Estimation of Population Parameters for Australian Prawn Fisheries

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Contents

Non-technical Summary

One of the main objectives of fisheries management is to ensure the sustainability of fished stocks. To reach this objective scientists have to adequately assess the status of fished populations with quantitative models of the fishery systems. Most of these models require estimates of population parameters such as growth rates, mortality rates and catchability (the proportion of the population caught by a single vessel each day). Most of these parameters are unique for each stock; unfortunately they are not easily estimated because marine organisms are inherently difficult to observe and study. Estimation is generally done through statistical analysis of catch data, either from the fishery or from research surveys.

Tropical prawns are fast growing organisms that reach maturity in a few months and tend to be predated upon or caught before they reach a year of age. Prawns are also animals for which age can not be easily determined because they have no hard structures that are retained through their life. As a result age can not be estimated and can only be inferred indirectly from their size. The combination of a short life-span and the inability to age individuals is a major difficulty in developing estimation methods for populations of tropical prawns. This is especially the case for those parameters that are time dependent (such as mortality and growth rates).

This document reports on two years of work devoted at developing new statistical methods for the estimation of population parameters in tropical prawn fisheries. The work was divided into five components:

1. Review of current methods of growth rate and mortality rate estimation
2. Development of new methods for the estimation of growth and mortality rate
3. Development of a method for the estimation of size-specific mortality rates
4. Study of the dynamics of prawn aggregations
5. Effects of effort and aggregation dynamics on catchability

In the review of current methods we investigated three models that use length frequency data to estimate growth and mortality. The first two of these methods ignore differences in size for individuals of the same age and assume all prawns recruit at the same time. As a consequence the methods result in substantially biased estimates of population parameters. The last method considered did accommodate different sizes at age and gave unbiased results. This last method, however, provided very uncertain estimates, with large confidence limits suggesting that estimates were accurate but not precise. This review concluded that it was imperative to develop new methods, more appropriate for the life history and fishery characteristics of tropical prawn fisheries.

A new method was then developed for estimation of mortality rates and growth parameters from length frequency data by incorporating individual growth variability within the model. The method is flexible enough to accommodate for different recruitment patterns, length-specific gear selectivity and varying fishing effort over time. This method is statistically robust and was tested with data for grooved tiger prawns from Northern Australia.

All the methods mentioned above make the fundamental assumption that the natural mortality rate does not change with the age or size of the prawn. We used data for common banana prawns to show this assumption is certainly not correct for juvenile prawns. We found considerable changes in the natural mortality of juvenile prawns, from 40% mortality per week for the smallest juveniles (4mm carapace length) to only 5% mortality per week for the larger ones (12mm carapace length). This suggests that there is a need to revise the evidence for size-independence of natural mortality rates for larger prawns.

Schooling is a well-known behavioural trait in fish but it is less common in prawns. In Australia, there is at least one group of prawns that form dense schools, the banana prawns. Other prawn species aggregate but in much smaller densities. We have used logbook data to describe the dynamics of prawn schools. We found that the apparent biomass of schooling banana prawns decreases due to fishing more rapidly than that of non-schooling banana prawns. This implies that the density and catchability of banana prawn stocks decreases as the season progresses. This possibly invalidates earlier assessments of banana prawn stocks which assumed catchability was constant throughout the season.

At larger spatial scales we examined the relation between the effects of non-random distribution of fishing effort and abundance. Models used to analyse the catch and effort data from the Northern Prawn Fishery suggest that there has been an increase in catchability due to the reduction in abundance of tiger prawns and the tendency of tiger prawns to aggregate.

In conclusion this project has made substantial progress in developing appropriate methods for parameter estimation for tropical prawn stocks. Some of these methods have been successfully used to show that previous estimates of growth parameters, mortality rates, and catchability may have been subject to substantial bias or relied on untenable assumptions. This research has therefore contributed to correct such estimates at the same time as providing a set of new statistical tools that can be used for other Australian prawn stocks.

Background

Australian prawn fisheries include state managed and Commonwealth managed fisheries. The total annual gross production is worth about $ 250 million (Australian Fisheries Statistics 1993). Stock assessment plays an important role in making decisions for management of these fisheries. Stock assessment relies, to a great extent, on the knowledge of population parameters including mortality rates (natural mortality and total mortality) and catchability coefficients. The latter are a measure of fishing efficiency.

Methods of estimating these population parameters were developed between the 1950s and 1970s. They are based on the abundance (or catch) of different age groups in the successive years, or alternatively, from tagging data (Ricker 1975; Gulland 1983). Despite increasing awareness of problems with these techniques (see below) there has been little methodological progress since that time.

The existing methods for estimating mortality in the literature have strong limitations and disadvantages (Vetter 1988), consequently, little progress has been made in obtaining estimates of adult mortalities for Australian prawn fisheries. At present, the NPF is assessed on the basis of untested estimates of mortality rates (Wang and Die, 1995). The Queensland Prawn Fishery faces the same problems.

Prawns are short-lived crustaceans and cannot be aged. Most species have extended spawning periods with seasonal patterns. These distinctive features obscure age groups in catch samples and make the traditional methods inappropriate for estimating population parameters. Tagging experiments are not ideal for prawns unless one can quantify the tagging mortality, tag shedding rate and reporting rate, albeit they are useful for estimating movement, migration and possibly growth.

A few authors have suggested using age or size specific mortality for marine fish stocks (Vetter 1988; Beyer 1989; Caddy 1991). For Australian prawn fisheries, the natural mortality rates are always assumed to be constant with size for each life history stage. It seems reasonable to assume constant mortality for adult prawns. But for earlier life history stages, the mortality is more sensitive to the change of size. CSIRO research has suggested that the mortality rate for juveniles is much higher than that for sub-adults or adults (Haywood and Staples 1993; O'Brien 1994). This suggests that for prawns, like marine fish, the natural mortality is a declining function of age or size.

Describing prawn population dynamics with models which use mortality as a function of size or age will provide more accurate results. A relationship between the mortality rate and size can then be established for the whole life cycle. Such a life cycle model will increase our ability to describe changes in survival, and hence obtain a better understanding about inter-annual variations in prawn abundance. Size-dependent mortality will also be very useful in future stock enhancement projects to determine the number and size of the prawns to be released.

The traditional approach to catch and effort data is based on the well known catch equation (Gulland 1983, p.105). This presumes that fish are evenly distributed on the fishing ground, or that fishing effort is randomly distributed. This is clearly not the case for most fisheries because of (a) the aggregation behaviour of fish, and (b) targeting on fishers. In such cases, the traditional catch equation is inappropriate to describe the relationship between catch and effort (Crecco and Overholtz 1990; Richards and Schnute 1992; Paloheimo and Chen 1993). In Australian prawn fisheries, banana prawns are known to aggregate to a great extent. Although species aggregate to a lesser extent, fishers rely on this behaviour, their experience and modern searching devices to increase their catch rate. Therefore, the catchability will depend on the distribution of fishing effort in relation to the distribution of prawns. Density-dependent catchability should be incorporated in the estimation methods and the population models. This will enable us to estimate effective effort on the different species of prawns more accurately. Accurate estimates of effective effort are essential for stock assessment models.

The concept of density-dependent catchability is not new. Paholeimo and Dickie (1964) suggested density-dependent catchabilities for Georges bank haddock, and Crecco and Overholtz (1990) tested and supported their theory.In fact, Paholeimo and Dickie (1964) argued that density-dependent catchability exists for most demersal and pelagic fisheries. However, no research on density-dependent catchability has been done for Australian prawn fisheries. If the theory of density-dependent catchability is applied to the prawn fisheries, better indices of abundance than the catch per unit of effort will be produced, and catch-effort data such as commercial log book data will be used more efficiently.

Need

The main management objectives of most Australian prawn fisheries are to comply with ecological sustainable development and maximise economic efficiency. To attain these objectives fisheries managers have relied on the advice provided by fishery scientists on the status of prawn stocks and on the effects of fishing upon these stocks.

Estimation of the status of prawn stocks and the advice to management depends on knowledge of biological parameters and the processes that affect abundance.

Current methods for the estimation of population parameters from fisheries data are unsatisfactory and produce unreliable estimates because they do not incorporate the distinctive features of the prawn fisheries.

In Australian prawn fisheries, great uncertainties are associated with the population parameters (Wang and Die 1995; Somers and Wang 1995). These uncertainties and possible bias in population parameter estimates are serious obstacles to the precise assessment of the status of prawn stocks. Such imprecise assessments lead to uncertain advice on the impacts of fishing upon the stock, and force fishery managers to take risky decisions.

Natural mortality and catchability are two critical and fundamental parameters in stock assessment and management strategy evaluations. In Australian prawn fisheries research, scientists often have to ignore the assumptions required by the traditional methods in order to obtain some approximate parameter estimates. However, the results are of limited use because of substantial bias induced by the violation of the assumptions. These traditional techniques often generate results that out of feasible range. Too often, the parameter values used for scientific inference and decision making are based on subjective experience, rather than on objectively verifiable procedures.

Therefore it is necessary to develop some new approaches for estimating mortality and catchability for Australian prawn stocks based on the length frequency data and catch-effort data. Many such data sets have been collected in the past from scientific trawl survey, commercial logbooks and catch sampling programs. This project will generate better estimates of population parameters, and management strategies will be evaluated more reliably.

Objectives

To establish a new framework for prawn stock dynamics and develop new statistical methods for estimation of population parameters, which will improve the management of Australian prawn fisheries by increasing confidence in decision support tools and reducing the risk associated with decisions based on stock assessment.

Chapter 1

Estimation of Mortality and Growth Parameters from Length Frequency Data

We consider estimation of mortality rates and growth parameters from length-frequency data of a fish stock when there is individual variability in the von Bertalanffy growth parameter L_∞, and investigate the possible bias in the estimates when the individual variability is ignored. Three methods are examined: (i) the regression method based on the Beverton and Holt's equation (1956, Rapp. P.v. Reun. Cons. Int. Explor. Mer. 140: 67–83); (ii) the moment method of Powell (1979, Int. Explor. Mer 175: 167–169); and (iii) a generalization of Powell's method which estimates the individual variability to be incorporated into the estimation. It is found that the biases in the estimates from the existing methods are, in general, substantial, even when individual variability in growth is small and recruitment is uniform; and the generalized method performs better in terms of bias but is subject to a larger variation. There is a need to develop robust and flexible methods to deal with individual variability in the analysis of length-frequency data.

1.1 Introduction

Stock assessment plays an important role in making decisions for management of fisheries. Stock assessment relies, to a great extent, on the knowledge of growth and mortality parameters. Length-frequency based methods are important for estimating population parameters when aging is either not possible or very expensive.

Traditional methods assume a deterministic relationship between size and age for the population. It is more realistic to assume there is individual variability in growth (Sainsbury, 1980). For example, using tag-recapture data, Wang, Thomas and Somers (1995) found substantial individual variability for the tiger shrimp species *Penaeus semisulcatus.*

Although it is well understood that variability leads to increased uncertainty in estimates, it is less well recognized that variability can also lead to bias, particularly in the analysis of length-frequency data. It is therefore of interest to investigate the effect of individual variability.

In this chapter we describe two existing methods (regression and Powell's method) and a modified Powell's method that takes individual variability into account. The objective of this chapter is to investigate the bias in these methods due to individual variability in growth. The methods are evaluated in a simulation study using a model that incorporates individual variability. The aspects we focus on are the bias and variability of the estimates and the robustness to violations of distributional assumptions.

1.2 Estimation Methods

We assume that the growth of individuals follows a von Bertalanffy curve so that the length at age a is given by

$$L(a) = L_\infty(1 - e^{-ka}). \tag{1.1}$$

We also assume that the population undergoes constant mortality z. A few methods are available to estimate the ratio $\theta \equiv z/k$, a key parameter in population dynamics. These methods, based on Beverton and Holt (1956), assume that recruitment is continuous and constant throughout the year, leading to a population with an exponentially distributed age structure with mortality as the parameter of the distribution. Under this assumption, the length-frequency distribution is expected to have declining proportions over sizes.

1.2.1 Regression method

Beverton and Holt (1956) first derived an expression for estimating z from length-frequency data and growth parameters (k, l_∞),

$$z = k\frac{l_\infty - \bar{L}}{\bar{L} - L_m}, \tag{1.2}$$

where $\bar{L}$ is the mean length of individuals with length above L_m, and L_m is any value such that individuals with length above L_m are fully vulnerable to the fishing gear. This method was established under the assumption that all individuals follow the same von Bertalanffy growth curve.

The Beverton-Holt equation (1.2) can be rearranged into the following regression form:

$$\bar{L} = \alpha + \beta L_m, \tag{1.3}$$

where $\alpha = l_\infty/(1+\theta)$ and $\beta = \theta/(1+\theta)$. Estimates of (α, β) can be obtained by regressing $\bar{L}$ on different L_m values. A weighting function that takes account of correlations between the observed means may be used to improve the estimation efficiency (Wetherall, Polovina and Ralston, 1987). However, we will simply take the number of fish used to calculate the mean as the weight in the regression. If $(\hat{\alpha}, \hat{\beta})$ are the estimates so obtained, we can estimate (l_∞, θ) by

$$\hat{\theta} = \frac{\hat{\beta}}{1-\hat{\beta}} \quad \text{and} \quad \hat{l}_\infty = \frac{\hat{\alpha}}{1-\hat{\beta}}.$$

1.2.2 Powell's two-moment method

Powell (1979) first examined the effect of variability in L_∞ on the estimates of θ assuming constant recruitment and constant mortality. We denote the density function of L_∞ as $p(x)$, which has a mean of l_∞ and a variance of σ^2.

If all the recruits have the same size l_0 and mortality is constant, then the density function of L, $f(l)$, satisfies

$$f(l) = \theta \int_l^\infty \frac{(x-l)^{\theta-1}}{(x-l_0)^\theta} p(x|L_0 = l_0)dx. \tag{1.4}$$

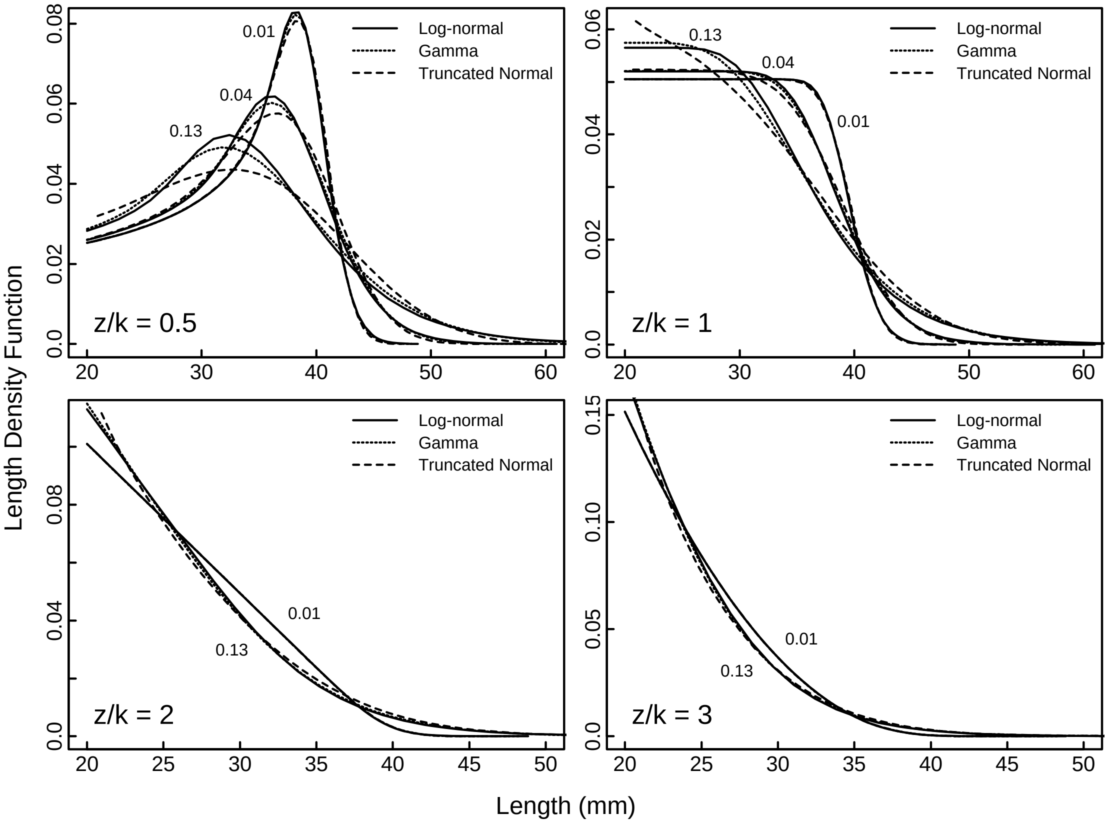
The derivation is given in 1.4 (see also Powell (1979)). In this case, we can just write $p(x|L_0 = l_0)$ as $p(x)$, which represents the distribution of the maximum length of an individual with recruitment length l_0. Note that, under this model, recruitment of individuals with length $L_m(> l_0)$ is also constant. Fig. 1.1 shows examples of some length density functions for several values of σ^2 and various distributions of L_∞.

The moments of the length distribution about l_0 satisfy

$$m_n = \mathrm{E}\{(L-l_0)^n\} = \frac{\Gamma(n+1)\Gamma(\theta+1)}{\Gamma(n+\theta+1)} \mathrm{E}\{(L_\infty - l_0)^n\}. \tag{1.5}$$

Note that the moments of the length distribution are simply proportional to the moments of the L_∞ distribution, with constant of proportionality dependent on

Fig. 1.1 Length density functions for the case of constant fixed-length recruitment and constant mortality. Each plot corresponds to a different value of $\theta = z/k$. We use the values 0.5, 1, 2 and 3, as studied by Powell (1979). Groups of curves within a plot are labeled by the value of the coefficient of variation of L_∞. Each group consists of a curve from each of the three distributions as shown in the legend. The recruitment length is 20 mm.



θ. Note that the first moment estimation equation ($n = 1$) is equivalent to the Beverton-Holt eq. (1.2) with $L_m = l_0$. However, when $L_m > l_0$, eq. (1.2) is no longer valid because of the conditioning of the distribution of L_∞ on L_m (see Discussion).

Powell (1979) used the first two moment equations to obtain

$$\left\{\begin{array}{lcl} \theta & = & \dfrac{2(m_2 - (1+\rho^2)m_1^2)}{2(1+\rho^2)m_1^2 - m_2}, \\ & & \\ l_\infty & = & l_0 + \dfrac{m_2 m_1}{2m_1^2(1+\rho^2) - m_2}, \end{array}\right. \tag{1.6}$$

where ρ is the coefficient of variation of $L_\infty - l_0$. Powell noticed that the bias in the estimates of (θ, l_∞) is $O(\rho^2)$, and may be ignored if ρ^2 is small. Then, approximately

$$\left\{\begin{array}{lcl} \theta & = & \dfrac{2m_2 - m_1^2}{2m_1^2 - m_2}, \\ \\ l_\infty & = & l_0 + \dfrac{m_1 m_2}{2m_1^2 - m_2}, \end{array}\right. \tag{1.7}$$

and (θ, l_∞) can be estimated by replacing the true moments on the right-hand side with the moments of the observed length distribution.

1.2.3 The third-moment method

In some cases, the individual variability in growth may be substantial and the $O(\rho^2)$ term cannot be assumed to be zero. Furthermore, it is useful to obtain an estimate of ρ^2 and hence of the variance of L_∞. We can do this by making use of the third moment and assuming a distributional form for L_∞. If $L_\infty - l_0$ is log-normally distributed then

$$\left\{\begin{array}{lcl} \theta & = & \sqrt{\dfrac{1}{1-\tau}} - 2 \\ \\ l_\infty & = & l_0 + \left(\sqrt{\dfrac{1}{1-\tau}} - 1\right) m_1 \\ \\ \rho^2 & = & \dfrac{m_2}{2m_1^2(1 - \sqrt{1-\tau})} - 1 \end{array}\right. , \tag{1.8}$$

where $\tau = 3m_2^3/4m_3m_1^3$. These equations are derived by expressing the moments in terms of the parameters, $(\theta, l_\infty, \rho^2)$, and solving for them. The moments are given by equation (1.5) and Table 1.2.

Note that distributions other than the log-normal may be used for L_∞. 1.4 provides details for three alternative distributional assumptions. The log-normal version will be used in the simulation study.

1.3 Simulation Studies

It is well known that estimates by the moment method are consistent when the model is correctly specified. Therefore Powell's method and the regression method give consistent estimates only when there is no individual variability, whereas the third-moment method should provide consistent estimates when the underlying distribution is correctly specified.

We now evaluate the three estimation methods by applying them all to simulated length-frequency data. Since these methods assume constant recruitment, we shall limit our study to the constant recruitment case in order to focus on the effect of individual variability.

We model the individual variability by assuming $L_\infty - l_0$ is log-normally distributed for a range of values of the coefficient of variation. We simulate length-frequency data by sampling from the theoretical length distribution that is derived from the L_∞ distribution. We then generate estimates from the simulated data set for each method. The sampling is repeated 100 times to give a reasonable estimate of the sampling variation in $\hat{\theta}$ and $\hat{l}_\infty$.

We can also find the asymptotic value of the estimates when the sample size is infinite and the length distribution is known without error. This asymptotic value is found by computing the estimate directly from the theoretical length distribution.

We then test the robustness of the log-normal distributional assumption by repeating the simulation for data sampled from different underlying distributions. In this case all three methods are biased. We consider two alternative cases for the distribution of L_∞: the gamma distribution and the truncated normal.

We also carry out a test of the robustness of the assumption of fixed k by repeating a subset of the simulation for data sampled with additional variation in k.

All the simulation work reported here was implemented in S-plus; the code is available via anonymous ftp at ftp://bne.marine.csiro.au/pub/wan032/f9515/zk.

Comparison of methods

We now aim to predict the distribution of real-data estimates by simulation. We follow Powell's example by considering the values $\theta = 0.5$, 1, 2 and 3. We assume $\log(L_\infty - l_0) \sim N(\mu, \sigma^2)$. The parameter σ is approximately the coefficient of variation ρ. We consider values of ρ ranging from 0% to about 36% (which we believe to be a reasonable range for our prawn fishery). Given ρ, we choose μ so that $\mathrm{E}(L_\infty) \equiv l_\infty = 40\,\mathrm{mm}$. The length of recruits, l_0, is 20 mm and recruitment is assumed to be uniform. (The actual choice of units is based on carapace lengths typical for tiger shrimps.)

For each θ and ρ we sample 1000 times from the distribution $f(l)$. This is actually implemented as a sampling from the L_∞ distribution, $p(\cdot)$, followed by a sampling from the age distribution conditional on L_∞ and L_0 given by eq. (A.3). The sampled lengths are then grouped into 1-mm length classes starting at 20 mm. We then apply each of the three estimation methods to the resulting length-frequency data set. We repeat the procedure 100 times for each θ and ρ.

