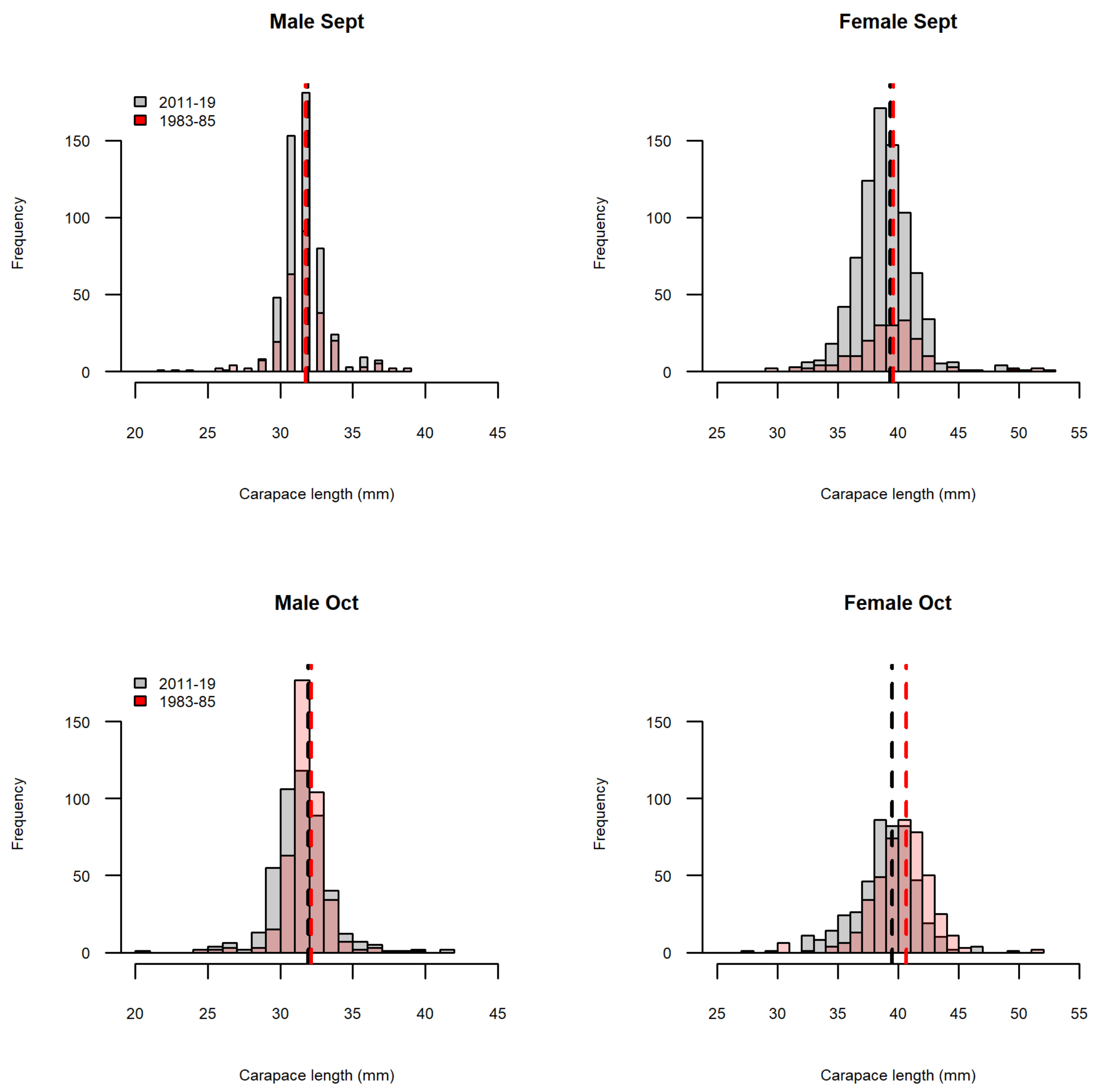

Figure 23. Comparison of red endeavour prawn length frequency distributions for two months between 2010s and 1980s. The recent data come from Scientific Observer program collected between 2011-2019 commercial fishing seasons. The earlier data are those from the Maxim surveys used in this report. The vertical dashed lines are the mean carapace length for the two periods respectively.

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