The asymptotic (infinite sample) estimates for each method are derived from the length density function $f(l)$, which is computed from eq. (1.4) by numerical integration using a fourth-order scheme. The summation is carried out over a grid that is uniform with respect to the quantiles of the lognormal distribution, except in the neighborhood of the lower limit of the integral; here the integration scheme is modified to handle the integrable singularity in the cases when $0 < \theta < 1$.

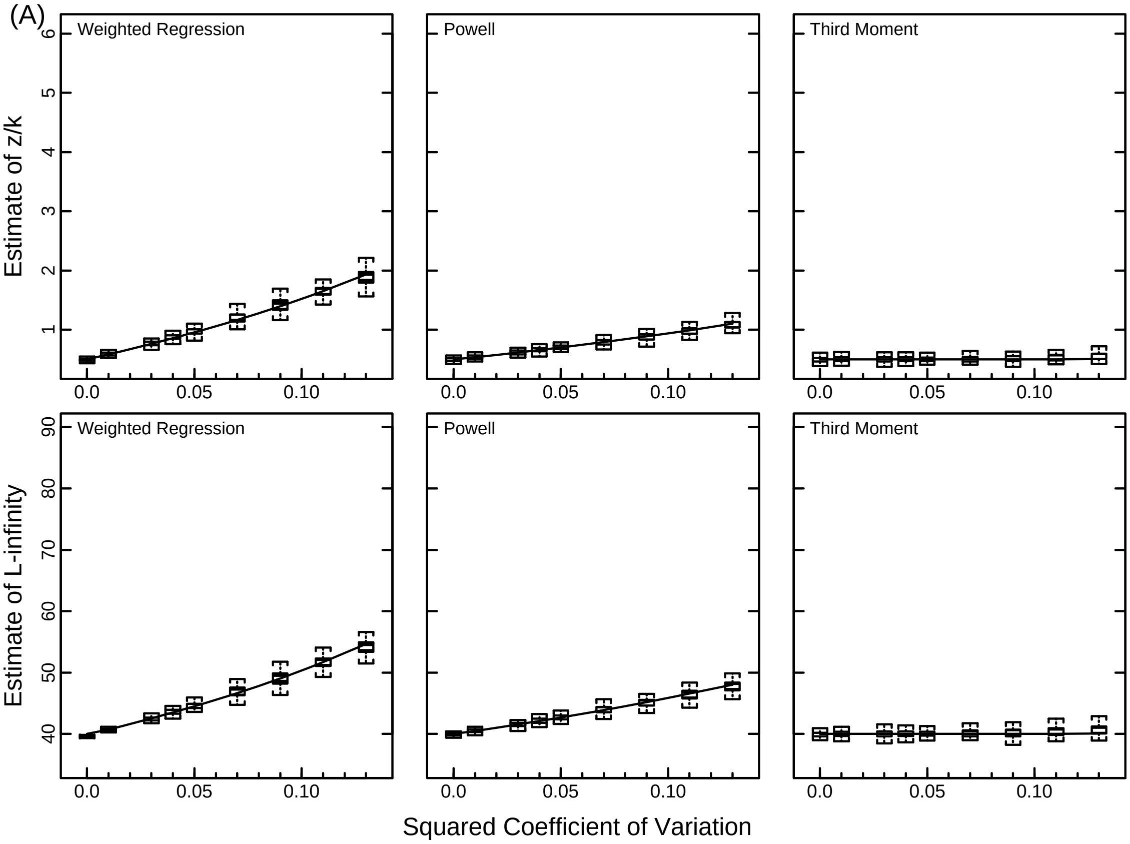
The regression method works by regressing mean length, $\bar{L}$, on truncation length, L_m. We adopt a weighted regression scheme with weights equal to the proportion of the population exceeding the truncation length. In practice, regression may be done by inspecting the graph of $\bar{L}$ vs L_m and rejecting points that look out of place beyond some cut-off L_m. Rejection is usually justified on the basis of the violation of some assumption (e.g. uniform vulnerability). However, in our simulation, all the basic assumptions are satisfied, so there is no need to resort to *ad hoc* inspection of graphs, which, in any case, would be difficult to implement.

The results of the simulations for $\theta = 0.5$ and 2 are shown (Fig. 1.2). Each graph shows box plots of the estimates over the range of ρ^2 values for a particular estimation method. The median, inter-quartile range and approximate 5th and 95th percentiles of the 100 estimates are represented in the box plots as a central line, a box and whiskers respectively. A curve showing the asymptotic estimates is overlaid on each graph. For ease of comparison, estimates are plotted on the same scale for all three methods and both values of θ. It is reassuring to see that the asymptotic curves agree well with the means of the box plots. This indicates that the accuracy of the numerical calculation of asymptotic bias and the number of simulations (100) for the box plots are adequate.

With simulated or real data we may sometimes find $\tau > 1$ (see eq. (1.8)), in which case the third-moment estimates become imaginary. This is a potentially serious drawback to the method. However in our simulations it is a rare occurrence. We found $\tau > 1$ occurred only for the case $\theta = 3$ (not shown) and $\rho^2 \geq 0.09$ and the incidence rate was 6 times in 300 simulations.

It is evident that the weighted regression and Powell methods display positive bias that increases with ρ and θ. Indeed, as Powell said, the bias in his method is almost linear in ρ^2. However, the $O(\rho^2)$ term that has been omitted in eq. (1.7) is not negligible even for small ρ. The variation of the estimates also increases with both ρ and θ. The third-moment method, on the other hand, is unbiased for all ρ and θ. As for the variance of the estimates, there is a small increase with ρ and a much more substantial increase with θ. For all methods, the variation can be reduced by increasing the sample size. Note that for $\rho = 0$ (when all methods are unbiased) the third-moment method is the most variable. This is because, as one referee pointed

Fig. 1.2(a) Estimates of $\theta = z/k$ (*top*) and l_∞ (*bottom*) from 100 simulations of length-frequency data using the three estimation methods. In each simulation 1000 individuals were generated according to constant recruitment at 20 mm, constant mortality z (with $\theta = 0.5$) and L_∞ randomly sampled from a log-normal distribution with mean 40 mm, lower cut-off 20 mm and squared coefficient of variation of L_∞ ranging from 0 to 0.13. The distribution of estimates is displayed as box-and-whisker plots, which show the median, interquartile range and approximate 5th and 95th percentiles. The theoretical estimates obtained from the density function are overlaid as a solid line.

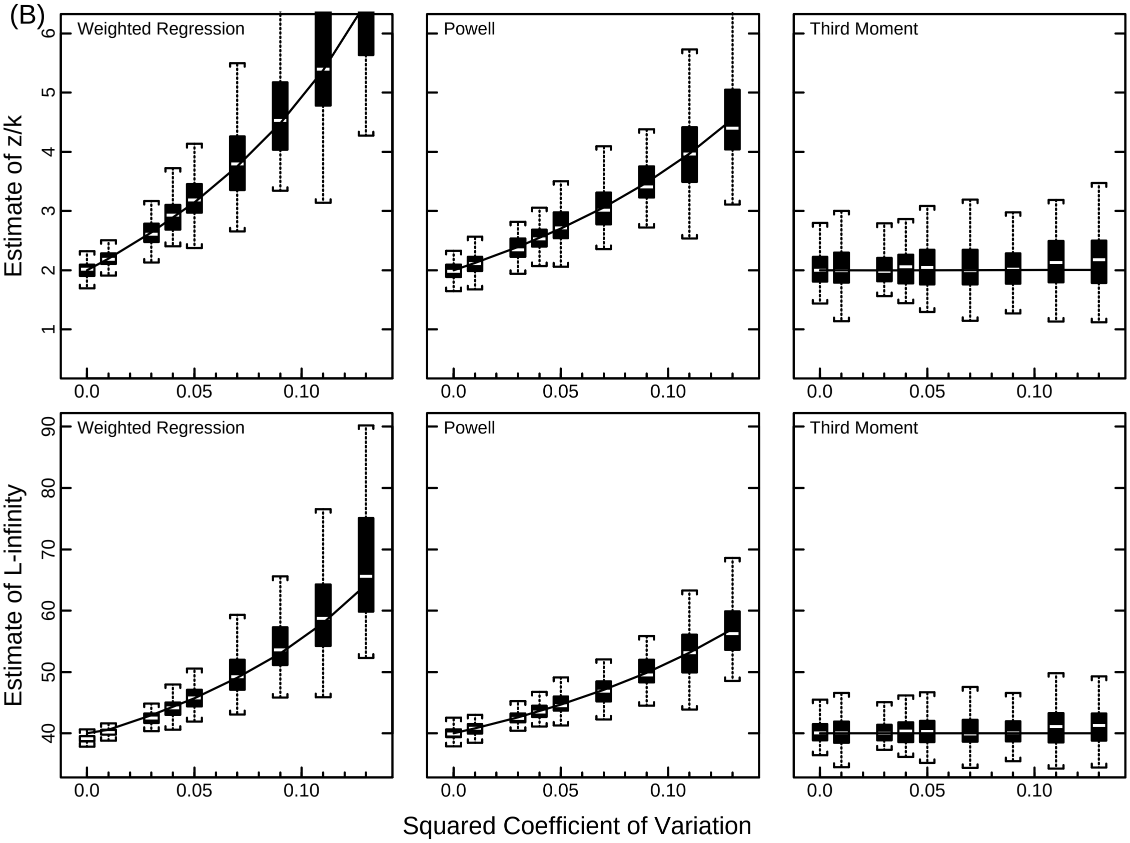


out, the third-moment estimates depend more sensitively on the tails of the length distributions, for which there are fewer observations.

1.3.1 Robustness of the distributional assumption

The third-moment method depends on the log-normal distributional assumption. We test the robustness of the third-moment method by applying the methods to simulated data generated from the log-normal distribution and two other distributions: the truncated normal and the gamma. In order for the distributions to be comparable, we constrain them to have the same mean and coefficient of variation.

Fig. 1.2(*b*) As Fig. 1.2(*a*) but with $\theta = 2$.



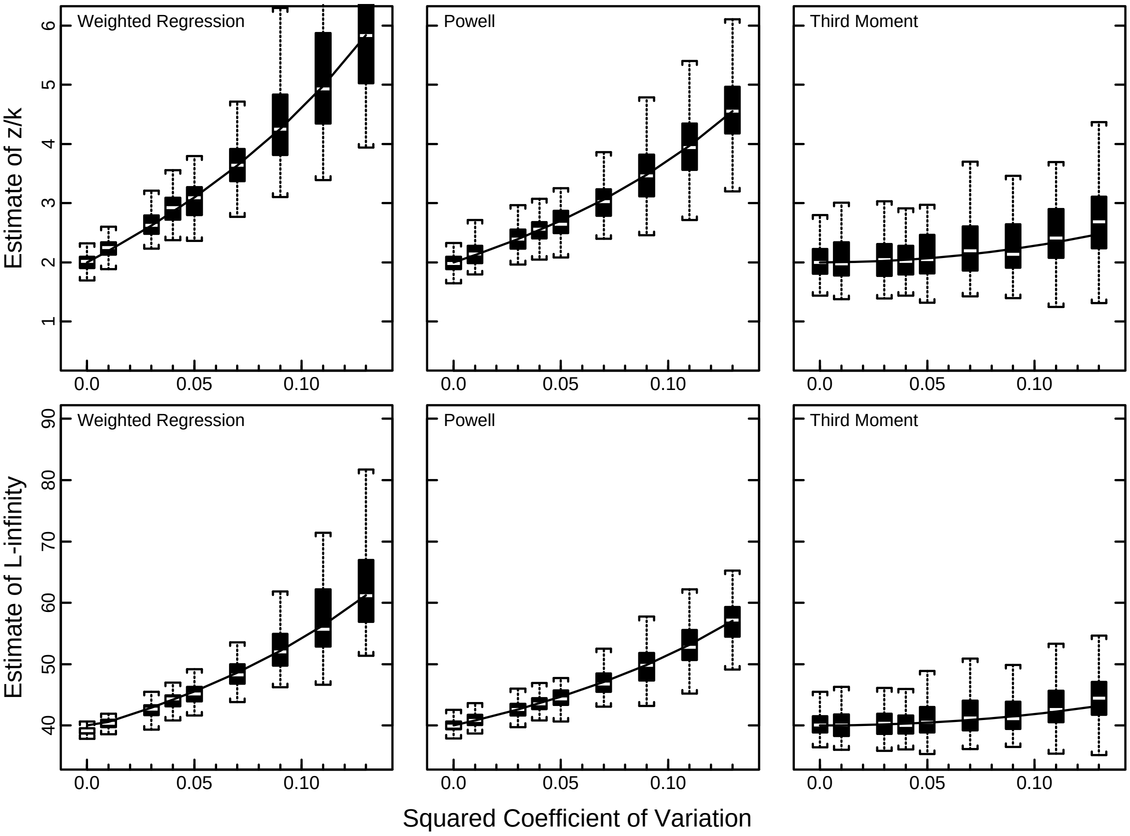
Note that eq. (1.5) therefore implies that the three length distributions under comparison are identical in their first two moments. Properties of the distributions are summarized in 1.4. In particular, this Appendix shows how we can obtain the parameters of the distribution if we know the mean and coefficient of variation.

For small ρ^2 the length density functions arising from the three distributions are fairly similar (Fig. 1.1). For larger ρ^2 the three densities take on their own character, with the log-normal and gamma densities resembling each other more closely than the truncated normal.

Simulation results using data generated from the underlying gamma distribution have been obtained, again for $\theta = 0.5$ and 2. We show the results for $\theta = 2$ in Fig. 1.3, where the same scale has been used as in Fig. 1.2. The results are very similar to the results for the log-normal distribution. There is a small positive bias for the third-moment method, which increases with ρ and θ. However, this bias is much less than that for Powell's method or the regression method.

The results for an underlying truncated normal distribution are shown in Fig. 1.4. Curiously, the weighted regression estimates have improved. The bias in the third-moment method is now larger still because the truncated normal distribution is even

Fig. 1.3 Estimates of $\theta = z/k$ (*top*) and l_∞ (*bottom*) when the underlying L_∞ distribution is gamma, whereas the third-moment and maximum likelihood methods erroneously assume an underlying lognormal. 100 simulated length-frequency data sets of 1000 individuals were generated according to constant recruitment at 20 mm, constant mortality z (with $\theta = 2$) and $l_\infty = 40$mm. The theoretical estimates obtained from the density function are overlaid as a solid line.

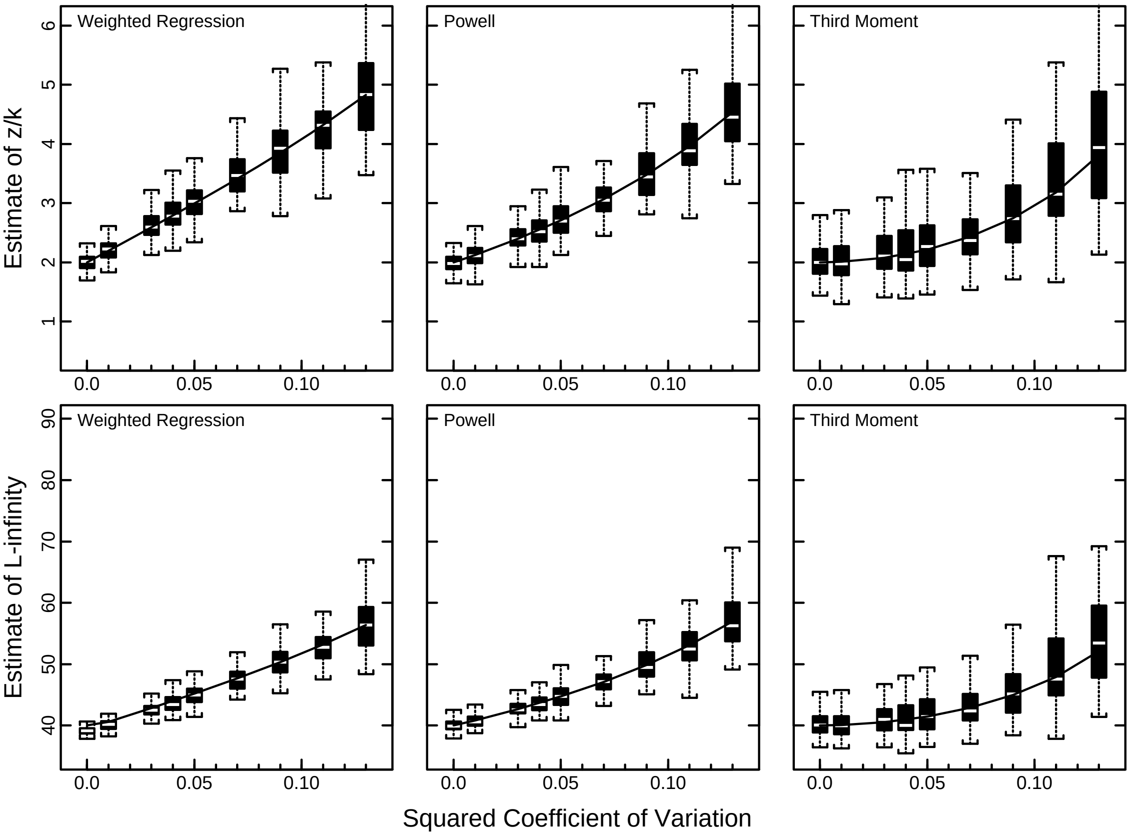


more different from the log-normal than the gamma distribution. The third-moment method is still less biased than Powell's method for $\theta = 0.5$. However, for $\theta = 2$ the improvement becomes less clear-cut for $\rho^2 > 0.10$ ($\rho > 32\%$).

1.3.2 Robustness of the fixed-k assumption

We have assumed that the parameter k is the same for all individuals. We test this assumption by allowing k to be a log-normal random variable. As in the previous robustness study, we have run all the estimation methods on simulated data generated under the additional property of random k. This means that, for each simulation we have taken 1000 samples from the k distribution, independently of the samples for L_∞ and age. We let k have mean $3\,\mathrm{yr}^{-1}$ and we allow two levels (10%, 20%) for the coefficient of variation ρ_k. We consider two cases for the mor-

Fig. 1.4 Estimates of $\theta = z/k$ (*top*) and l_∞ (*bottom*) when the underlying L_∞ distribution is truncated normal, whereas the third-moment method erroneously assumes an underlying log-normal. 100 simulated length-frequency data sets of 1000 individuals were generated according to constant recruitment at 20 mm, constant mortality z (with $\theta = 2$) and $l_\infty = 40$mm. The theoretical estimates obtained from the density function are overlaid as a solid line.



tality: $z = 1.5$ and 6 corresponding to $\theta = 0.5$ and 2, where now $\theta = z/\mathrm{E}(k)$. The underlying L_∞ distribution is log-normal with two levels of variation: $\rho_{L_\infty} = 10\%$ and 20% (the subscript L_∞ is added to avoid confusion with ρ_k). The simulations of the comparison study provide control cases corresponding to $\rho_k = 0\%$.

The means and standard deviations of the estimates of θ and l_∞ over 100 simulations are shown in Table 1.1. The effect of variable k is to add a positive bias to all the estimates. The size of the extra bias increases with ρ_k, ρ_{L_∞} and θ and is approximately independent of the method. The bias in the third-moment method caused by random k is the same order of magnitude as the bias due to the truncated normal distribution.

Table 1.1 Mean and standard deviations (in parentheses) of (θ, l_∞) from each of the three methods under comparison for different values of the true parameters θ, ρ (here referred to as ρ_{L_∞}) and ρ_k. The underlying distribution of L_∞ is log-normal and $l_\infty = 40\,\text{mm}$. The case $\rho_k = 0\%$ is the case of fixed k, which corresponds to the data in Fig. 1.2a and 1.2b with $\rho^2 = 0.01$ and 0.04.

Estimate of θ

θ	ρ_{L_∞}	ρ_k	WR	Powell	3rd M
0.5	10%	0%	0.59 (.033)	0.54 (.038)	0.50 (.050)
		10%	0.59 (.031)	0.54 (.036)	0.51 (.049)
		20%	0.61 (.030)	0.56 (.038)	0.53 (.051)
	20%	0%	0.88 (.051)	0.66 (.045)	0.51 (.055)
		10%	0.87 (.056)	0.66 (.043)	0.51 (.047)
		20%	0.90 (.053)	0.69 (.044)	0.53 (.050)
2.0	10%	0%	2.20 (.156)	2.11 (.194)	2.06 (.429)
		10%	2.24 (.168)	2.15 (.206)	2.07 (.377)
		20%	2.34 (.186)	2.27 (.204)	2.23 (.424)
	20%	0%	2.94 (.299)	2.56 (.231)	2.06 (.341)
		10%	2.94 (.298)	2.59 (.274)	2.12 (.428)
		20%	3.10 (.320)	2.77 (.303)	2.34 (.563)

Estimate of l_∞

θ	ρ_{L_∞}	ρ_k	WR	Powell	3rd M
0.5	10%	0%	40.65 (0.21)	40.51 (0.29)	40.02 (0.49)
		10%	40.64 (0.21)	40.54 (0.30)	40.11 (0.51)
		20%	40.68 (0.20)	40.59 (0.30)	40.15 (0.51)
	20%	0%	43.57 (0.46)	42.18 (0.45)	40.07 (0.61)
		10%	43.47 (0.51)	42.11 (0.43)	40.04 (0.51)
		20%	43.61 (0.50)	42.26 (0.46)	40.17 (0.57)
2.0	10%	0%	40.17 (0.76)	40.80 (1.09)	40.44 (2.70)
		10%	40.34 (0.85)	40.95 (1.18)	40.42 (2.35)
		20%	40.80 (0.93)	41.57 (1.16)	41.36 (2.66)
	20%	0%	44.30 (1.64)	43.71 (1.43)	40.39 (2.18)
		10%	44.30 (1.63)	43.83 (1.64)	40.72 (2.69)
		20%	45.18 (1.63)	44.91 (1.73)	42.04 (3.54)

1.4 Discussion

The Beverton-Holt eq. (1.2) was originally derived under the assumption of constant L_∞. Later, Powell noticed that the equation still holds when L_∞ follows a distribution, provided the lower cut-off, L_m, equals the minimum recruitment length, l_0.

The result follows easily from eq. (1.5) after setting $n = 1$. We have assumed the cut-off chosen by the experimenter L_m and the minimum length of the recruited population l_0 are the same, thus avoiding more complicated conditional moment formulas. However, for $L_m > l_0$, eq. (1.2) is no longer valid because the length distribution must be replaced by a truncated distribution. In general, the truncated nth moment relative to L_m is given by

$$m_n = \mathrm{E}\{(L - L_m)^n | L \geq L_m\} = \frac{\int_{L_m}^{\infty} (l - L_m)^n f(l) dl}{\int_{L_m}^{\infty} f(l) dl}. \tag{1.9}$$

The numerator of the right-hand side of this equation becomes

$$\begin{aligned} &\mathrm{E}\{(L - L_m)^n I(L \geq L_m)\} \\ &\quad = \frac{\Gamma(n+1)\Gamma(\theta+1)}{\Gamma(n+\theta+1)} \mathrm{E}\left\{ \frac{(L_\infty - L_m)^{n+\theta}}{(L_\infty - l_0)^\theta} I(L_\infty \geq L_m) \right\}, \end{aligned} \tag{1.10}$$

where $I(\cdot)$ is an indicator function. The denominator is given by the same expression with $n = 0$. Therefore, the truncated moments of the length distribution are no longer simply proportional to the moments of the L_∞ distribution; instead a weighting term $\{(L_\infty - L_m)/(L_\infty - l_0)\}^\theta$ must be introduced. This weighting term has the effect of increasing the overall slope of $\bar{L}$ against L_m, thus leading to an overestimate of β and so of θ.

In this chapter we have used the methods on a very idealized case, namely uniform recruitment at constant length and constant mortality, an assumption which is unlikely to be true in practice. It is also probably true that both (k, L_∞) may vary between individuals. However, as pointed out by Wang, Thomas and Somers (1995), it is generally adequate to allow L_∞ to vary to account for individual variability. The simplified models investigated here allow us to see more clearly the effect of individual variability. It would serve little purpose to compare the methods on a more complicated model with, say, seasonal recruitment and effort because the inaccuracy in the methods would be due to several causes.

The simulation studies show that all methods are biased when distributional assumptions are violated. The third-moment method, although performing better in terms of bias, is not wholly satisfactory. Other modifications to Beverton and Holt's method (Ssentongo and Larkin, 1973; Ebert, 1980; Hoenig, 1987) have strong limitations and disadvantages, as pointed out by Vetter (1988). Therefore, we believe there is a need to develop more comprehensive models to accommodate general aspects. We have developed a maximum-likelihood approach incorporating individual variability and arbitrary recruitment pattern and time-varying mortality (Wang and Ellis, 1998).

Appendix 1.1. Derivation of eq. (1.4)

If $f(l)$ is the probability density function of L at any time, then

$$f(l) = \int_l^\infty p(x) f(l|L_\infty = x)dx, \tag{A.1}$$

where $f(l|L_\infty = x)$ is the probability density function of L at time t when L_∞ is known to equal x.

If L_∞ is known the the random variables L, age A and age at recruitment A_0 are deterministically linked by eq. (1.1). Therefore $f(l|L_\infty = x)$ can be expressed in terms of the conditional age density function, $h(a|L_\infty = x, A_0 = a_0)$, as

$$f(l|L_\infty = x) = \frac{1}{k(x-l)} h\left(-k^{-1}\log(1-l/x)\middle| x\right). \tag{A.2}$$

The age distribution satisfies

$$h(a|L_\infty = x, A_0 = a_0) = z e^{-(a-a_0)z}.$$

We therefore have

$$\begin{aligned} h(a|L_\infty = x) &= h\left(a|L_\infty = x, A_0 = -k^{-1}\log(1-l_0/x)\right) \\ &= z\left(\frac{x}{x-l_0}\right)^\theta e^{-az}, \end{aligned} \tag{A.3}$$

and equation (1.4) follows from (A.1), (A.2) and (A.3).

Appendix 1.2. Third-moment estimation under various distributional assumptions

The form of the third-moment estimators depends on the assumed distribution of L_∞. Table 1.2 gives properties of the log-normal distribution and the two other distributions that were used in the robustness study. The table shows how the two parameters of each distribution can be computed from the mean and coefficient of variation (note that $\mu_1 = l_\infty - l_0$). Also shown are the moments, μ_i, of the distribution in terms of its parameters.

The truncated normal case requires further explanation. The parameter x_0 is found by solving the equation for ρ^2: the solution x_0 is the limit of the sequence u_i ($i = 0$, $1, \ldots$), where

$$u_0 = 0 \text{ and } u_{i+1} = \frac{2(\psi(u_i)^2(1+\rho^2) - 1)}{\psi(u_i)(1+2\rho^2) + \sqrt{\psi(u_i)^2 + 4\rho^2}}.$$

We will use $\phi(\cdot)$ to denote the standard normal probability density function and $\Phi_c(\cdot)$ to denote the standard normal complementary cumulative density function. For convenience, we define $\psi(x) = \phi(x)/\Phi_c(x)$, $G(x) = \psi(x) - x$, $x_0 = (l_0 - \mu)/\sigma$ and $G_0 = G(x_0)$. Note that $\mu_i = \mathrm{E}\{(L_\infty - l_0)^i\}$ and $m_i = \mathrm{E}\{(L - l_0)^i\}$, the moments of the L_∞ and L distributions, respectively. Therefore, μ_i can be defined by this recurrence relation

$$\mu_n = (n-1)\sigma^2\mu_{n-2} - x_0\sigma\mu_{n-1}, \text{ with } \mu_0 = 1 \text{ and } \mu_1 = \sigma G_0. \tag{A.4}$$

The moments of the length distribution m_i depend on $p(\cdot)$ only through its moments μ_i thus

$$m_i = \frac{\Gamma(i+1)\Gamma(\theta+1)\mu_i}{\Gamma(\theta+i+1)};$$

this is a restatement of eq. (1.5).

The lower section of Table 1.2 shows the estimates of ρ^2, θ and l_∞ in terms of quantities derived from the first three moment estimates. The estimate of the auxiliary parameter x_0, namely $\hat{x}_0$, is the solution of the equation

$$M_3G(x)((x^2+2)G(x) - x) + M_2G(x)^2(1 - xG(x)) - 4(1 - xG(x))^2 = 0. \tag{A.5}$$

Being a non-linear equation in a single variable, this equation can easily be solved numerically, provided a root exists. We suspect, however, that it is possible to obtain data that leave this equation with no real solution.

Table 1.2 Properties of the log-normal, gamma and truncated normal distributions, which are candidate distributions for the von Bertalanffy parameter L_∞. $p(y|l_0)$ is the density function at $L_\infty = y$. Estimates are given in terms of the moment estimates $\hat{m}_i$ and dimensionless quantities derived from them: $\hat{\tau} = 3\hat{m}_2^3/4\hat{m}_3\hat{m}_1^3$, $M_2 = \hat{m}_2/\hat{m}_1^2$, $M_3 = 3\hat{m}_2^2/\hat{m}_1\hat{m}_3$, $M = M_2M_3$ and $\hat{G}_0 = G(\hat{x}_0)$. For definitions of μ_i, G, x_0 and $\hat{x}_0$, see text.

	Log-normal	Gamma	Truncated normal
1. Properties of the L_∞ distribution			
$p(y\|l_0)$	$\dfrac{\phi\left(\sigma^{-1}[\ln(y-l_0)-\mu]\right)}{y-l_0}$	$\dfrac{(y-l_0)^{\alpha-1}e^{-(y-l_0)/\beta}}{\beta^\alpha\Gamma(\alpha)}$	$\dfrac{\phi(\sigma^{-1}(y-\mu))}{\Phi_c(x_0)}$
ρ^2	$e^{\sigma^2}-1$	$1/\alpha$	$1/G_0^2 - x_0/G_0 - 1$
μ_i	$e^{i\mu}e^{(i\sigma)^2/2}$	$\dfrac{\Gamma(\alpha+i)\beta^i}{\Gamma(\alpha)}$	see eq. (A.4)
par. 1	$\sigma^2 = \ln(1+\rho^2)$	$\alpha = 1/\rho^2$	$\sigma = \mu_1/G_0$
par. 2	$\mu = {}^1\!/_2 \ln \dfrac{\mu_1^2}{1+\rho^2}$	$\beta = \mu_1\rho^2$	$\mu = l_0 - \mu_1 x_0/G_0$
2. Estimates from moments of the length distribution			
$\hat{\rho}^2$	$\dfrac{{}^1\!/_2 M_2}{1-\sqrt{1-\hat{\tau}}} - 1$	$\dfrac{M_3+M_2-4}{2(2-M_3)}$	$1/\hat{G}_0^2 - \hat{x}_0/\hat{G}_0 - 1$
$\hat{\theta}$	$\sqrt{\dfrac{1}{1-\hat{\tau}}} - 2$	$\dfrac{3M_2+M_3-2M}{M-M_2-M_3}$	$\dfrac{M_2\hat{G}_0^2+\hat{x}_0\hat{G}_0-1}{1-\hat{x}_0\hat{G}_0-{}^1\!/_2 M_2\hat{G}_0^2}$
$\hat{l}_\infty - l_0$	$\hat{m}_1\left(\sqrt{\dfrac{1}{1-\hat{\tau}}}-1\right)$	$\hat{m}_1\left(\dfrac{4M_2+2M_3-3M}{M-M_2-M_3}\right)$	$\dfrac{{}^1\!/_2 \hat{m}_1 M_2\hat{G}_0^2}{1-\hat{x}_0\hat{G}_0-{}^1\!/_2 M_2\hat{G}_0^2}$

Chapter 2

Maximum Likelihood Estimation from Multiple Length-Frequency Data

We consider estimation of mortality rates and growth parameters from length-frequency data of a fish stock, and derive the underlying length distribution of the population and the catch when there is individual variability in the von Bertalanffy growth parameter L_∞. The model is flexible enough to accommodate (i) any recruitment pattern as a function of both time and length, (ii) length-specific selectivity and (iii) varying fishing effort over time. The maximum likelihood method gives consistent estimates provided the underlying distribution for individual variation in growth is correctly specified. Simulation results also indicate that our method is reasonably robust to violations in the assumptions. The method is applied to real grooved tiger prawn data (*Penaeus semisulcatus*) to obtain estimates of natural and fishing mortality.

2.1 Introduction

Estimation of growth and mortality is fundamental in fisheries and other areas because stock assessment and management rely on the knowledge of these population parameters. Length-frequency based methods become important when aging is either not possible or very expensive. Existing methods such as that of Beverton and Holt (1956) assume that recruitment is continuous and constant throughout the year, which leads to a population with an exponentially distributed age structure. Existing modifications to Beverton and Holt's method use some simple recruitment patterns or distributions (Ssentongo and Larkin, 1973; Ebert, 1980; Hoenig, 1987;

Wetherall, Polovina and Ralston, 1987). As pointed out by Vetter (1988), the existing methods for estimating mortality in the literature have strong limitations and disadvantages. In particular, they require the following assumptions:

(A1) each individual follows the same von Bertalanffy growth curve;

(A2) the recruitment is either continuous and constant throughout the year (as in Beverton and Holt (1956) and Wetherall, Polovina and Ralston (1987)) or a pulse function in Hoenig (1987);

(A3) the total instantaneous mortality, z, is independent of time (i.e. both natural and fishing mortality rates are constant).

As pointed out by Sainsbury (1980), it is more realistic to allow individual variability in growth. For example, using tag-recapture data, Wang, Thomas and Somers (1995) found substantial individual variability for the tiger prawn species *P. semisulcatus*.

Although it is well understood that variability leads to increased uncertainty in estimates, it is less well recognized (among the fisheries community) that variability can also lead to bias. Wang and Ellis (1998) analysed the effect of ignoring individual variability in a simplified context of constant recruitment and a single length-frequency record. They found that, when L_∞ (with mean l_∞) was allowed to be a random variable, two existing methods gave positively biassed estimates for l_∞ and z/k, the bias increasing with the variance of L_∞. For example, for coefficient of variation 20% and $z/k = 2$ the weighted regression method of Wetherall, Polovina and Ralston (1987) gave an estimate of 2.94 ± 0.30. (Note that we use L_∞ to denote the *random variable*, and we reserve $l_\infty = \mathrm{E}(L_\infty)$ for the mean parameter.)

Estimation of mortality relies on the distribution of the length, which is determined by the age distribution, mortality rates and the individual variability in growth rates. If individual variability in growth is ignored, an inappropriate length distribution will be generated, which may lead to biases in parameter estimates. Further to the necessity of bias reduction, it is also biologically interesting to quantify the individual variability in growth, which has important implications in fisheries management.

In this study, we consider the length distribution when (i) there is individual variability in growth parameters; and (ii) the recruitment function is arbitrary. The model presented here is flexible enough to incorporate various sizes at recruitment and fishing selectivity function although we did not use these aspects in the analysis of tiger prawn data. Some analytical expressions are derived for these generalizations. A maximum likelihood approach is developed for estimation of mortality and growth parameters. Simulation studies are carried out to determine the performance of the method. The simulated data are generated from the recruitment pattern of the brown tiger prawn (*Penaeus esculentus*) in the Northern Prawn Fishery of Australia. Estimates of both natural mortality and fishing mortality are quite reliable when growth parameters are assumed known, because growth parameters are often available from other studies. Finally we apply the maximum likelihood method to real grooved tiger prawn data (*P. semisulcatus*), which were also collected from the Northern Prawn Fishery.

2.2 The Model

We assume that the growth of individuals follows a von Bertalanffy curve so that the length at age a (relative to some origin t_0) is given by (1.1). To provide a general treatment we relax each of the assumptions mentioned in the introduction. First we relax assumption (A1) by letting the maximum length, L_∞, vary within the population. We denote the density function of L_∞ as $p(x)$, which has a mean of l_∞ and a variance of σ^2. It is possible that recruits to the fishery have a range of sizes. To allow for this we let the size at recruitment, L_0, be a random variable with density function $u(s)$. In practice, one may be able to use information from other studies to arrive at an approximate parametric form for $u(s)$.

If $f_t(l)$ is the probability density function of L at time t, then

$$f_t(l) = \int_0^\infty \int_l^\infty p(x|L_0 = s) f_t(l|L_\infty = x, L_0 = s) u(s) dx ds, \tag{2.1}$$

where $f_t(l|L_\infty = x, L_0 = s)$ is the probability density function of L at time t when L_∞ is known to be x and the size at recruitment is s.

Denote the age at recruitment of an individual as A_0. From equation (1.1), $f_t(l|L_\infty = x, L_0 = s)$, which may be written as $f_t(l|x, s)$ for brevity, can be expressed using the conditional distribution of age (see Wang, Thomas and Somers (1995)), $h_t(a|L_\infty = x, A_0 = a_0)$

$$f_t(l|x, s) = \frac{1}{k(x-l)} h_t\left(-k^{-1}\log(1 - l/x) \middle| x, a_0\right). \tag{2.2}$$

We now generalize assumptions (A2) and (A3) by introducing the intensity function of recruitment, $r(t)$, and the total instantaneous mortality, $z(t)$, which are arbitrary functions of time t. The total mortality would depend on time through the fishing mortality component F, where $z(t) = M + F(t)$ and M is the constant natural mortality.

The age distribution satisfies

$$h_t(a|L_\infty = x, A_0 = a_0) \propto r(t - a + a_0) \exp\{-\int_{a_0}^a z(t - a + y) dy\}.$$

This equation states that the density of individuals of age a is proportional to the intensity of recruitment at the time when they were recruited, namely $t-a+a_0$, times a reduction factor due to mortality over the intervening period. We therefore have

$$\begin{aligned} h_t(a|x,s) &= h_t(a|L_\infty = x, A_0 = -\frac{1}{k}\log(1-s/x)) \\ &\propto \exp\left(-\int_{-k^{-1}\log(1-s/x)}^{a} z(t-a+y)dy\right) r\left(t-a-k^{-1}\log(1-s/x)\right) \end{aligned} \tag{2.3}$$

and equation (2.2) becomes

$$f_t(l|x,s) \propto \frac{1}{x-l}\exp\left(-\int_{t-k^{-1}\log(\frac{x-s}{x-l})}^{t} z(y)dy\right) r\left(t-k^{-1}\log\left(\frac{x-s}{x-l}\right)\right). \tag{2.4}$$

Let us consider the case of fixed recruitment length, i.e., $L_0 = l_0$, and define a parameter vector, $\boldsymbol{\beta}$, consisting of (k, l_∞, σ), and other parameters quantifying mortality and catchability. Equation (2.1) then reduces to a single integral over x,

$$f_t(l;\boldsymbol{\beta}) \propto \int_l^\infty p(x)\exp\left(-\int_{t-k^{-1}\log(\frac{x-l_0}{x-l})}^{t} z(y)dy\right) r\left(t-k^{-1}\log\left(\frac{x-l_0}{x-l}\right)\right)\frac{dx}{x-l}. \tag{2.5}$$

A more convenient form for computation arises after changing the integration variable from the asymptotic length x to time since recruitment,

$$\tau = k^{-1}\log\left(\frac{x-l_0}{x-l}\right). \tag{2.6}$$

The expression (2.5) then becomes

$$f_t(l;\boldsymbol{\beta}) \propto \int_0^\infty p(x(\tau))\exp\left(-\int_{t-\tau}^{t} z(y)dy\right) r(t-\tau)\frac{d\tau}{1-e^{-k\tau}}. \tag{2.7}$$

In the special case of constant recruitment, i.e., $r(t)=1$, and constant mortality, $z(t)=z$, $f_t(l;\boldsymbol{\beta})$ becomes independent of time. From expression (2.5), we obtain

$$f(l;\boldsymbol{\beta}) = \theta\int_l^\infty \frac{(x-l)^{\theta-1}}{(x-l_0)^\theta}p(x|L_0=l_0)dx, \tag{2.8}$$

in which $\theta = z/k$. This expression was first derived by Powell (1979).

2.3 Maximum Likelihood Estimation

Let $p_{ij}(\boldsymbol{\beta})$ be the expected proportion of individuals in the i-th length class $(l_{i-1}, l_i]$ on the j-th occasion, where $i = 1, 2, \ldots, N$; and let n_{ij} be the corresponding observed numbers. The value of $p_{ij}(\boldsymbol{\beta})$ can be obtained from the density function $f_t(l;\boldsymbol{\beta})$ given by equation (2.1). Thus

$$p_{ij}(\boldsymbol{\beta}) = \frac{\int_{l_{i-1}}^{l_i} f_j(x;\boldsymbol{\beta})dx}{\int_{l_0}^{l_N} f_j(x;\boldsymbol{\beta})dx}, \tag{2.9}$$

in which $f_j(x;\boldsymbol{\beta})$ is the (unnormalized) density function on the j-th occasion.

Under a multinomial model, estimation of the parameter vector $\boldsymbol{\beta}$ relies on the procedure:

$$\text{maximize} \sum_{i,j} n_{ij} \log p_{ij}(\boldsymbol{\beta}) \text{ with respect to } \boldsymbol{\beta}. \tag{2.10}$$

The sum is the log-likelihood function up to a constant independent of the parameters. The probability, p_{ij}, can be approximated as $f_j(l_{i+1/2})/\sum_i f_j(l_{i+1/2})$, which is the normalized value of the density function for the j-th occasion at the midpoint of the i-th length class.

If sampling effort is known and expected catch is assumed to be a known function of effort and population abundance, the log-likelihood function in (2.10) can be easily modified to incorporate effort information. For example, if the total number of individuals on each occasion, $n_j = \sum_i n_{ij}$, is assumed to follow a Poisson distribution, the log-likelihood function becomes

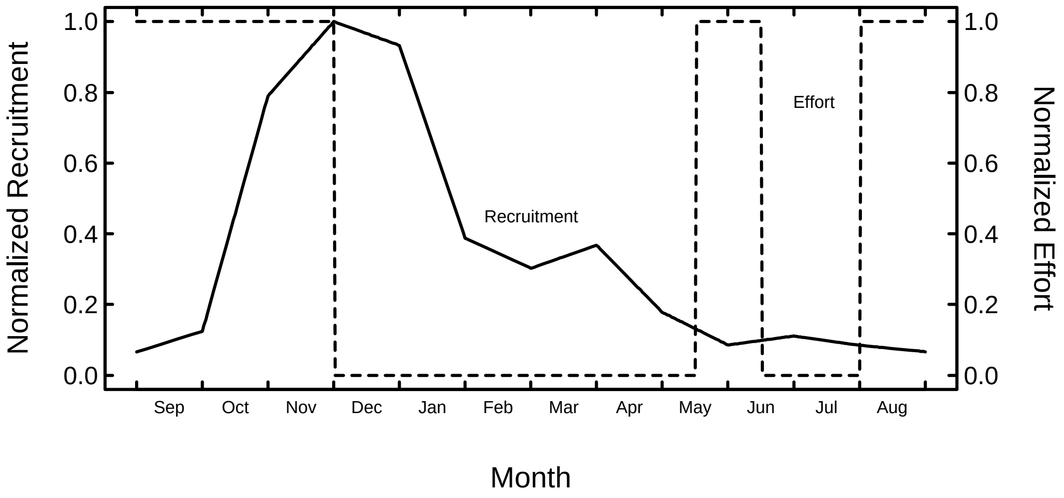
$$\sum_{i,j} n_{ij} \log p_{ij}(\boldsymbol{\beta}) + \sum_j \{n_j \log \lambda_j(\boldsymbol{\beta}) - \lambda_j(\boldsymbol{\beta})\}, \tag{2.11}$$

where $\lambda_j(\boldsymbol{\beta})$ is the expected total number in the sample on the j-th occasion and depends on effort. One way to model this dependence is $\lambda_j(\boldsymbol{\beta}) = \phi(\boldsymbol{\beta})p_j(\boldsymbol{\beta})e_j$, where e_j is the sampling effort and p_j is the expected proportion of individuals on the j-th occasion (i.e. the relative abundance), so that ϕp_j is the expected catch per unit effort. In this case we can obtain the maximum likelihood estimate of ϕ as $\sum_j n_j/\sum_j e_j p_j$. The probability, p_j, can be approximated as $\sum_i f_j(l_{i+1/2})/\sum_{i,j} f_j(l_{i+1/2})$. The second summation in (2.11) can be regarded as auxiliary information.

In our simulation and tiger prawn studies we specialize to the case of fixed, known recruitment length, l_0, and $f_j(x;\boldsymbol{\beta})$ is obtained from (2.5) or (2.7). For definiteness we set the constant of proportionality implicit in these equations to one.

The prototype implementation of our maximum likelihood method was written in S-plus. However, to improve the performance for a large number of simulations, the program was recoded in C using Powell's optimization routine (Press, Teukolsky, Vetterling and Flannery, 1992). The C code is available from ftp://bne.marine.csiro.au/wan032.

Fig. 2.1 The empirical recruitment pattern (solid line) of tiger prawns *P. esculentus* in the Northern Prawn Fishery of Australia and the fishing effort pattern (dashed line).



2.4 Simulation Studies

We simulated length-frequency data based on the recruitment pattern of tiger prawns, *P. esculentus*, in the Northern Prawn Fishery of Australia. This pattern has been derived from experimental trawls in which the number of individuals in the lowest length class are counted (Wang and Die, 1996). We assume the recruitment and effort patterns are the same in each year (Fig. 2.1). The effort pattern (dashed line) consists of two constant-fishing periods: May 15 to June 15, and August 1 to December 1. The unit of effort, E, depends on the unit of catchability, q, since qE must have unit yr^{-1}: therefore we just let $E = 1$ during the fishing season. Note that the proportion of the year that is fished is $\int E(t)dt = 5/12$.

The growth component of our models has $l_\infty = 40\,\mathrm{mm}$ and $k = 3\,\mathrm{yr}^{-1}$; the instantaneous natural mortality is $M = 2\,\mathrm{yr}^{-1}$; and the instantaneous fishing mortality, F, during the fishing season is $4\,\mathrm{yr}^{-1}$ (i.e., $q = 4$ since, in our units, $F = q$). The resulting annual mortality, $Z = \int z(t)dt$, is 11/3. The L_∞ distribution is truncated normal with standard deviation 4 mm. We assume that all recruits have length 19.5 mm. The values for mortality come from Somers and Wang (1997).

We generate 12 length-frequency data sets, one for the beginning of each month. Each monthly length-frequency data set is obtained by taking a sample of size 1000 from the theoretical length distribution that is derived from the L_∞ distribution. We then obtain parameter estimates from the twelve months of simulated data. The process is repeated 100 times to provide a reasonable estimate of the sampling variance of the parameters. In practice, (k, l_∞) can often be estimated from a different study. We therefore consider two models. In Model 1, we assume all five

Table 2.1 Mean parameter estimates and standard deviations (in parentheses) for simulated tiger prawn (*Penaeus esculentus*) data. The model assumes an underlying truncated normal L_∞ distribution. The data are generated from two underlying L_∞ distributions: the truncated normal and the lognormal.

Model[1]	k	l_∞	σ	Z	M	F
		(a) underlying truncated normal L_∞ distribution				
True	3	40	4	3.67	2	4
1	2.99 (.05)	40.00 (.19)	4.02 (.08)	3.65 (.05)	1.98 (.15)	3.99 (.34)
2	3	40	4.01 (.07)	3.65 (.04)	2.00 (.11)	3.95 (.28)
		(b) underlying lognormal L_∞ distribution				
True	3	40	4	3.67	2	4
1	3.02 (.07)	39.53 (.22)	4.28 (.08)	3.53 (.05)	1.51 (.16)	4.84 (.35)
2	3	40	4.14 (.07)	3.62 (.04)	1.93 (.11)	4.05 (.28)

[1] Model 1 assumes all parameters are unknown; Model 2 assumes (k, l_∞) known.

parameters are unknown, and, in Model 2, we assume that l_∞ and k are known and we estimate M, F and σ.

The results are summarized in part (a) of Table 2.1. All the parameters are quite well estimated, even for Model 1. There is a modest reduction in the standard deviation when (k, l_∞) are assumed known.

We have also tested for robustness by performing the estimation process on data generated from a lognormal distribution. The results are shown in part (b) of Table 2.1. For Model 1 the estimates of M and F have a large opposite bias, whereas the absolute bias for Z is somewhat smaller. Model 2 improves the estimates dramatically, despite the fact that an incorrect distribution (the truncated normal) is being used in the model. Note that the variation in the estimates of total annual mortality Z is somewhat less than that of F and M; this is because F and M are highly negatively correlated (typically 94%).

In this paper, we assume that natural mortality is independent of size. This is a reasonable assumption if the recruits have reached certain sizes, which is the case in our tiger prawn study (Somers, Crocos and Hill, 1987). It is possible to incorporate size-dependent mortality in our models.

2.5 Application to Tiger Prawns (*P. semisulcatus*)

The data for this application consist of a six-year sequence of experimental length frequency data from the trawling region around Albatross Bay in the eastern Gulf of Carpentaria, Australia. The data consist of catches from 11 mm to 59 mm (carapace length) for each of 69 times ranging from March 1986 to March 1992. The catch for each time is obtained by aggregating the catches from several stations covering the trawling region. Sampling was done roughly every lunar month.

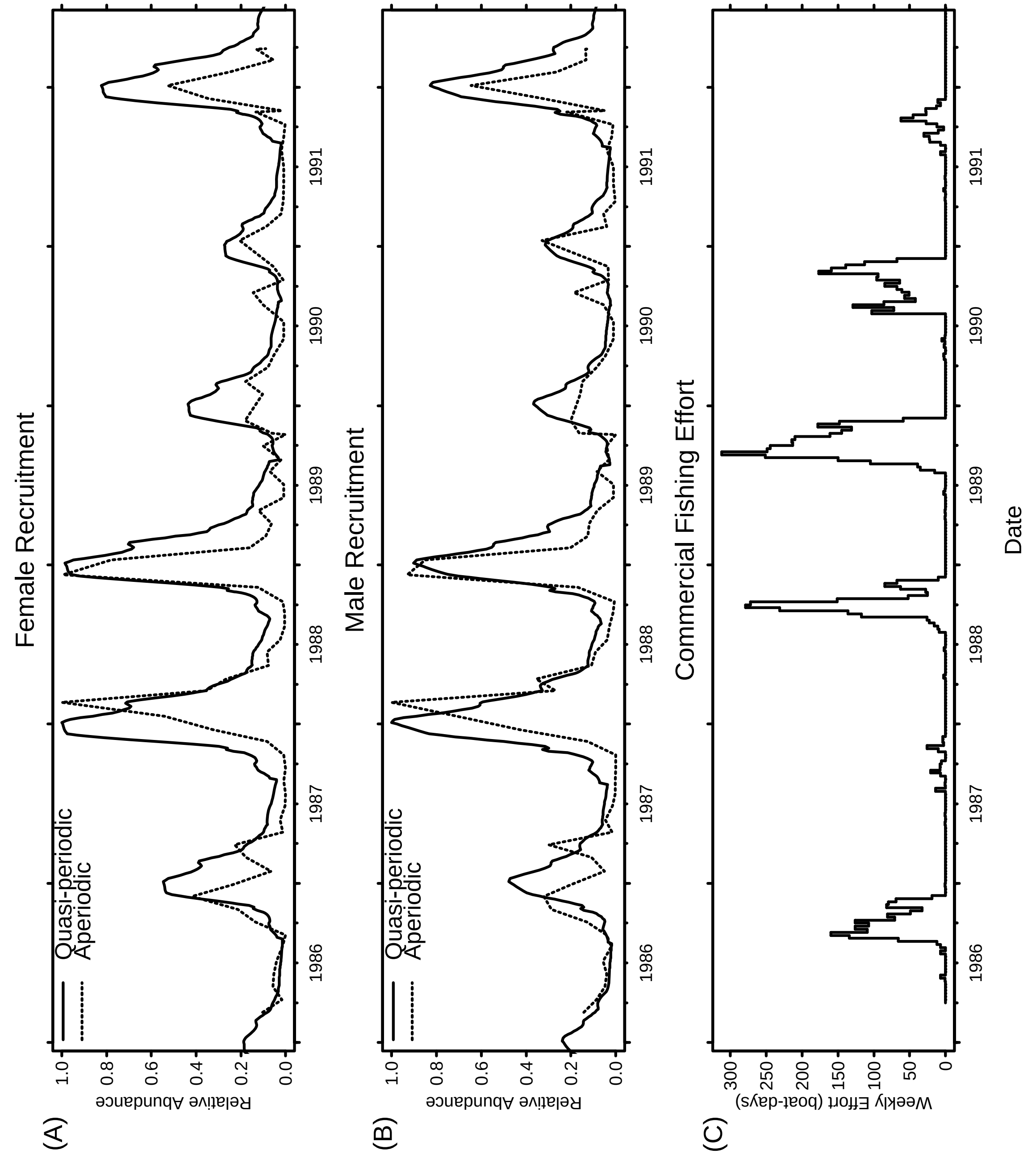
We use the catch data for the smaller size classes to obtain two types of recruitment pattern: the *aperiodic* pattern and the *quasi-periodic* pattern. The aperiodic pattern is constructed by summing over all individuals with length 20 mm or less for each time. The resulting sequence of time points is then joined up by straight lines. The quasi-periodic pattern is generated from the aperiodic pattern by averaging corresponding points across years to give a single annual pattern. The pattern for all six years is generated from the annual pattern by applying, for each biological year, a scale factor that is found by averaging the catch over all size classes within the year. The start of the biological year is defined as the time when the annual pattern reaches its minimum (see Fig. 2.2).

The effort pattern comes from commercial log books collected from fishers for the period from 1986 to 1992 in the area. Effort is measured in boat-days (see Fig. 2.2(C)). There is substantial contrast in the effort both within years (due to seasonal closures) and across years. This contrast may allow us to separate fishing mortality from natural mortality.

The instantaneous fishing mortality $F(t)$ is assumed to be $qE(t)$. The mean total mortality $Z = M + q\bar{E}$, where $\bar{E}$ is the mean effort over the study period. Given the results of the simulation study, we expect the parameter Z may be more reliably estimated than either M or q, whose estimates are negatively correlated.

We further assume the L_∞ distribution is truncated normal. This choice is based on the shape of the observed length distribution during July to September, the period when this distribution should approximate the asymptotic length distribution. The truncated normal distribution is simply a normal distribution that is cut off below the recruitment length l_0 and then renormalized. The truncated normal can therefore be reparameterized in terms of the mean $l_{\infty *}$ and variance σ_*^2 of this underlying normal distribution. It is more convenient to use these parameters than the mean l_∞ and variance σ^2 of the truncated normal distribution. Note that l_∞ is always larger than $l_{\infty *}$ and σ is always less than σ_*. However, in this application the two sets of parameters are nearly interchangeable, since over the range of estimated values l_∞ exceeds $l_{\infty *}$ by at most 0.5 mm and σ_* exceeds σ by at most 0.6 mm (see Table 2.2).

Fig. 2.2(A) Quasi-periodic (solid line) and aperiodic (dashed line) recruitment patterns for female tiger prawns *P. semisulcatus* in the study area; (B) as (A) but for male tiger prawns; (C) the weekly fishing effort pattern in the study area.



We define a recruit to be an individual with length l_0, which can be chosen at discretion. We examine a range of candidate values of l_0 between 19.5 mm and 27.5 mm, to find out which values provide the most suitable definition of recruitment for this data set, i.e. that which leads to the least violation of model assumptions.

If we are to consider different recruitment lengths then we must allow for the timing of the recruitment pattern to vary; recall that the recruitment pattern was derived from size classes 21 mm or less. If we use this pattern at say 23.5 mm then we need to shift the pattern slightly to later times. It is not apparent by how much we should shift, therefore we shall estimate it. We call this parameter the *lag*. We expect the lag to increase with l_0. Also note that the derived recruitment pattern is an average over different size classes and hence it is an average over different times. The absolute timing of the pattern is therefore uncertain and so the lag parameter adopts the role of estimating this uncertainty.

We do have sampling effort information, so that it would be reasonable to consider incorporating into the likelihood the Poisson term for the total catch as mentioned in section 3. Information on total catch per occasion would improve estimates of mortality. However, preliminary analysis found that there was a mismatch of the expected total catch with the observed total catch. Therefore, it appears to be unrealistic to assume that the catch is proportional to the sampling effort. In other words, ϕ (see section 3) is not constant in time. In the subsequent data analysis we use the form of the log-likelihood in (2.10), which uses the shape of the observed distribution and takes the total catch as given.

Initially we tried to estimate all the parameters k, $l_{\infty *}$, σ_*, M, q and the lag simultaneously (Model 1). However, the estimates of k and $l_{\infty *}$ were unrealistic, i.e., k was too high and $l_{\infty *}$ was too low (see Table 2.2). We therefore re-ran the estimation for k fixed at each of the feasible values 2, 3 and 4. The estimates of $l_{\infty *}$ were still too low.

The reason could be that the estimate is dominated by the length-frequency records during the recruitment season (January to March) where the highest catches are (see Fig. 2.4). These records contain little information on the asymptotic length; for this parameter we require catches during the fishing season (August to November) where the larger size classes predominate. However, the catches during this period are smaller than those between January and March, and so they contribute less to the sum of log-likelihood in (2.10).

Finally we re-ran the estimation for both k and $l_{\infty *}$ fixed at each of three feasible values (Model 2). For k we used 2, 3 and 4 as before. For $l_{\infty *}$ we were guided by estimates of (k, l_∞) in the the following papers: Somers and Kirkwood (1991); Wang, Thomas and Somers (1995); Wang (1997). We simply fit a straight line to these estimates for each sex and read off the l_∞ value for each value of k. The

Table 2.2 Parameter estimates and jackknifed standard deviations (in parentheses) for real tiger prawn (*Penaeus semisulcatus*) data. F_{89} is the estimated fishing mortality in 1989. The last column is the jackknifed correlation between M and F_{89}.

Model[1]	k	$l_{\infty *}$	σ_*	Z	M	F_{89}	cor(M, F_{89})
Males: Quasi-periodic recruitment							
1	9.3 (1.2)	33.4 (0.5)	4.5 (0.2)	5.2 (0.7)	4.1 (1.0)	2.3 (0.8)	–0.82
2	2	39.3	5.1 (0.4)	3.1 (0.3)	2.9 (0.4)	0.3 (0.6)	–0.78
2	3	37.7	4.3 (0.5)	3.9 (1.1)	3.7 (0.5)	0.6 (2.5)	–0.35
2	4	36.1	4.3 (0.2)	4.4 (0.7)	3.4 (0.4)	2.1 (1.4)	–0.25
Males: Aperiodic recruitment							
1	5.0 (0.6)	32.6 (0.5)	4.8 (0.2)	2.0 (0.4)	1.3 (0.5)	1.6 (0.6)	–0.67
2	2	39.3	5.8 (0.3)	3.0 (0.3)	2.8 (0.4)	0.4 (0.5)	–0.79
2	3	37.7	4.7 (0.2)	3.7 (0.3)	3.7 (0.5)	0.1 (0.5)	–0.81
2	4	36.1	4.5 (0.2)	3.7 (0.4)	3.5 (0.5)	0.5 (0.6)	–0.64
Females: Quasi-periodic recruitment							
1	5.6 (0.6)	42.2 (1.0)	7.1 (0.4)	5.0 (0.4)	4.2 (0.5)	1.7 (0.5)	–0.65
2	2	53.1	8.3 (1.4)	4.1 (0.2)	3.9 (0.4)	0.3 (0.5)	–0.83
2	3	47.4	6.9 (0.4)	4.3 (0.3)	4.0 (0.4)	0.7 (0.5)	–0.66
2	4	41.7	7.7 (0.3)	3.3 (0.2)	2.7 (0.4)	1.3 (0.6)	–0.71
Females: Aperiodic recruitment							
1	4.9 (0.5)	39.2 (0.8)	8.2 (0.4)	3.0 (0.3)	2.6 (0.5)	0.9 (0.5)	–0.67
2	2	53.1	13.5 (1.3)	4.0 (0.3)	3.9 (0.4)	0.1 (0.5)	–0.80
2	3	47.4	9.7 (0.9)	4.4 (0.3)	4.3 (0.4)	0.1 (0.6)	–0.70
2	4	41.7	8.1 (0.4)	3.4 (0.3)	3.0 (0.4)	0.8 (0.5)	–0.71

[1] Model 1 assumes all parameters are unknown; Model 2 assumes $(k, l_{\infty *})$ known.

resulting fixed values of $(k, l_{\infty *})$ we used in the estimation were, for males, (2, 39.3), (3, 37.7) and (4, 36.1), and for females, (2, 53.1), (3, 47.4) and (4, 41.7).

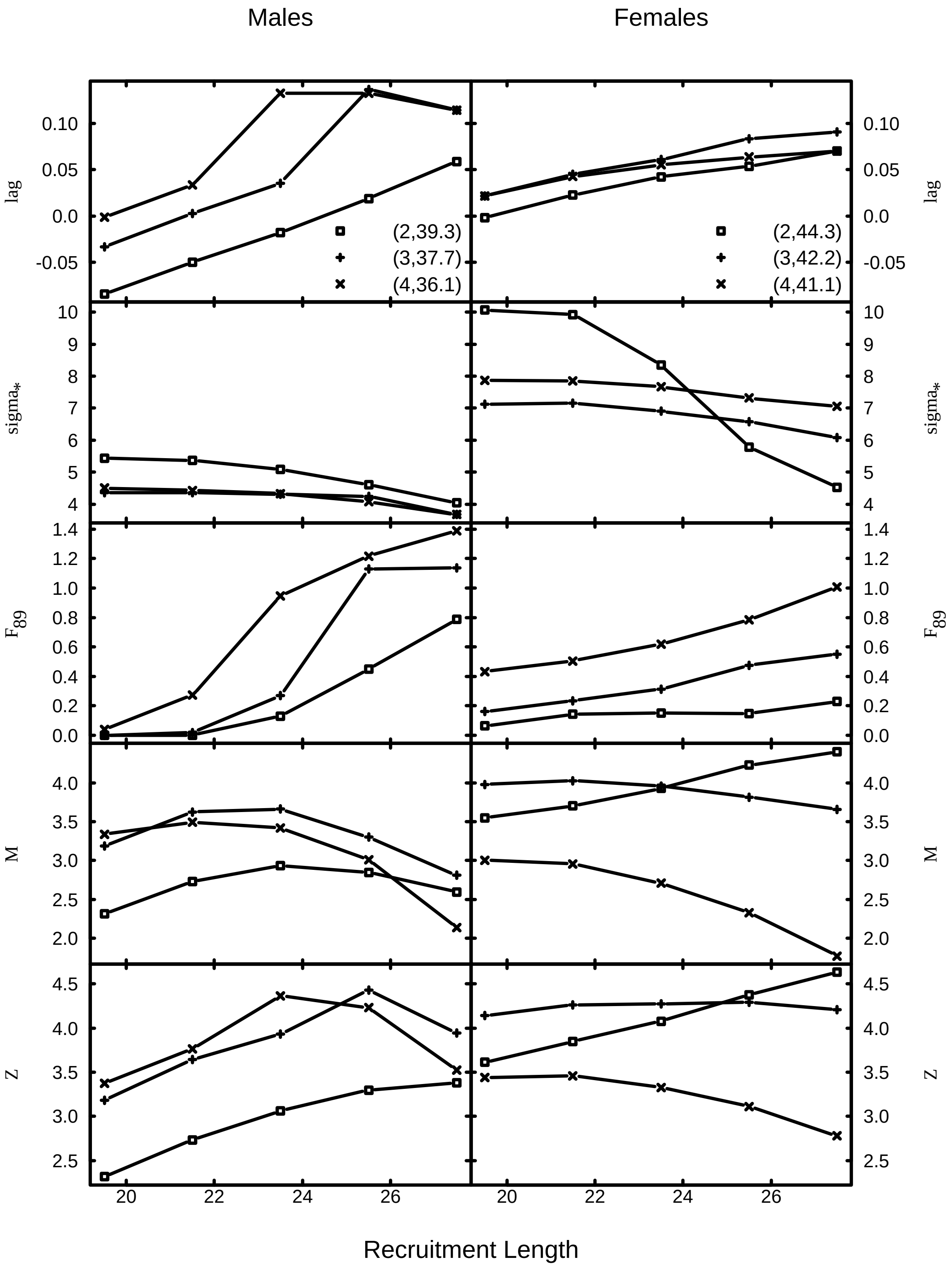
It is clear from the data (see Fig. 2.4) that recruitment actually occurs over a range of lengths between 20 mm and 30 mm. However, our model assumes recruitment at a fixed length, l_0, so we need to choose this value. If l_0 is too small, individuals recruiting at larger lengths will be unaccounted for in the model and the catchability of individuals with size above l_0 will no longer be constant. On the other hand we wish to make l_0 as small as possible in order to make full use of the data. Wang and Somers (1996) have also used l_0 to account for continuous recruitment in estimating growth parameters, and have provided guidelines for choosing l_0. Note that parameter estimates are consistent for given l_0 provided all model assumptions are satisfied. However, when l_0 is too small or too large, there is bound to be a violation of those assumptions. In the case of assumption violation, we would expect the estimates to change more rapidly.

In Fig. 2.3 the parameter estimates for fixed $(k, l_{\infty *})$ are plotted against l_0 for the quasi-periodic recruitment model. In the light of the above discussion, we say the most reasonable value for l_0 is that for which the estimates are most slowly varying in the immediate neighbourhood of l_0. On the basis of σ_*, M and Z for the males $l_0 = 23.5$ would be a reasonable choice. We exclude q from consideration because its standard deviation is comparable to its magnitude (see Table 2.2). Also we exclude the lag because we expect it to increase approximately monotonically with l_0, as indeed it does. There is no clear choice for females so we choose $l_0 = 23.5$, the same as for males. This choice is consistent with the consideration that l_0 should be somewhere between 20 mm and 30 mm, but in the lower half of the range so that more data can be included in the estimation (since lengths must exceed l_0). The results of Fig. 2.3 can be regarded as a sensitivity study on the effect of changing l_0. The purpose of this sensitivity study is not to estimate l_0, but rather to check that the model assumptions have not been violated for the given l_0.

The parameter estimates for all cases with $l_0 = 23.5$ are shown in Table 2.2. Also shown are jackknife estimates of the standard deviations. The jackknifing is done by dropping the length-frequency record from each occasion in turn and re-estimating the parameters. From the over-all estimate $\hat{\theta}$ and the jackknife estimate $\hat{\theta}_i$ from dropping the i-th occasion we get a pseudo-value $\hat{\theta} - (n-1)\hat{\theta}_i/n$, where in our case $n = 69$. The jackknifed standard deviation is simply the standard deviation of these pseudo-values. We also show the jackknifed correlation between M and q, which is simply the correlation between the corresponding pseudo-values. In most cases there is a large negative correlation.

The parameter F_{89} is the estimated fishing mortality in 1989, the year of peak effort; F_{89} is simply proportional to q with constant of proportionality 2865, the number of boat-days of effort in that year. The mean total annual mortality Z is

Fig. 2.3 Parameter estimates against recruitment length l_0 for real tiger prawn data using quasi-periodic recruitment under Model 2. The mean annual total mortality Z is equal to $M + 0.46F_{89}$, where F_{89} is the fishing mortality in 1989.



$M + 0.46F_{89}$ since the mean annual effort was 1320 boat-days. The mostly high negative correlations between M and F_{89} (equivalently, q) may explain why Z tends to have a smaller standard deviation than either M or F_{89}.

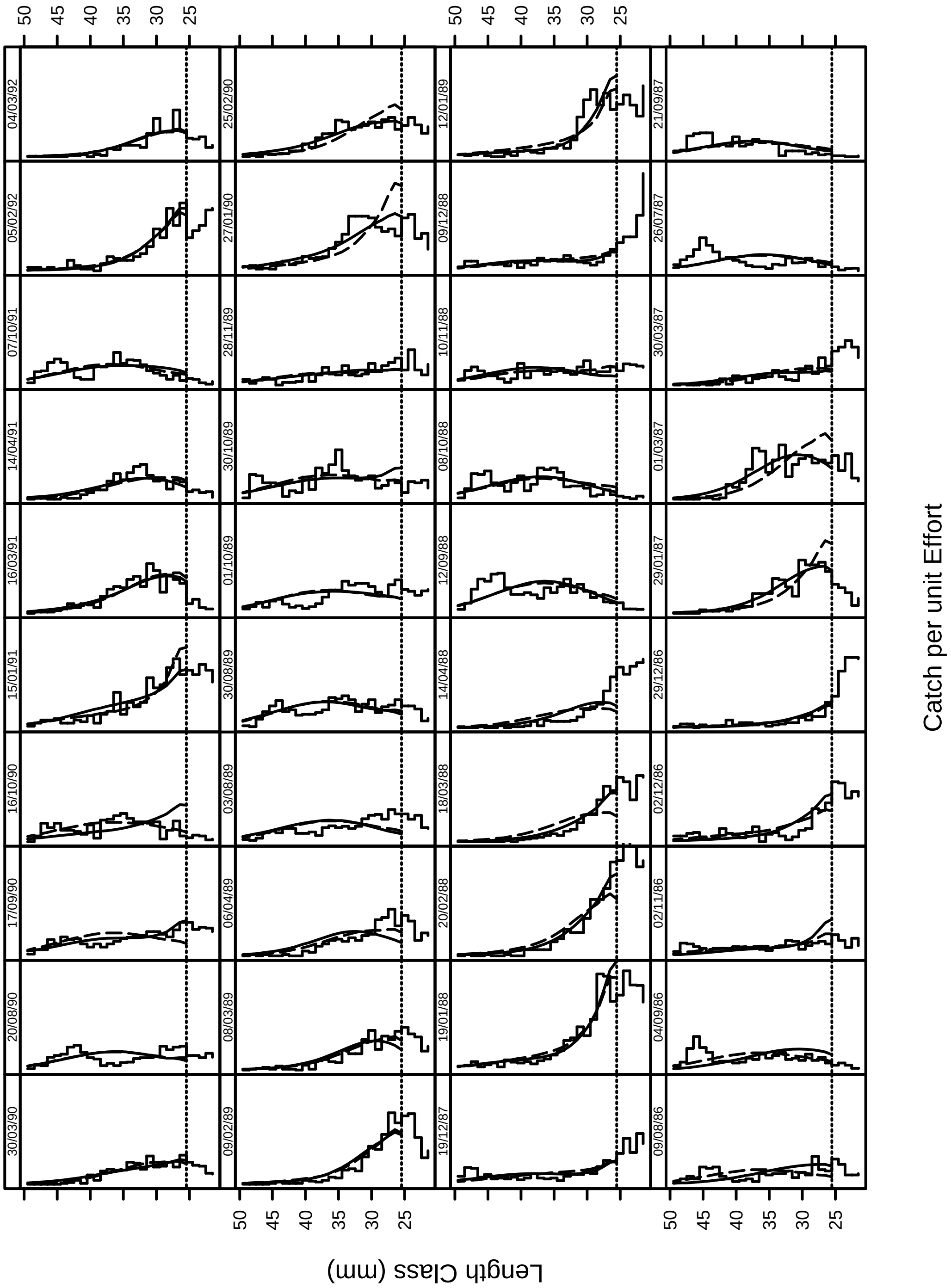
The results are fairly similar for the two recruitment models although there are differences: the quasi-periodic recruitment model gives larger F_{89} estimates and smaller σ_* estimates. Our method assumes that the recruitment pattern is known without error, therefore the preferred recruitment pattern should be the one with less error. Let us suppose that the true recruitment pattern consists of a periodic pattern with random variation both within years and between years. If the within-year variation is sufficiently large in comparison with the between-year variation, then the quasi-periodic pattern should be used. On the other hand, if the between-year variation is large then the aperiodic pattern is preferred.

Fig. 2.4 shows the 40 length-frequency records for females with the largest total catch. Overlaid is the expected catch (given the total catch) from the models with $(k, l_{\infty *})$ fixed at (3, 47.4) for quasi-periodic recruitment (solid line) and for aperiodic recruitment (dashed line). Because the integral for the expected length distribution is singular in the neighbourhood of l_0, the first few size classes are omitted from the estimation; only data with length above $l_0 + 2$ are used in the estimation. The fit is mostly reasonably good. However, for the quasi-periodic model, there tends to be a lack of fit during January, which is the start of the recruitment season. This seems to be a consequence of choosing a recruitment length too low to account for all recruits; some individuals recruit at lengths above 23.5 mm. Also the fit is poor in April 1988 when recruitment occurred later than usual (see Fig. 2.2); the aperiodic model fits better here. On the other hand, the aperiodic model does not fit well in October 1990, which suggests that the aperiodic pattern is in error just before that time. This would be consistent with the increased variability of the pattern in late 1990 (see Fig. 2.2(A)).

2.6 Discussion

Methods such as Macdonald and Pitcher (1979), ELEFAN (Pauly, Ingles and Neal, 1981) and Sparre (1987) operate on multiple length-frequency data and attempt to identify cohorts in the frequency pattern. Essentially they estimate the growth parameters by tracing cohorts in time, then they estimate mortality by measuring the evolution in abundance of a cohort. For mortality estimation these methods need catch per unit effort data. Sparre's method bears some similarity to ours because it attempts to fit the length distribution of a cohort to a normal distribution whose variance is a parameter to be estimated. Our method does not require separation of cohorts. Another advantage of our method is that it is not necessary to

Fig. 2.4 Female length-frequency records for the 40 occasions with the largest total catch (stepped line). The smooth solid curve is the expected catch (given the total catch) from Model 2 with $(k, l_{\infty *})$ fixed at (3, 47.4) and quasi-periodic recruitment at length 23.5 mm. The dashed curve is the expected catch for the aperiodic recruitment model. Only data above the dotted line are included in the fit. The temporal sequence of the panels is from left to right, then from bottom to top.



have information about sampling effort, which may greatly reduce the complexity of sampling.

Deriso and Parma (1988) and Sullivan, Lai and Gallucci (1990) have reported methods based on stochastic growth. Sullivan (1992) also applied Kalman filter approach for estimating population parameters. Their models differ from ours in the way random variation is incorporated in the growth model. In their models the length increment from one time step to the next follows a distribution, whose mean is given by a fixed growth model. As Wang and Thomas (1995) have demonstrated, this is equivalent to assuming that the growth rate changes randomly from time to time. In our model each individual follows a deterministic growth curve whose L_∞ parameter is chosen from a random distribution. An individual with larger than average growth at one time step will have above-average growth at subsequent time steps. Perhaps further modelling effort could be directed into combining these approaches.

Our methods are based on distributional assumptions that must be tested for robustness, because, in practice, the L_∞ distribution of real prawn populations will not equal any of our mathematical distributions. We have found that, even for our ideal model, akin to any other existing model, biases occur for moderate to large coefficients of variation when violation of distributional assumptions occur.

However, our research experience in fisheries tells us that it may be too ambitious to estimate all the parameters simultaneously. For instance, Ebert (1973) even found estimation of two parameters (natural and fishing mortality) unreliable and had to assume one of them. This is perhaps why traditional cohort analysis assumes the natural mortality to be known. Also Askland (1994), one of the most recent cohort-analysis methods, requires known M. Nevertheless, in practice, (k, l_∞) may be estimated from different types of data. The results based on Model 2 (assuming (k, l_∞) known) indicate that both M and F can then be estimated more reliably. Assuming that growth parameters are known greatly reduces the complexity of estimating the remaining unknown parameters, and improves the performance of the proposed methods.

Chapter 3

Size-dependent natural mortality

While it is generally accepted that natural mortality of marine invertebrates is very high in the early life history stages and decreases in later life history stages, it is often assumed to be constant within a given life history stage. The analysis is based on the data collected at 2 weekly intervals at four sites over a period of six years (between September 1986 and March 1992). We assume mortality to be a parametric function of size rather than a constant. Another complication is that a significant proportion of the juvenile *P. merguiensis* population emigrates from the study area each year. We have accounted for this effect by incorporating the size-frequency pattern of the emigrants in our analysis. The extra parameter in the model required to describe the dependence of mortality on size was found to be significantly different from zero, and the instantaneous mortality rate varies from 0.02 to 0.89/week.

3.1 Introduction

Many species of marine animals suffer very high initial natural mortality rates that decrease rapidly until sexual maturity. Following this, natural mortality plateaus, although it may increase for old animals (Beverton and Holt, 1956; Hoenig, Pepin and Lawing, 1990; Caddy, 1996). In fisheries stock assessment, most modellers assume that natural mortality (M) is constant for exploited age (or size) groups. As long as exploited age groups are similar in their position in the food chain this is probably a valid assumption (see Vetter (1988) for a review of the issues). In general there is so much uncertainty about the value of M itself that for exploited age groups trying to estimate how much and if it changes with size is probably not warranted for most exploited stocks (Vetter, 1988).

It is generally accepted that M may change abruptly between life history stages as animals' susceptibility to the agents of M (predation, disease, environmental extremes etc.) change as they migrate or metamorphose. However, even a small change in M during an early life history stage can have a significant effect on the numbers of individuals surviving to spawn (Gosselin and Qian, 1997). Mortality in the juvenile stages has been shown to regulate population size in lobsters (Smith and Herrnkind, 1992), crabs (Eggleston and Armstrong, 1995) and oysters (Roegner and Mann, 1995). Although in other species such as cod (Gadus morhua) year-class strength is mainly determined before the early juvenile stage (Sundby, Bjoerke, Soldal and Olsen, 1989).

In some species of penaeids (eg. tiger prawns: *Penaeus semisulcatus* and *P. esculentus*), year class strength is partially determined by parental stock size whereas in banana prawns (*P. merguiensis*) it is mainly determined by environmental conditions (rainfall) and to a lesser extent, the numbers of juveniles (Staples and Vance, 1986; Vance, Haywood, Heales, Kenyon and Loneragan, 1998). So while mortality is not the major factor determining year class strength it is nevertheless important in explaining interannual variation given similar environmental conditions.

In the Gulf of Carpentaria, *Penaeus merguiensis* spawns between September and November and again from February to March (Rothlisberg, Crocos and Staples, 1988). The eggs hatch within a day and the planktonic larvae move onshore, arriving on the coast as postlarvae 2 to 3 wk after spawning. Postlarvae settle in mangrove-lined estuaries and remain there for between 1 and 3 mo. Postlarvae and juveniles are exposed to high rates of predation by fish when they are in the mangrove nursery areas (Salini, Blaber and Brewer, 1990). There is also some suggestion that the vulnerability of juvenile penaeids to predation by fish is a function of penaeid size (Haywood, Heales, Kenyon, Loneragan and Vance, 1998).

There is an annual emigration of juveniles from the estuaries to the inshore coastal region during the wet season (January to March) (Vance, Haywood, Heales, Kenyon and Loneragan, 1998). The fishing season opens early in April each year. Exploitation rates are very high, with 90% of the stock being taken within 4 to 5 weeks of the season's beginning (Lucas, Kirkwood and Somers, 1979). Average annual catch is about 4 000 t, worth approximately A$25 million (Somers and Wang, 1997).

Previous studies have assumed constant a M for populations of juvenile penaeids (Haywood and Staples, 1993); O'Brien (1994)). A few authors have suggested using age- or size- specific mortality for marine fish stocks (Vetter, 1988; Beyer, 1989; Caddy, 1991). More recently, Caddy (1996) emphasised the importance of modelling the relationship between natural mortality and size for short-lived invertebrate stocks. In this paper, we will use a method similar to the catch-curve analysis (Chapman and Robson, 1960) but our method is based on the size distribution rather than the age distribution to estimate natural mortality. Mortality is assumed to be a parametric function of size. The analysis also takes account of the effect of emigration by incorporating the emigration pattern as a function of the size of prawns collected in the same period.

3.2 Materials and methods

3.2.1 Juvenile Habitat

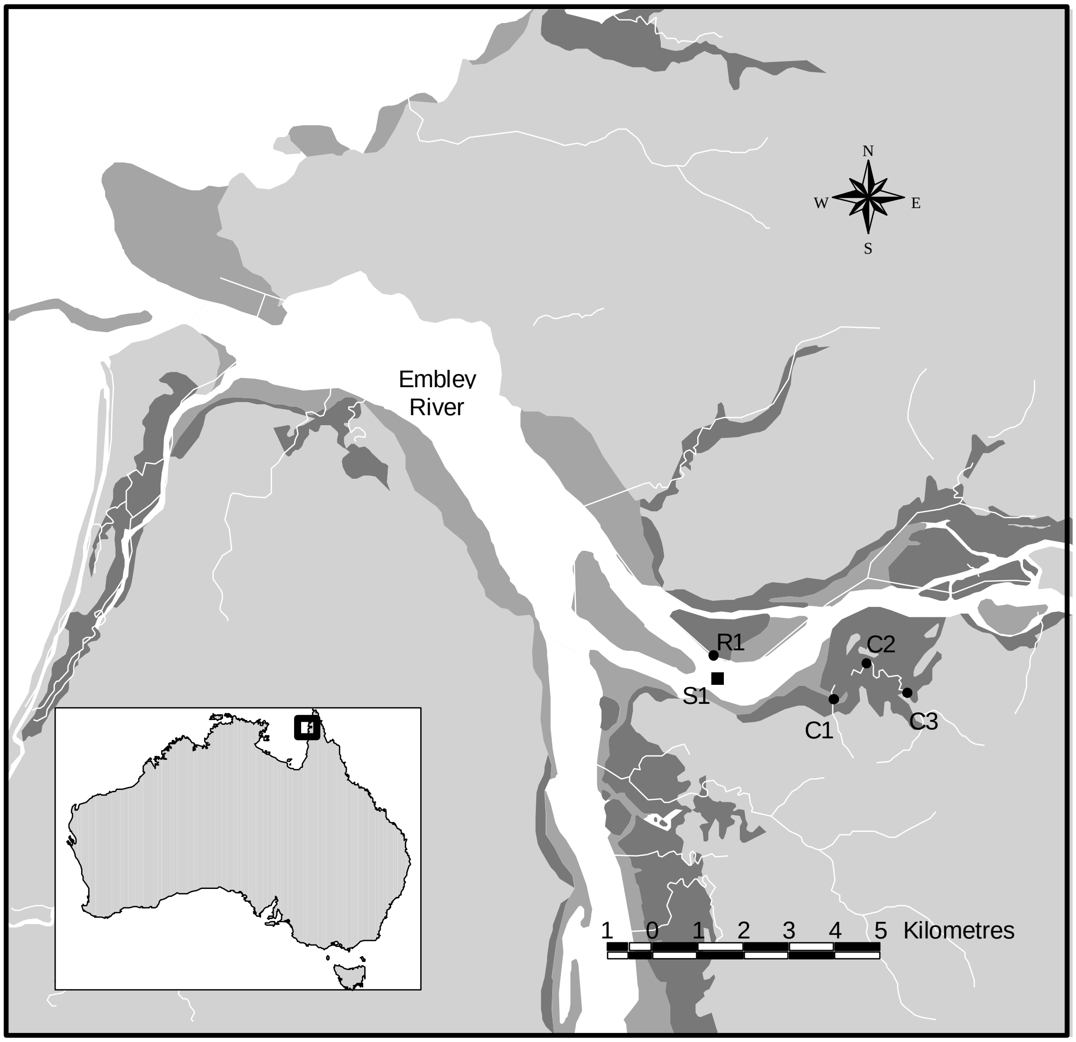
Earlier work (Vance, Haywood and Staples, 1990) demonstrated differences in the length distributions of juvenile *Penaeus merguiensis* found in small creeks compared to the main river. When estimating population parameters such as mortality, it is important that sampling is unbiased and representative across different habitats. To estimate the relative extent of river-lined and creek- lined mangrove habitat we measured the lengths of both from the AUSLIG (Australian Surveying and Land and Information Group) 1:100 000 scale digital topographic chart of Australia using a Geographical Information System (GIS). For the Embley River system the length of mangrove-lined river bank was 208 km and mangrove-lined creek bank was 233 km ie a ratio of 1.12 (creek : river).

Total area trawled in the creek during each sampling session was 270 m2 compared to 240 m2 (see details below) in the river ie 1.12, ensuring our sampling was representative of the banana prawn populations in the different habitats.

3.2.2 Data collection

Resident juvenile *Penaeus merguiensis* were sampled at 2 weekly intervals at four sites in the Embley River (Figure 3.1) over a period of 6 y (between September 1986 and March 1992); except for the periods April to August 1990 and June to August 1991. These periods were not sampled as data from the first 4 y of the project showed that very few prawns were resident within the estuary at these times (Haywood and Staples, 1993; Vance, Haywood, Heales, Kenyon and Loneragan, 1998). One site (R2) was on a mangrove-lined bank of the river, while the other 3 sites (C1, C2, C3) were on a small creek that drains into the Embley River 10 km from its mouth (Figure 3.1). These sites were respectively about 0.8, 2.5 and 3.0 km upstream from the creek mouth. Benthic postlarval (< 3 mm CL) and juvenile (≥ 3 mm CL) prawns were collected at the four sites with a beam trawl (mouth dimension 1.0×0.5 m, fitted with a 2 mm mesh net and 1 mm mesh cod end). Trawls were completed within 2 h of low water during spring tides because the catchability of *P. merguiensis* is highest at this time (Staples and Vance, 1979). One trawl parallel to the bank and four trawls at right angles to it were done at each site. Parallel

Figure 3.1. Map of the Embley River, north-eastern Gulf of Carpentaria showing beam trawl sampling sites for resident *Penaeus merguiensis* in the main river (R1) and creek (C1, C2, C3) and the set net site for sampling emigrating *P. merguiensis* (S1).



trawls were made as close as possible to the water's edge (within 2 to 5 m) in 0.4 to 0.6 m depth. They were made in the direction of the prevailing current (speed approximately 0.5 m/s), and were 200 m in length at the river site and 50 m at the creek sites. Right-angle trawls of 10 m length, from the water's edge towards the middle of the river or creek, were made at randomly chosen sections of the bank at each site. Samples were immediately placed on ice and frozen upon return to the laboratory. Postlarval and juvenile *Penaeus merguiensis* were counted and recorded to the nearest 1.0 mm CL, using an ocular micrometer fitted to a binocular microscope. Catches from all four benthic sites were summed to analyse the length frequency data. This procedure reduces any biases introduced by the migration of juveniles between the river and creek sites (Vance, Haywood and Staples, 1990).

Juvenile banana prawns emigrate from the estuarine nursery areas during the wet season each year. To account for the effect of emigration on our estimation of mortality, we sampled emigrating prawns every 2 wk, using a pair of nets anchored in the main channel of the river at site S1, where the depth was about 4 m (Figure 3.1). The nets were 1.0×0.5 m and 1.0×2.0 m across the mouth, and were fitted with 2 and 28 mm mesh respectively. Buoys fastened to the top horizontal bar of each net frame kept the nets on the surface. Previous work in the south- eastern Gulf of Carpentaria has shown that 80% of emigrating *Penaeus merguiensis* do so within 0.5 m of the surface (Staples and Vance, 1986). Two different-sized nets were used to ensure that we sampled the full size range of emigrating prawns. The nets were set immediately after high water left in place throughout the ebb tide (usually 6 h). The analysis is based on the pooled data over six years.

3.2.3 The statistical model

Prawns less than 4 mm CL did not emigrate. Emigration peaked between 7 and 15 mm CL (Figure 3.2). To account for the effect of emigration in the analysis, we first estimated the relative probabilities of emigration for each size class by taking the ratio of the frequencies of residents to emigrants.

Let $m(l)$ be the instantaneous mortality rate at size l. The probability of death during $(t, t+\Delta t)$, given that it is still alive at time t, is To account for size-dependent mortality, we will assume

$$m(l) = \alpha e^{\beta l},$$

where $\beta \leq 0$, and $\beta = 0$ indicates size-independent mortality. Let $\eta(l)$ be the size-specific emigration rate over the size of interest 2 mm CL $\leq l \leq$ 15 mm CL, which has a similar effect to mortality on the resident-population size distribution. The marginal distribution function is then

$$\exp\left[-\int_{l_0}^{l}\{m(x)+\gamma\eta(x)\}dx\right],$$

in which γ is the scale parameter.

The distribution of abundance as a function of size is related to the growth rate. If we assume that the growth rate is constant g (which is quite appropriate for juvenile prawns), we will have the proportion of survival from size l_0 to l as

$$\exp\left[-\int_{l_0}^{l}\left(\frac{\alpha e^{\beta x}+\gamma\eta(x)}{g}\right)dx\right].$$

Note that the preceding expression is still valid when the growth rate, g, is a function of size, which is generally the case. If N_0 is the total number of the population with size l_0, the expected number of prawns that survive up to length l, N_l, satisfies

$$\log(N_l)=\frac{\alpha}{g}\int_{l_0}^{l}\exp(\beta x)dx-\frac{\gamma}{g}\int_{l_0}^{l}\eta(x)dx+\log(N_0),$$

which can be written in the form

$$A\exp(\beta l)+B\int_{l_0}^{l}\eta(x)dx+C.$$

In the special case of constant mortality rate $m(l)=m$, the above expression has the form

$$al+b\int_{l_0}^{l}\eta(x)dx+c.$$

As we can expect, if no emigration occurs, the $\log(N_l)$ is a linear function in size l in this special case. This is not true in general, however. The parameter estimates were obtained using PROC NLIN (SAS version 6.11) after logarithmic transformation. The 95% confidence contours were obtained using Delta-Method (Armitage and Berry, 1987), which gives the standard error of the estimated mortality at size l,

$$e^{-\hat{\beta}l)}\sqrt{S_\alpha^2-2\hat{\alpha}\hat{\beta}S_{\alpha\beta}+\hat{\alpha}^2\hat{\beta}^2S_\beta^2}.$$

3.3 Results

Overall, 339119 prawns were caught in the beam trawls and 2240 were caught in the set nets. The length-frequency plot of the resident population clearly shows a

Figure 3.2. *Penaeus merguiensis.* Pooled length frequency of emigrating prawns caught in the set nets in the Embley River between September 1986 and March 1992

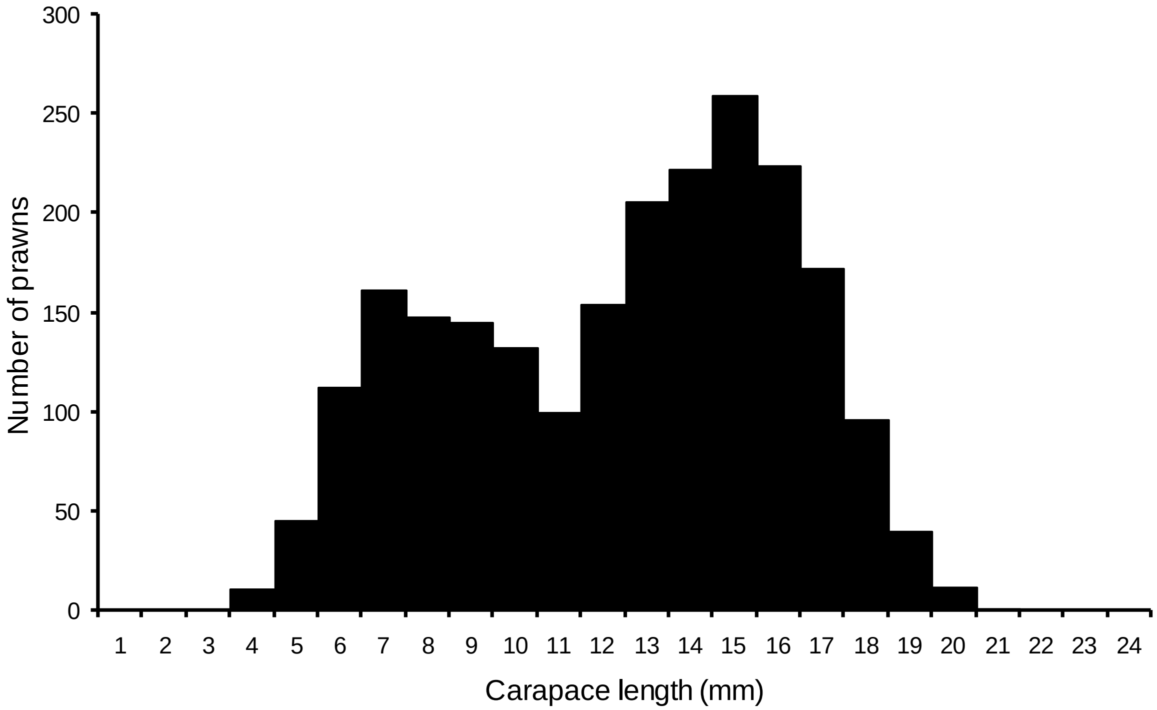


Figure 3.3. *Penaeus merguiensis*. Observed and predicted carapace length frequency incorporating emigration, assuming constant and size-dependent mortality

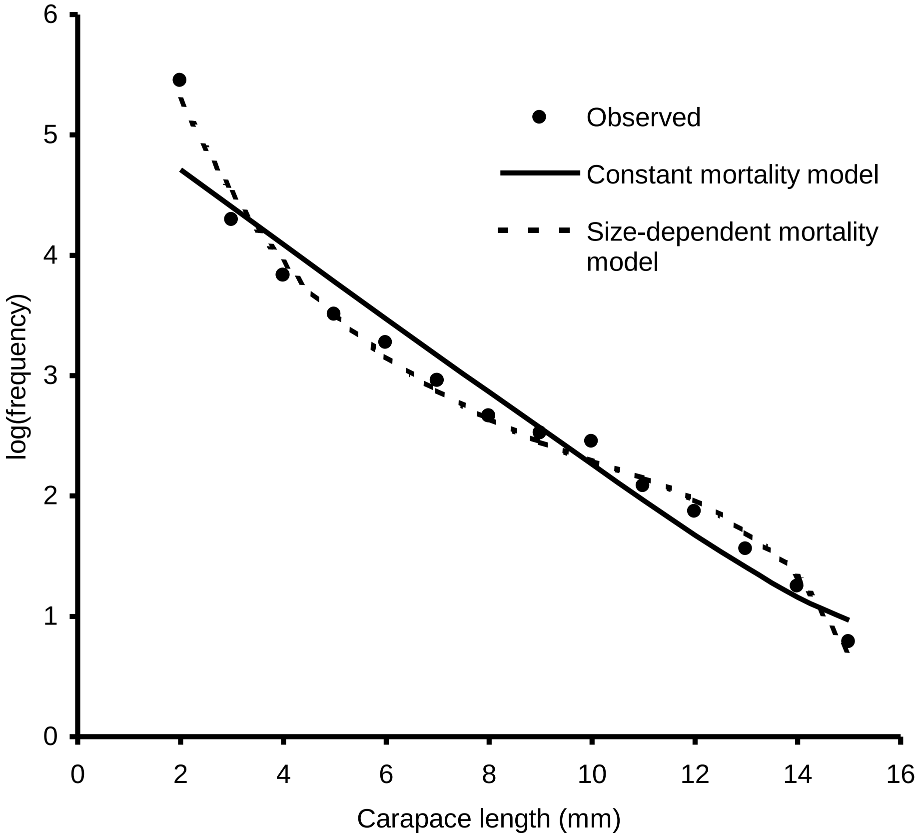


Table 3.1 *Penaeus merguiensis.* Parameter estimates (Est) and corresponding asymptotic standard errors (SE) from non-linear regression.

	Parameter	Est	SE	95% C.I.
Constant M (i.e. $= 0$)				
	α	0.31	0.0363	0.24, 0.38
	γ	0.31	0.520	-0.73, 1.35
Size-dependent M				
	α	1.59	0.282	0.96, 2.22
	β	0.29	0.038	0.21, 0.38
	γ	1.63	0.240	1.09, 2.16

declining trend, but with a hump at 10 mm CL, which indicates a strong emigration effect (Figure 3.3). The number of prawns caught that were > 15 mm CL is very low due to mortality and emigration. We therefore restricted our analysis to the prawns between 2 and 15 mm CL.

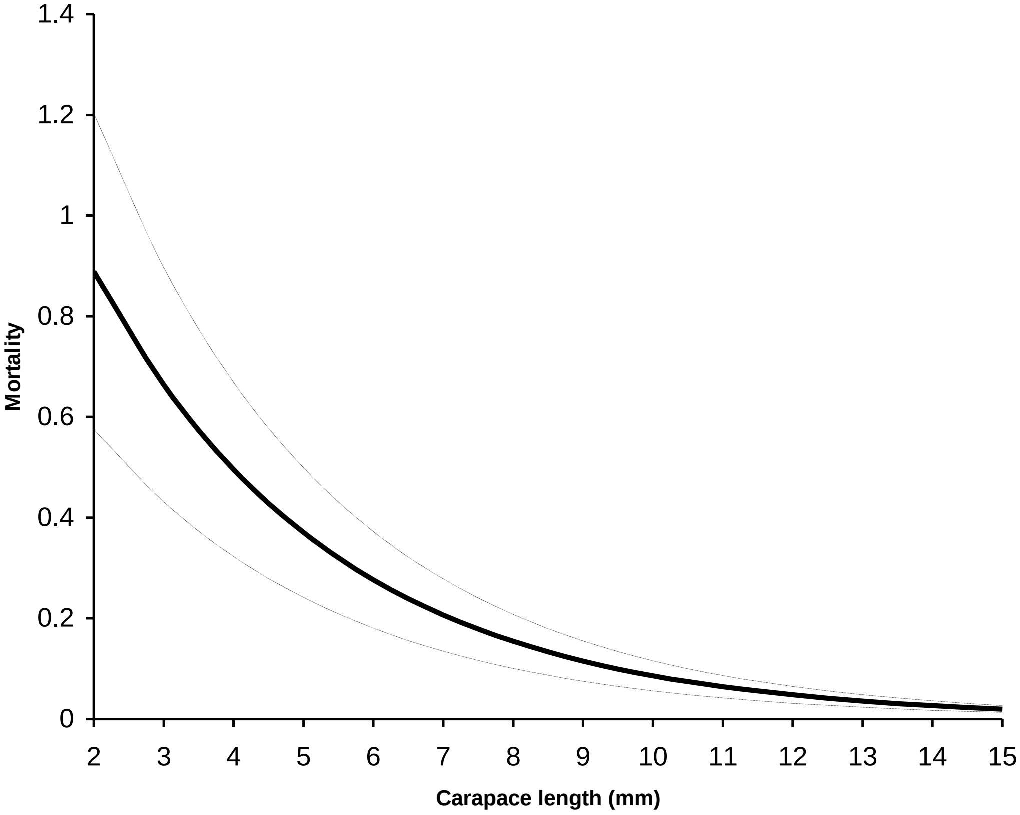
The model explained 126.223 sum of squares out of 126.412($R^2 = 0.99$) and all parameter estimates were significant (Table 3.1). The estimated mortality function is $M(l) = 1.59e^{-0.292l}$, and the correlation between $\hat{\alpha}$ and $\hat{\beta}$ is -0.86. The estimated mortality at size 2 mm CL is as high as 0.89 wk^{-1}, while that at 15 mm CL is 0.02 wk^{-1} (Figure 3.4), if we assume that the growth rate is 1 mm wk^{-1} (Haywood and Staples, 1993). If the growth rate is believed to be as high as, 1.5 mm wk^{-1}, say, then the corresponding mortality rates are 50% higher.

3.4 Discussion

Understanding the survival rates of fish stocks is critical for their management. Most life-history mortality occurs during the egg and larval stages, and these combined with the early post-metamorphic stage are the periods most likely to determine annual recruitment levels (Caddy, 1991). Traditionally, mortality of size classes recruited to the fishery is assumed to be constant. This may be reasonable for adult animals, but for the earlier life-history stages, the mortality rate is highly correlated with size. We have assumed that the growth rate is mm CL week^{-1}. This may not be the case since growth of marine animals is often affected by a number of environmental factors that include temperature and salinity. However, statistical evidence is not affected by the g value because g is a scale parameter in the mortality estimation, i.e., other values of g will lead to a similar conclusion.

The current research work in the Northern Prawn Fishery on seasonal closures and the stock recruitment relationship (Wang and Die, 1996) is impeded by the great

Figure 3.4. *Penaeus merguiensis.* Estimated weekly instantaneous mortality rate (solid line) and 95% confidence intervals (dashed lines).



uncertainties in the mortality rates (Somers and Wang, 1997). For instance, the value for mortality used in current stock assessments for 25 mm CL prawns (estimated from tagging studies; Lucas, Kirkwood and Somers (1979)) is 0.05. This is twice the value estimated using our length-dependent model for 15 mm CL prawns (0.02). Note that the length range in the data we used is 2–15 mm CL. Application of the method described here to a dataset with a wider length range would be of interest. We hope that a more accurate description of the mortality rate may lead to a more precise stock assessment and improve the resultant management strategies.

Size-dependent mortality is also potentially useful in sea ranching and restocking studies. In these cases, the change of mortality rates in size will have an important role in assessing the stock status and identifying the optimal size at release. For example, the restocking program may be interested in producing a final stock of 10 million prawns at 10 mm CL: how many should be released at 5 mm CL or 2 mm CL to achieve this goal? The numbers given by the size-dependent mortality model and the constant dependent model are 26.5 and 47.6 million juveniles at size 5 mm CL, or 156.6 and 121.5 million at size 2 mm CL.

Chapter 4

Schooling dynamics in penaeid fisheries: Banana prawns (*Penaeus merguensis*) in the Australian Northern Prawn Fishery

A shallow-water, daylight fishery in the Gulf of Carpentaria fishes banana prawns (*Penaeus merguiensis*). These prawns form dense schools that are targeted by the fishing fleet with the help of small airplanes and colour sounders. Such schooling behaviour is rare in penaeids and, as in other fisheries for schooling fish, may lead to an inverse relationship between catchability and stock size.

We have used a sample of commercial logbook data containing trawl-shot records to identify the location, time of capture and biomass of over 600 banana prawn schools during the period 1991–92. The number of these schools decreases by 83% in the first three weeks of the fishing season. The average biomass of a school decreases even more rapidly than the number of schools and, after three weeks of fishing, it has been reduced by 93%. The apparent decrease in the biomass of schooling prawns during the first three weeks of the season is, therefore, in the order of 99%. This is considerably greater than the 66% decrease that can be estimated from catch per unit of effort data, and implies that assessment models which assume that catchability is independent of stock size are not appropriate for this fishery.

4.1 Introduction

Schooling is one of the most widespread behavioural mechanisms used by marine species to reduce natural predation. On the other hand, schooling behaviour often facilitates fishing because it aggregates the fish and the schools are easier to detect and catch than are individual fish. In fisheries for schooling organisms the capture of fish is only a small part of the fishing operations: searching for schools often represents the largest part of time spent at sea. Populations of schooling fish often show a relationship between stock size and vulnerability to fishing impact. As stock size decreases, it becomes easier and easier to catch the few remaining schools, and the proportion of the stock removed by one unit of effort (= catchability) increases. Unfortunately, schooling behaviour is rarely accounted for during stock assessments; therefore, many schooling stocks suffer from underestimation of the impact of fishing and from overly optimistic management, which often leading to overfishing and stock collapse (Hilborn and Walters, 1992).

Schooling is not restricted to fish; some marine invertebrates of commercial fishery importance form schools for eaxample, krill and squid. Very few penaeids, however, show schooling behaviour (Lucas, Kirkwood and Somers, 1979). Dall, Hill, Rothlisberg and Staples (1990) report that the group of white shrimp that occurs over muddy substrates (*Penaeus setiferus*, *P. indicus*, *P. merguiensis* and *P. chinensis*) "occasionally show schooling behaviour". Van Zalinge (1984) reports that in Kuwait *P. semisulcatus* sometimes form schools. Unfortunately, little research has been conducted on this aspect of penaeid behaviour and the work by Munro (1975) and Somers (1977) on *P. merguiensis* remain the only detailed published accounts describing penaeid shrimp schools.

P. merguiensis is an Indo-Pacific species harvested by trawl and artisanal fleets from the Persian Gulf to the East Coast of Australia (Grey, Dall and Baker, 1983). In Australia this prawn is harvested from the Exmouth Gulf in the west to Northern New South Wales in the east, but most of the catch comes from the Gulf of Carpentaria, the main fishing ground of the Northern Prawn Fishery. The Northern Prawn Fishery (NPF) is the most valuable fishery managed by the Commonwealth of Australia, and covers the area between Cape York in Northern Queensland and the Kimberly coast in Western Australia. The fishery started in the 1960s when schools of banana prawns (P. merguiensis) were discovered in the south-east Gulf of Carpentaria. Presently 128 vessels target a mixture of prawn species (banana prawns, tiger prawns, endeavour prawns and a few king prawns), but also harvest small quantities of squid, bugs, scallops and some fish. Annual prawn catches average around 8000 t, whole weight.

Early in the fishing season (April), and during the day, the fleet targets banana prawns that form very dense schools. As the banana-prawn catch declines, vessels switch to night-time fishing and start targeting tiger and endeavour prawns with trawl-shots of 3 to 4 h duration. The switch between fishing effort for banana prawns and fishing effort for tiger prawns has been described with a simple exponential model by Somers and Wang (1997).

Schools of banana prawn are sometimes visible during the day as 'mud boils' that can be seen from long distances, thus lending themselves to aerial spotting. Spotter planes are used for the first two or three weeks of the season, although vessels may search for banana-prawn schools for one or two weeks after that. Crews look for schools by eye, but also use colour echo-sounders to identify marks on or above the seabed that show the presence of banana prawns. Once a school is located, vessels either launch their main gear (twin otter trawls) or their try-gear (4-metre wide trawl) to test the presence of banana prawns. If the catch includes banana prawns the vessel(s) will fish the school and track it using the sounder until catches drop to non-economic levels. Trawl shots are short, often of less than 30 min, and trawl nets are set to fish light—that is with a large vertical opening and little drag on the bottom (by using floats in the headrope, twice as many meshes on the sides of the net and long fly-wires). Often other vessels join in to fish the same school.

The stock of banana prawns has been assessed as being fully exploited since the 1970s (Lucas, Kirkwood and Somers, 1979) and there is no evidence of recruitment overfishing. The long-term annual catch has been estimated from the median catch over the last 25 years and is 4000 t (Die and Taylor, 1996). There is a high year-to-year variation in catches (between 2000 and 8000 t) that has been linked to rainfall within the riverine catchments of the Gulf of Carpentaria (Vance, Staples and Kerr, 1985).

Lucas, Kirkwood and Somers (1979) estimated that in 1971 the fleet harvested 90% of the available stock. Since then the NPF, has changed considerably, one change being a decrease in the relative proportion of banana prawns in the mixed prawn catch. We do not know, however, whether the current fishing fleet is affecting the stock at the same rate as the fleet was in the early 1970s. Neither do we know whether school dynamics have any impact on the proportion of the stock harvested by each unit of effort—that is, whether catchability changes throughout the fishing season.

Given the large impact of the environment on recruitment of common banana prawns, management of this fishery focuses on maximising the yield obtained from each yearly cohort by controlling when the fishery harvests the stock. The fishery is closed while the banana prawns are small, not having reached adult size (the season starts on April 1 each year).

This paper aims at developing a method to identify common banana prawn stocks and investigate the changes in the number and size of these schools during the first few weeks of the NPF fishing season. We also compare these changes with those that occur in catch per unit of effort.

4.2 Methods

4.2.1 Data sources

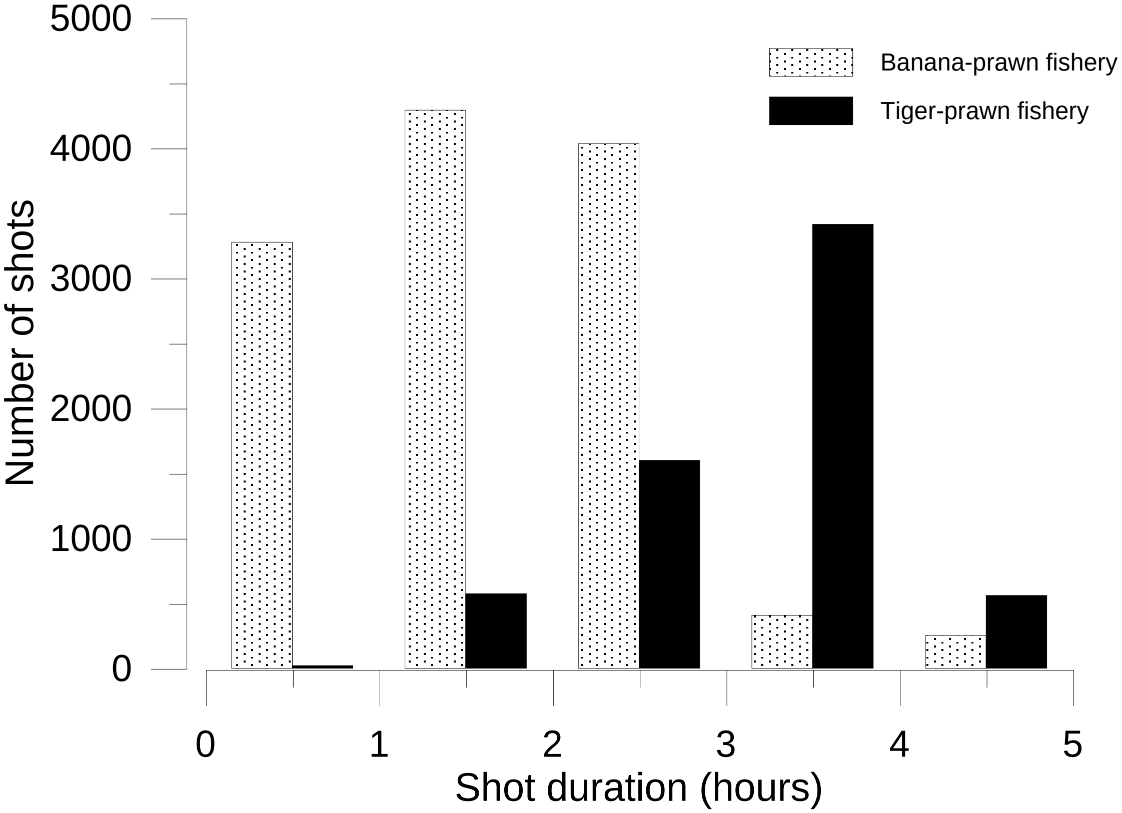
Fishers in the NPF are required to keep logbooks of information on daily catches by species group, together with the location of the highest catch (Robins and Somers, 1994). In the 1990s the catch recorded in logbooks represented 95% of the NPF landings. Presently, prawn discards are negligible; therefore logbooks are a very reliable and precise source of information on the nature of catches and their location. From 1981 to 1993, it was also possible to record in the logbooks catch data for every trawl-shot. However, these data were not entered in the computerised logbook database maintained by the Australian Fisheries Management Authority (AFMA). We have obtained trawl-shot data from the NPF logbooks for the period 1991–92 and placed it in a computerised database. The trawl-shot data correspond to 20% of the total fishing days of 1991–92 and we have assumed that these data constitute a representative sample of all fishing operations in the NPF.

Trawl-shot records contain information on the trawl-shot number, starting time, ending time and trawl-shot duration of each trawl-shot made during the fishing day. The number of cartons and/or weight of the catch by species group is also recorded. The latitude and longitude of each trawl shot is recorded with one minute precision (roughly equivalent to one nautical mile).

In the NPF, fishing days are classified as banana-prawn fishery days if the catch of banana prawns exceeds the catch of all other species groups or if the daily catch is zero (in which case it is assumed that the fisher was searching for banana prawns but did not catch any). During the first month of the fishing season (March or April, depending on the year) most fishing days are classified as banana-prawn fishery days because the fleet actively targets banana prawns during the day.

Not all trawl shots conducted during the peak of the banana prawn fishery are short, and 40% of banana-prawn fishery trawl shots are longer than two hours (Figure 4.1). This may be because fishing is directed at banana prawns that are not aggregated, or because some nightly trawl-shots are directed at catching tiger prawns. The tiger-prawn fishery trawl shots during this period clearly last longer than those for the banana-prawn fishery (Figure 4.1). For this study of schools of banana prawn we selected data corresponding to trawl shots lasting less than one hour that were made during banana-prawn fishery days.

Fig. 4.1. Trawl-shot duration (hours) for NPF vessels fishing during April 1991 and 1992 in the banana-prawn (grey bars) and tiger-prawn (solid bars) fisheries. The number of trawl shots from the trawl-shot database were raised to the total number of trawl shots in the fishery by using the ratio of the number of fishing days represented in the trawl-shot data and the total number of fishing days recorded in the logbooks.



4.2.2 Analysis

To define the characteristics of schools of banana prawn and the process of fishing them, we used a six-step process. From the trawl-shot data, we first identified schools and, in the process, characterised the number of schools individual vessels target each day. Secondly, also from the trawl-shot data, we investigated how much the daily catch records tolds us about the catch made by individual vessels in the largest schools they fished. Thirdly, we used the daily catch records to identify any other vessels that may have fished the schools identified in the first step. Fourthly, we estimated the overall size of the school from the combined catch of all vessels that fished a particular school. Fifthly, we compared abundance estimates inferred from catch per unit of effort data with those obtained from school abundance and school-size data. Lastly, we also investigated prawn densities within schools.

1. Identifying schools

   The skippers always record the position of the first trawl shot of the day, but often neglect to record any position for subsequent trawl shots. We therefore assume that subsequent trawl shots are at the same position, provided either (a) the depth does not change or (b) the time interval between winching up and the next trawl shot is less than 1 h.

   A daily sequence of trawl shots from a single vessel need not be targeting the same school. We assume that a trawl shot targets a new school if (a) the time since the start of the last trawl shot exceeds 4 h, or (b) the position changes by more than a minute in either latitude or longitude. The final stage in identifying schools is to amalgamate any trawl-shot sequences from two or more vessels that overlap in space and time. We assume that two vessels fished the same school if their trawl shots have identical position and differ in time by less than 4 h.

2. Relating daily catch to schools

   Let's define $C_{n,d,s}$ as the catch of vessel n in day d for trawl-shot s, and $C_{n,d,\cdot}$ as the daily catch of vessel n. For those vessels that filled daily logbooks only we know the overall daily catch and the location of the greatest catch. For the vessels that provided trawl-shot records, we also know how many schools were fished and the locations of these schools. We used the latter group of vessels to estimate the proportion of a vessel's total catch that was actually caught at the location of greatest catch, $P_{d,\max}$, where

   $$P_{d,\max} = \frac{\max(C_{n,d,s})}{\sum_s C_{n,d,s}}.$$

   These proportions indicate how informative the daily data are about the position and size of schools captured.

3. Identifying other vessels that fished schools

   Only the daily logbook data for 1992 were used in this analysis because, during 1991, many vessels did not report the location of the greatest catch at the precision (1 minute) required for matching with trawl-shot data. Even in 1992 only half of the vessels that provided their daily catch recorded the position of greatest catch with 1-minute accuracy; the other half recorded it at 6-minute accuracy. This lack of precise catch-location information from the latter group meant that their catches could not be directly associated with particular schools. On the other hand, for those vessels that did provide precise catch-location information but did not provide trawl-shot data, we did try to allocate their catch to specific schools. For vessels where the position of greatest catch (as reported in daily logbooks) coincided with the position of a school identified from the trawl-shot data, we assumed that the vessel was fishing that school.

4. Size of schools

   We assume that each school is completely fished out. The size of a school is, therefore, the total catch from all vessels fishing it. We assume the total catch is the sum of three components: (a) the catch from the i vessels that provided trawl-shot data; (b) the catch from the j vessels that provided daily data at 1-minute precision; and (c) the catch from the k vessels that provided daily data at 6-minute precision. The first component is simply computed from the sum of the catch of all trawl shots associated with a given school a: $\sum_s \sum_{n=1}^{i} C_{a,n,d,s}$. Given that the daily catch of the j vessels is assumed to correspond to a single school, the second component is the daily catch $C_{n,d,\cdot} = C_{a,n,d,\cdot}$. Clearly this second component will give an overestimate of the school size because some vessels that provided only daily data may have fished more than one school in a day.

   To estimate the third component, we first calculated the total grid-level daily catch made by vessels that provided daily data at the 1-minute level, $\sum_{n=i+1}^{i+j} C_{g,n,d,\cdot}$, and at the 6-minute grid level, $\sum_{n=i+j+1}^{i+j+k} C_{g,n,d,\cdot}$, where $C_{g,n,d,\cdot}$ denotes the daily catch made by vessel n in the 6-minute grid g.

   We then estimate, from the data at the 1-minute level, the proportion P_a of the total daily grid-level catch assigned to school a:

   $$P_a = \frac{\sum_{n=i+1}^{i+j} C_{a,g,n,d,\cdot}}{\sum_{n=i+1}^{i+j} \sum_a C_{a,g,n,d,\cdot}},$$

   where $C_{a,g,n,d,\cdot}$ denotes the daily catch made on school a by vessel n in the 6-minute grid g. Finally, we assign proportional fractions of the daily grid catch at the 6-minute level to all schools lying in that grid during that day:

   $$C_{a,*,d,\cdot} = P_a \sum_{n=i+j+1}^{i+j+k} C_{g,n,d}.$$

Some of the schools found in a 6-minute grid may not have been fished by the group of vessels that provided trawl-shot data and would not therefore, be identified in this analysis. This would also suggest that our overall estimates of school size,

$$C_{a,d} = \sum_{s} \sum_{n=}^{i} C_{a,n,d,s} + \sum_{n=i+1}^{i+j} C_{a,n,d} + C_{a,*,d}.$$

are overestimates.

5. Abundance estimation

   As an estimate of the biomass of aggregated banana prawns, we simply use the catch of all schools. Such an index assumes that catch is independent of effort and reflects population biomass. The fishing effort directed to the banana-pawn fishery decreases as the first month of the season proceeds. We believe, however, that the chance of detection of individual schools does not decrease because the available search capacity always exceeds the time required to search through the area (we assume that search effort is heavily saturated).

   We then compared these estimates of abundance with more traditional measures such as the catch per hour trawled and the catch per day fished.

   We also estimated densities of prawns within schools by combining data on catch rates (kg/min) with data on gear size and prawn size. The volume of water sampled by a banana prawn net was assumed to be the product of headrope length (metres), trawl speed (metres per minute), trawl duration (winch-up time from logbooks, minus shoot-away time from logbooks, minus 5 minutes to account for duration of winching process), and a factor representing the ratio between the area of the opening of a banana prawn net and the headrope (this factor equals 0.05 × headrope—Steve Eayrs, Australian Maritime College, personal communication). The density (number of prawns m^{-3}) was then calculated from the biomass density (kg m^{-3}) and data on the average size of banana prawns caught during April in 1991 and 1992 (40 prawns kg^{-1} according to Brian Taylor, CSIRO, unpublished data).

4.3 Results

1. Identifying schools

   The data used comprised 1024 records of trawl shots that targetted schools of banana prawns and contained location information corresponding to 510 fishing days. In 71% of cases, vessels did less than 3 trawl shots per day, and in only 3% of cases did vessels do more than 5 trawl shots per day (Table 4.1).

Table 4.1. Number of trawl shots per day made by NPF vessels targeting banana prawn schools.

No. trawls per shot-day	1	2	3	4	5	6+
Frequency	282	80	61	52	20	15

Table 4.2. Number of trawl shots per school made by NPF vessels targeting schools of banana prawns.

No. trawl-shots per vessel per school	1	2	3	4	5	6+
Frequency	482	97	44	33	7	9

   We identified 420 (Figure 4.2) schools during the initial nine weeks of the fishing season for 1991 and 209 during the same period in 1992. Most vessels did only one trawl shot per school (Table 4.2), and only in 14% of cases did an individual vessel undertake more than two trawl shots in a school.

2. Relating daily catch to schools

   For 77% of the fishing days, vessels that targetted schools fished only one school per day, and on only 7% of the fishing days did vessels fish more than two schools per day. Therefore, on 77% of the fishing days the daily catch was made from a single school and the reported location of the daily catch will be the school's location. In the other cases, part of the catch came from other schools and, thus, other locations (Table 4.3). For these other days, the catch made at the largest school ranged from 38% to 99% of the total daily catch (Figure 4.3). However, more than half of these days the catch made at the largest school represented more than 60% of the daily catch. This suggests that our assumption, in the absence of other data, that the whole daily catch was caught at the location of the greatest catch will be correct in 77% of cases. In a further 13% of cases, this assumption will overestimate the catch by up to 40%. In only 10% of cases will the assumption overestimate the catch by more than 40%. Overall, the catch taken at the location of the greatest catch was 90% of the total daily catch of the vessels that provided trawl-shot data (Table 4.3).

Fig. 4.2. Location of schools of banana prawn found in trawl-shot data. Schools are classified according to the number of recorded trawl shots within each school.

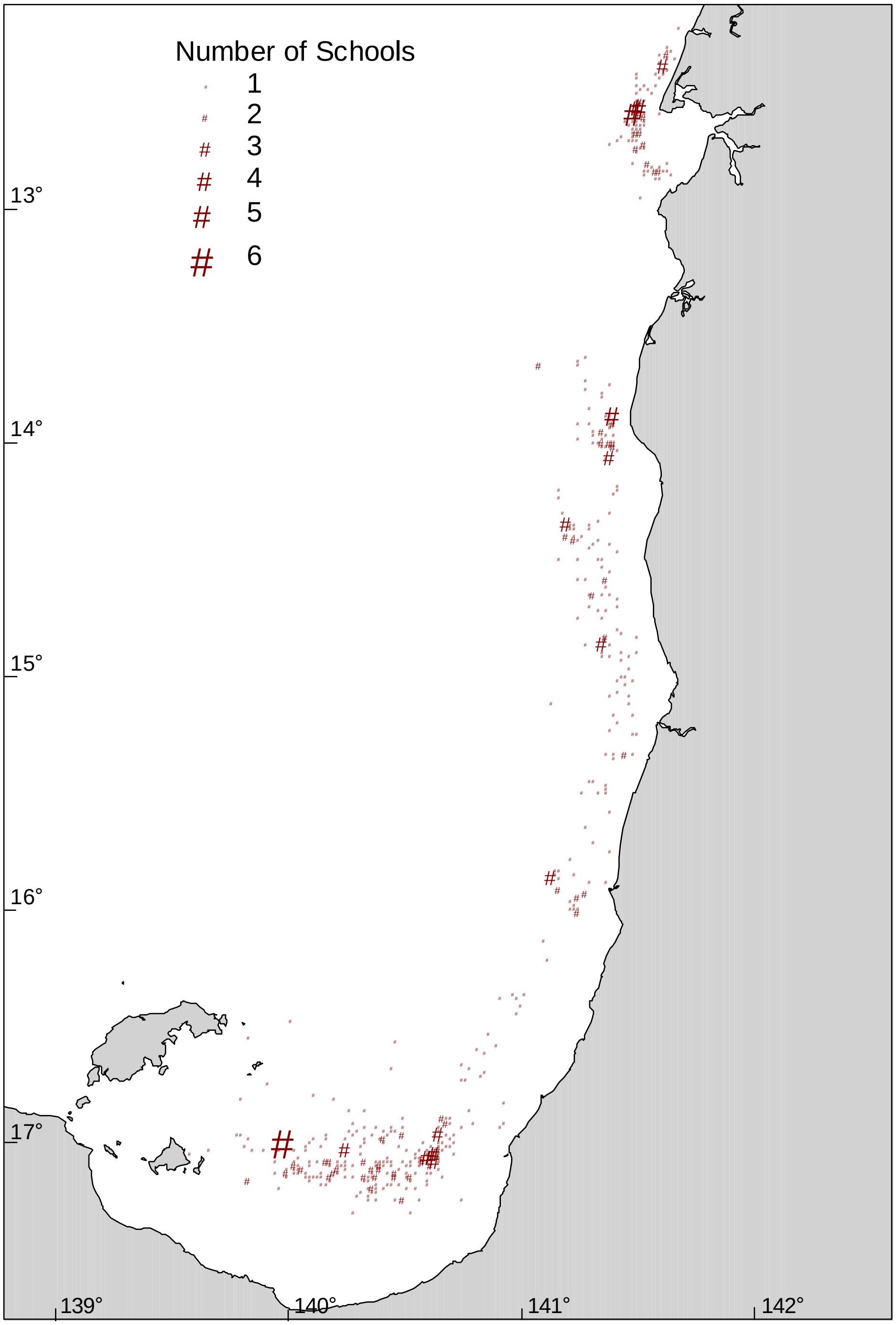


Table 4.3. Number of schools fished per vessel per day, catch made at the location of greatest catch (tons), total daily catch (tons) and percentage of daily catch caught at the location of greatest catch.

No. schools	Frequency	Greatest catch	Daily catch	% catch
1	399	497.2	497.2	100
2	71	78.6	113.7	69
3	33	28.5	48.3	59
4	4	6.8	13.5	51
5	3	2.9	6.8	42
Total	510	613.9	679.4	90

3. Identifying other vessels that fished schools

   For 1992, we identified 206 fishing days where vessels recorded daily catches and positions at the 1-minute level such that the catch could be associated with one of the schools identified by the trawl-shot data. The total catch of banana prawns associated with these fishing days was 189 t, compared with the 105 t already associated to these schools from the trawl-shot data. Finally we allocated an extra 3.5 t of catch to these schools from the 20 fishing days where vessels recorded daily catches only at the 6-minute grid level.

4. Size and number of schools

   The school size, identified from trawl-shot data alone in 1991, ranged from less than 10 kg to over 10 t (Figure 4.4). For 1992, the range of school sizes is similar to those in 1991; but this may be largely because many of the larger schools identified in 1992 contain daily as well as trawl-shot data (Figure 4.4). The average size of 1992 schools that were identified by trawl-shot data only is 50% smaller than the average size of those identified in 1991.

   School size decreased quickly during the initial nine weeks of the fishing seasons (Figure 4.4) at an exponential rate equivalent to halving the size every 5 days. The number of schools fished also decreased exponentially, halving each week for the first four weeks of the season (Figure 4.5).

5. Abundance estimation

   The catch per day for the first month of the 1977 and the 1991 seasons follows a very similar pattern, whereas the catch per day for the first month of the 1992 season was always smaller (Figure 4.6). In 1977, the catch per day decreased exponentially as a function of time at a rate of 4% per day. Similarly, catch per day decreased by 5% in 1991. These decreases equate to a halving of the catch rate every 14 17 days. By contrast, during 1991 the catch per day from schools decreased exponentially by 21% per day, therefore halving every 3 days.

Fig. 4.3. Histogram of percentage of total daily catch accounted for by the catch (kg) from the largest school fished in each day. The histogram is based on 490 fishing days. On 379 of these days only one school was fished, whereas on the other 109 days more than one school was fished.

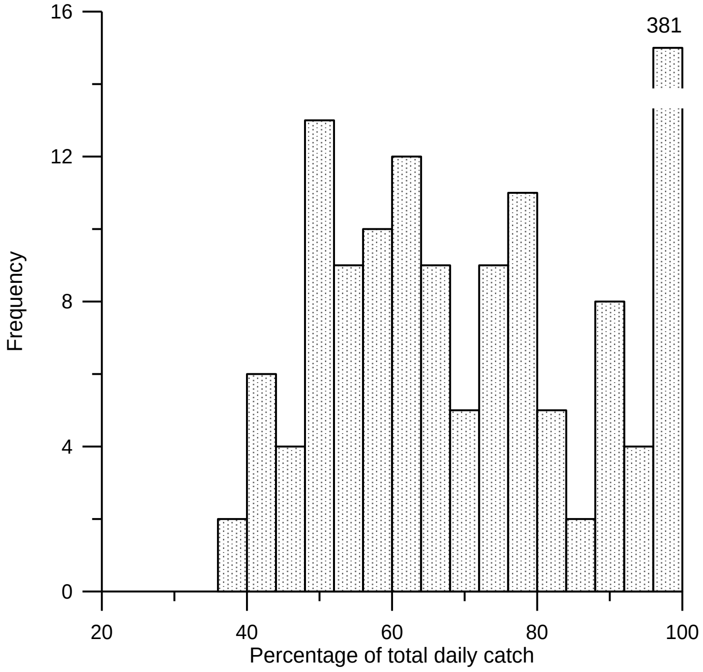


Fig. 4.4. School sizes (kg) for the 1991 and 1992 seasons. Circles indicate schools that incorporate both trawl-shot and daily data. Crosses indicate schools that only incorporate trawl-shot data. The sizes of the former are overestimated and those of the latter are underestimated.

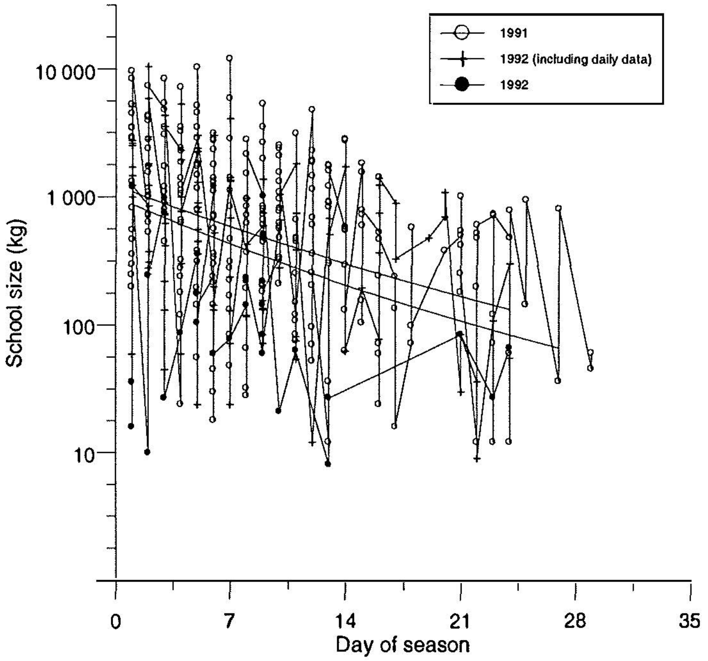


Fig. 4.5. Number of schools identified in trawl-shot data for the initial 9 weeks of the season in 1991 and 1992. Season begins April 1.

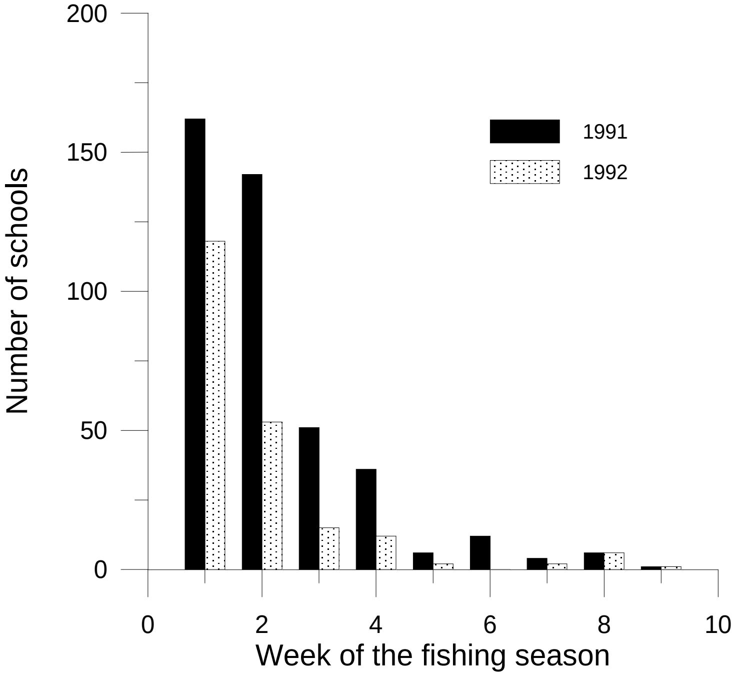
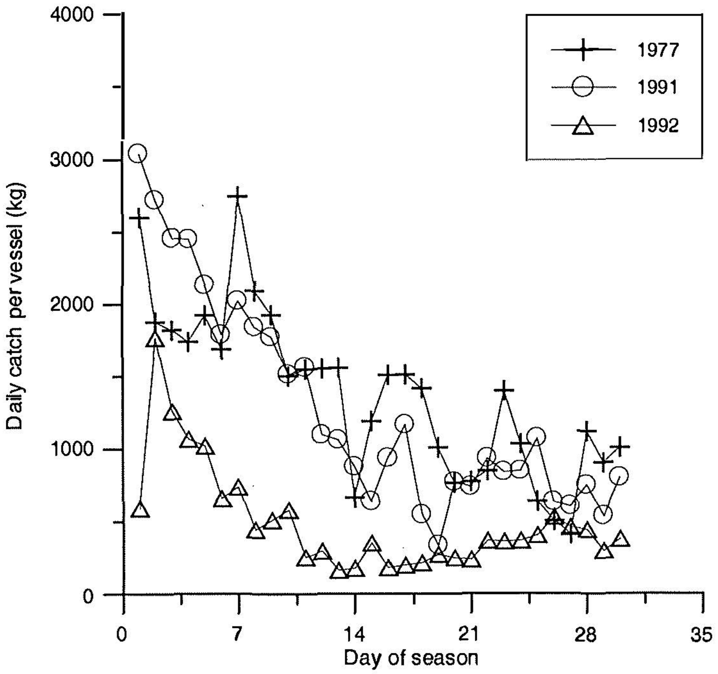


Fig. 4.6. Banana prawn catch per day (kg) in the first five weeks of the fishing season of the NPF banana-prawn fishery for the years 1977, 1991 and 1992.



The duration of trawl shots is reduced as school densities increase (Figure 4.7) which suggests that trawlers shorten their trawl shots when schools are very dense to avoid bursting the nets. The highest densities were estimated to be 167 g m^{-3} or 6.6 prawns m^{-3} and densities of 7 g m^{-3} or 0.35 prawns m^{-3} were not uncommon (90% percentile).

4.4 Discussion

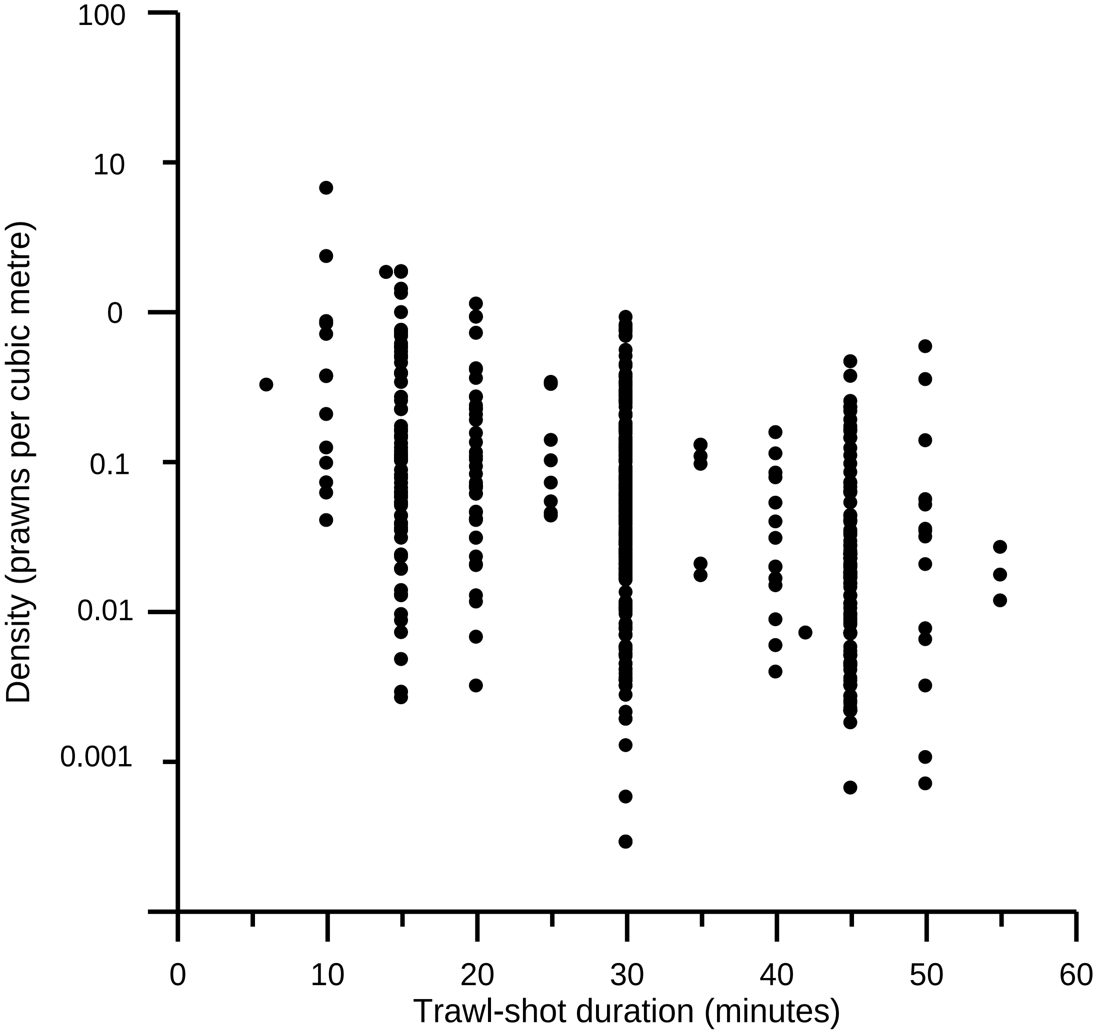
The impact of fishing on the abundance of highly aggregated stocks of mobile species is notoriously difficult to assess unless the relationship between catch per unit of effort and overall abundance is well known. Many authors have investigated this relationship on theoretical terms (Clark and Mangel, 1978) and have fitted the resulting population models to their catch per unit of effort data. We, on the other hand, have chosen to describe the dynamics of schools of banana prawns. This description may later help to build an empirical model of the relationship between catch per unit of effort and overall abundance.

Sharp (1978) investigated the origins of tuna schools of different sizes and described the relationship between primary schools, secondary (those derived from the amalgamation of primary schools) and mixed schools of tuna and dolphins. Sharp associated each purse seine set with a single school. We relaxed this assumption in our work because in the NPF large schools of banana prawn can be fished by several trawl shots and by more than one vessel.

Munro (1975) reports that sub-adult *P. merguiensis* start schooling when they leave the rivers and that catch rates of 90 kg per 30 min trawl shot can be made, which corresponds to about 9000 small prawns (unfortunately Munro does not report the type of gear used in his work). Between March and September these prawns grow into adults and school actively until late September in waters between 13 and 20 m deep. Schools are almost monospecific and remain 1 m above the bottom, either as a 2–4 metre ball, or dispersing vertically in the shape of a Xmas tree. Sediments are lifted by the schools, which helps fishers to detect them from the surface that is why they are called mud-boils. Munro suggests that schooling tends to occur in slack water conditions, around the neap tides, and did not find evidence to associate mating or moulting with schooling behaviour.

It must be pointed out that schools of banana prawn, although dense in comparison to other penaeids, are much less dense than those of demersal fish. For example, Crawford and Jorgenson (1996) used sonar to measure artic cod schools containing 70–90 m^{-3} and 500–600 t per hectare. The density of schools of banana prawns is also less than that of pelagic fish such as herring, which pack in schools of up to 19

Fig. 4.7. Density (prawns m^{-3}) of banana prawns in schools identified from trawl-shot data as a function of the duration of trawl shots.



fish m^{-3} but average 4.25 fish per cubic meter (Misund, Aglen and Fronaes, 1995). By comparison, the highest densities estimated for schools of banana prawns in our study are 6.6 prawns m^{-3} and 3 t per hectare. Some of the above differences may be because our estimates are likely to be underestimating real density. Trawl gear is always deployed in the water ahead of the school to ensure that the trawl is fully open before it comes in contact with the school. The gear is also left on the bottom for a few minutes after the school has been overtaken by the net. This means that the total volume sampled by the net is greater than the volume of the school that issampled; thus the density is underestimated.

In our analysis we assume that the total catch made from a school represents the initial biomass of that school. Future detailed investigation of the catch rate from large schools may reveal whether this is a reasonable assumption. Otherwise echo sounders may be used to determine the size of the school. Robins and Sachse (1994) report a large school detected by echo sounder in April 1974 that was estimated to contain 19 t of banana prawns. This is only twice the size of the largest school detected by us in 1991–92. Somers (1977) surveyed NPF skippers in 1977 and asked them to estimate the size of schools of banana prawns fished during that year. School size ranged from 4 t to a maximum of 180 t. Somers (1994) suggests that, given that 1977 was not a year of record catches, schools of up to 400 t are not unthinkable. Similarly, Lucas, Kirkwood and Somers (1979) report that schools of banana prawns "typically occupy an area up to several thousand square meters and a total catch of several tonnes although very much greater catches from a single school have been taken".

The banana-prawn catch in 1977 was 6300 t, similar to the 1991 catch of 6700 t and much larger than the 2200 t caught in 1992. Therefore, the biomass of banana prawns in 1977 and 1991 was probably similar. The number of schools we identified in 1991 was 420, greater than the estimate of 257 obtained by Somers (1977) for 1977. According to Somers, the modal size of schools in 1977 was 4 t, much larger than the modal size of 1 t identified from our 1991 data. It is possible that there were more small schools in 1991 than in 1977, but it is also possible that the differences in the size and number of schools between the two years are a result of the different methods used by us and Somers.

In our study we chose to define schools according to the length of the trawl shot (< 1 h) and to whether most of the catch of that day was made up of banana prawns. In 1983–1985, Ian Somers and David Carter (see Hill (1994)), during work designed to establish the opening of the fishing season, used a different criterion to define banana prawn schools: those trawl shots made with a 6 m try-net where the catch rate was more than 10 prawns per minute. This is equivalent to 160 kg of banana prawns per one h trawl shot, which is two to three times larger than the size of the smallest schools (about 50 kg) identified by us for 1991–1992 (Figure 4.4).

Many other published reports about fisheries for schooling penaeids report strong stock declines or complete fishery collapses, suggesting that schooling penaeids are generally prone to over-fishing. During the early times of the prawn fishery in Kuwait Van Zalinge (1984) reported catch rates of 1100 to 4400 kg per hour for *P. semisulcatus*, 120 to 1200 kg for *Metapenaeus affinis* and 225 to 660 kg for *Penaeus stylifera* in a fishery that used vessels and gear similar to that of the NPF. Mathews and Abdul-Ghaffar (1986), however, suggest that *P. semisulcatus* schools are no longer a feature of the Kuwait fishery, and suggest that this is due both to overfishing and to environmental disturbance.

A small but similar banana-prawn fishery to that of the NPF took place in Exmouth Gulf in Western Australia where schools were targeted with the aid of spotter planes. As in Kuwait, schools of banana prawn disappeared from Exmouth Gulf by the end of the 1960s and the daylight fishery for *P. merguiensis* was replaced by a night-time fishery for *P. esculentus* and *P. latisulcatus* (Penn, 1984). Moffet (1967)—quoted by Penn—reports schooling may have contributed the decline of P. setiferus in Texas. Penn reports on other large declines for fisheries based on schooling penaeids in the Yellow Sea for *P. orientalis* (cites Kristjonsson (1969)), for *P. indicus* in Madagascar (cites Marcelle (1978)), and in SW India (cites Kristjonsson). Penn suggests that high effort may alter schooling behaviour, but acknowledges that this may be just an erroneous impression resulting from stock declines.

Our decision to base our schooling criterion on the length of the trawl shot reflects the operations of commercial vessels in that fishers are likely to use short trawl shots only when they expect that the prawns are highly aggregated. Short trawl shots allow fishers to steam back quickly to the original location of the school and shoot again, prevent nets from bursting, and minimise losses of prawn quality because of excessive catch in the codend. A portion of the banana-prawn catch is taken in trawl shots longer than 1 h during pattern trawling. We assume this mode of fishing does not target schools. According to our trawl-shot data, more than 99.9% of the NPF banana-prawn catch for the months of April 1991 and April 1992 was taken during the banana-prawn fishery (when more than 50% of the daily catch comprised banana prawns). Two thirds of these banana prawns were caught in schools (with trawl shots less than 1 h) and one third was caught by pattern trawling (trawl shots longer than 1 h). Less than 0.1% of the NPF banana-prawn catch was caught in the tiger-prawn fishery. However, because it is much easier to catch aggregated prawns, the preceeding figures cannot be used as an indication of the relative proportions of the total biomass found in schools and outside schools. for inferences to be made about the relative contribution of aggregated prawns to the total biomass of the population, further knowledge on the schooling process itself is required.

By comparing the changes in relative abundance as estimated from logbook data on catch per day with changes as estimated from the daily catch of schooling prawns, it seems obvious that the decrease in biomass of schooling prawns is much faster than the decrease in biomass of non-schooling prawns. This is clearly caused by fishers targeting schools. It also seems obvious that stock size determines the size of the schooling population and that there are fewer and smaller schools in the years of small stock size. This suggests that catchability (the portion of the stock harvested by a unit of effort) must decrease as stock density decreases, which implies that not only does catchability decrease as the season progresses, but also that catchability is smaller in years of small stock size than in years where stocks are large.

The relationship between school size and total biomass has been shown to be crucial in determining the impact of fishing on a harvested stock (Clark and Mangel, 1978). Many authors suggest that the inverse relation between catchability and stock size is a general phenomenon of all fisheries and not of only pelagic stocks (Crecco and Overholtz, 1990; Condrey, 1984; Winters and Wheeler, 1985). This relationship between catchability and stock size has not been proven for prawn stocks in the NPF. In fact Wang and Die (1996), in their assessment of NPF tiger-prawn stocks, assumed that catchability was constant and independent of stock size. Our present study suggests that, in the NPF fishery for banana prawns, fishers' targeting of schools is likely to result in catchability being inversely related to stock size. Therefore, the inference from this study is that assessment methods which assume that catchability is independent of stock size—such as the method used by Lucas, Kirkwood and Somers (1979)—may not be appropriate for modelling the effects of fishing on the NPF banana-prawn stock.

Acknowledgments

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Chapter 5

Effects of abundance distribution and effort distribution on catchability

We examine the effects of abundance distribution and effort distribution on the catchability coefficient. Using the framework of Swain and Sinclair (1994, Can. J. Fish. Aquat. Sci. 51: 1046-1054), we investigate the effect of aggregation for a given pattern of fishing effort and the effect of targeting. Some analytic expressions are derived. In particular, we propose evaluating three indices: the catchability ratio, knowledge parameter and the aggregation index to understand the causes of the density dependent catchability. We also analyze the commercial catch-effort data from the Northern Prawn Fishery. It appears that the density-dependence has increased the catchability by 10% and the stock of tiger prawns has a declining aggregation.

5.1 Introduction

The traditional approach to catch and effort data is based on the well known catch equation Gulland (1983), p.105). This presumes that fish are evenly distributed on the fishing ground, or that fishing effort is randomly distributed. This is clearly not the case for most fisheries because of (a) the aggregation behaviour of fish, and (b) targeting by fishers. In such cases, the traditional catch equation is inappropriate to describe the relationship between catch and effort (Crecco and Overholtz, 1990; Richards and Schnute, 1992; Paloheimo and Chen, 1993). Paloheimo and Dickie (1964) suggested density-dependent catchabilities for Georges bank haddock, and Crecco and Overholtz (1990) tested and supported their theory. Shardlow (1993) also found that the catchability increased with abundance in a Salmon fishery. In fact, Paloheimo and Dickie (1964) argued that density-dependent catchability exists for most demersal and pelagic fisheries. Density-dependent catchability should be incorporated in the estimation methods and the population models to obtain more accurate estimates of effective effort, which are essential for stock assessment models.

In Australian prawn fisheries, banana prawns are known to aggregate to a great extent. Although species aggregate to a lesser extent, fishers rely on this behaviour and on their experience and modern searching devices to increase their catch rate. Therefore, the catchability will depend on the distribution of fishing effort in relation to the distribution of prawns. If the theory of density-dependent catchability is applied to the prawn fisheries, better indices of abundance than the catch per unit of effort will be produced, and catch-effort data will be used more efficiently.

In this paper, we will examine both effects of fish distribution (aggregation) and effort distribution on catchability in a similar way as in Swain and Sinclair (1994) and Swain and Morin (1996). We describe the effort distribution using a parameter which measures the knowledge about the abundance distribution. The change in catchability is a joint effect of aggregation of fish and knowledge of fishers. We also analyze the commercial catch-effort data from the Northern Prawn Fishery in Australia.

5.2 Relative Abundance Distribution

Swain and Sinclair (1994) (subsequently denoted as SS) assume that abundance at the geographic position x is given by

$$d_x = Nf(x),$$

where $f(x)$ can be given by a density function so that $\int f(x)dx = 1$.

If $e(x)$ is the effort spent at position x, the expected catch is

$$c(x) = qe(x)d(x),$$

where q is a constant independent of x. If a total of $\int e(x)dx = E$ effort is spent over the area $\mathcal{A}$, the average catchability is defined to be

$$q_e = \frac{C}{NE} = \frac{\int_{\mathcal{A}} c(x)dx}{NE}. \tag{5.1}$$

SS considered three models for fishing effort.

(i) uniform fishing or equivalently fishing is random over the area $(-x_T, x_T)$ where the fish density exceeds some threshold;

(ii) fishing effort at position x is proportional to the abundance at x for $x \in (-\infty, \infty)$;

(iii) fishing only at the location where the abundance is maximum, i.e, at $x = 0$.

In model (i), it is assumed that fishers have no knowledge about the distribution of the fish stock (except that it exceeds some threshold density within a finite area). The corresponding catchability can therefore be regarded as a bench-mark. We would expect the catchability in model (iii) is the highest, and the model (ii) is probably a more realistic case.

Assuming $f(x) = \sigma^{-1}\phi(x/\sigma)$, the normal density function with a variance σ^2, SS obtained the corresponding catchabilities for the three effort models as

$$\begin{aligned} q_0 &= \frac{q\int_0^{x_T} f(x)dx}{x_T}, \\ q_1 &= q\int_{-\infty}^{\infty} f^2(x)dx = \frac{q}{2\sigma\sqrt{\pi}}, \\ q_\infty &= \frac{q}{\sigma\sqrt{2\pi}}. \end{aligned}$$

Note that in case (i) the fishing area $(-x_T, x_T)$ depends on both the abundance distribution and the total abundance N. This is why SS concluded that spatially uniform changes in abundance also affect the catchability to some extent. In fact such effect is due to changes in distribution of fishing effort.

If $f(x)$ is the relative abundance distribution as a function of position, what is the proportion of fish distributed in areas with density $\leq r$? This proportion, $F(r)$, is given by

$$F(r) = \int_{Nf(x)\leq r} f(x)dx.$$

It may appear that characterization of the abundance by a one-dimensional function $f(x)$ is overly restrictive. However this is not the case if we reinterpret the x variable. Note that $F(r)$ does not depend on the actual spatial arrangement of density, since the x-axis could be segmented and arbitrarily rearranged to give the same $F(r)$. This infinite family of spatial density distributions can be represented by the unique function $f(x)$ in which the densities are sorted in decreasing order. For instance, the normal density $\phi(x)$ can be represented by a one-sided normal density $2\phi(x)I(x > 0)$, where $I(\cdot)$ is an indicator function. Furthermore, $f(x)$ can also represent two-dimensional densities, since these can be binned, sorted and laid out in one dimension. The integration element dx should then be reinterpreted as an area element.

We will use R to denote the corresponding random variable that has the cdf $F(r)$. After some algebra, we also have for any n,

$$\mathrm{E}\left(\frac{R}{N}\right)^n = \int f^{n+1}(x)dx, \tag{5.2}$$

which will be used later.

If $f(x)$ is the standard normal density, the above integration is

$$\frac{1}{(\sqrt{2\pi}\sigma)^n\sqrt{n+1}}.$$

5.3 Effect of Aggregation

From (5.1), we have

$$q_e = \frac{\int_{\mathcal{A}} e(x)f(x)dx}{E}. \tag{5.3}$$

We now consider how the catchability changes when the distribution of abundance changes for a given fishing pattern $e(x)$. The $e(x)$ is assumed to be
(a) a constant over a fixed area $(-X, X)$,where $X > 0$;
(b) $e(x) = \phi(x)$;
(c) $e(x) = \phi(x)/\{2\Phi(X) - 1\}$ for $x \in (-X, X)$.

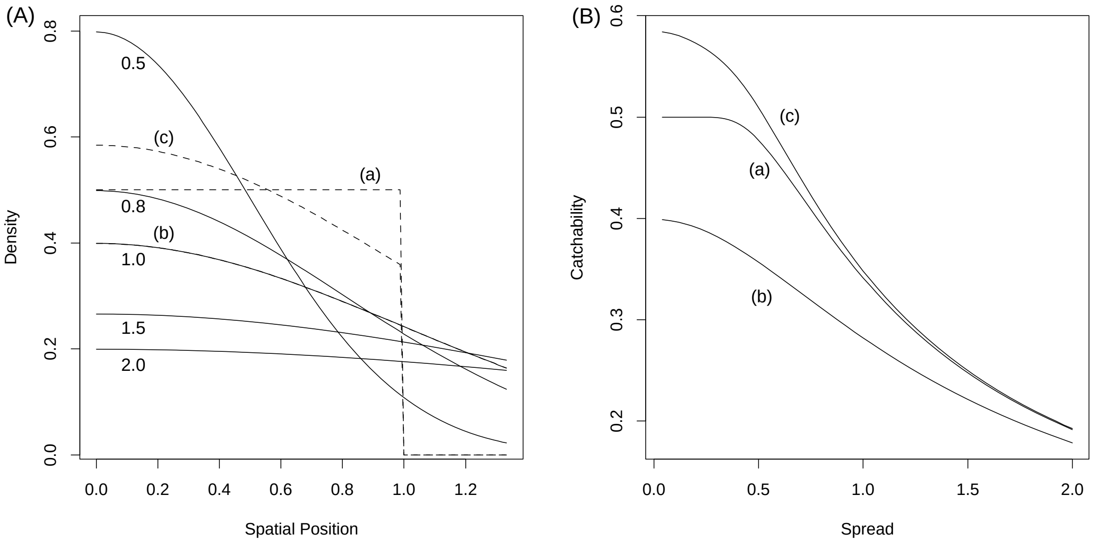
Unlike the case (i) considered by SS, the fishing area here is fixed in (a). The case (b) is slightly different to the case (ii) considered by SS in which the effort pattern changes as the abundance changes. In our cases here, fixing the fishing effort function and allowing the abundance distribution to change, q_e shows the effect of aggregation on catchability.

If we assume $f(x) = \sigma^{-1}\phi(x/\sigma)$, we have the corresponding catchabilities for the above three fishing-effort functions

$$q_a = q\frac{\Phi(X/\sigma) - 0.5}{X},$$

$$q_b = \int_{-\infty}^{\infty} \phi(x)\frac{1}{\sigma}\phi(x/\sigma) = \frac{q}{\sqrt{2\pi(1+\sigma^2)}}.$$

Fig. 5.1. (A) Abundance distribution for a range of values of the spread σ. Overlaid (dashed line) are the effort patterns (a), (b) and (c). (B) ratio of catchability to q vs spread for each effort pattern.



Here $\Phi(\cdot)$ is the standard normal cumulative density function (cdf). Similar algebra leads to

$$q_c = q_b \frac{2\Phi(X\sqrt{(1+\sigma^{-2}}) - 1}{2\Phi(X) - 1}.$$

We demonstrate how catchability varies with aggregation in Fig. 5.1. Fig. 5.1(A) shows the abundance distribution for a range of values of the spread σ. More highly aggregated distributions have smaller values of σ. The effort pattern in (b) is identical to the distribution labeled 1.0. In (a) and (c) we let $X = 1$, as shown by the dotted line. Fig. 5.1(B) shows the ratio of catchability to q against spread for the three effort patterns. In all cases the catchability decreases with spread. Case (a) is not very sensitive to σ for small spreads until $\sigma \approx X$ because almost the entire population lies inside X. On the other hand, targeted patterns are more sensitive to σ. The catchability is higher for (c) than for (a) because, although both patterns cover the same area, the effort pattern (c) exploits the aggregation more. Similarly q_c is higher than q_b because the effort used in (b) outside X is used more efficiently in (c) inside X. The catchability of (a) relative to (b) depends on X; for sufficiently large X, q_a is less than q_b.

We can define a dimensionless aggregation index in terms of the variance of R thus

$$\lambda = \mathrm{var}(R/\bar{R}), \tag{5.4}$$

where $\bar{R} = N/A$, the mean density. If f is a normal distribution then $\lambda \propto 1/\sigma^2$. Hence large values of λ imply a small spatial spread, so that it is appropriate to regard λ as an index of aggregation.

5.4 Effect of Effort Distribution

We will assume that the effort distribution is a power function of the abundance, i.e., $e(x) \propto f^{\gamma}(x)$. The constant of proportionality is $E/\int f^{\gamma}(x)dx$ to obtain a total effort of E. Without loss of generality, we will simply assume $E = 1$. We will refer to γ as the knowledge parameter. Higher values of γ provide more effort in higher abundance areas and result in greater catches. The three models discussed by SS correspond to the cases when γ =0, 1, and ∞, respectively. The general expression for the catchability is

$$q_{\gamma} = q\frac{\int_{\mathcal{A}} f^{\gamma+1}(x)dx}{\int_{\mathcal{A}} f^{\gamma}(x)dx}.$$

For random fishing $\gamma = 0$, and the catchability becomes

$$q_0 = qn_A/A,$$

where n_A is the proportion of the population inside the region $\mathcal{A}$ with area A.

From eqn. (5.3), the ratio of the two catchabilities generated from effort functions $e_1(x)$ and $e_2(x)$ is

$$l = \frac{\int e_2(x)f(x)dx}{\int e_1(x)f(x)dx}.$$

In particular, we shall be interested in quantifying the increase in catchability of a fishing pattern $e(t)$ relative to the catchability from random fishing. If $e(x) \propto f^{\gamma}(x)$,

$$l(\gamma) = \frac{A\int_{\mathcal{A}} f^{\gamma+1}(x)dx}{n_A\int_{\mathcal{A}} f^{\gamma}(x)dx}. \tag{5.5}$$

An alternative expression for $l(\gamma)$ can be found in terms of the abundance distribution, using the moment equations (5.2) thus:

$$l(\gamma) = \frac{A\mathrm{E}(R^{\gamma})}{N_A\mathrm{E}(R^{\gamma-1})}, \tag{5.6}$$

in which N_A is the population within $\mathcal{A}$. This form will prove useful in estimating $l(\gamma)$ assuming known γ.

In the case when $f(x)$ is the normal density function, and $\mathcal{A} = \{x : |x| \leq z_\alpha \sigma\}$,

$$\begin{aligned} l(\gamma) &= \frac{2z_\alpha \sigma \int_{\mathcal{A}} f^{\gamma+1}(x)dx}{n_A \int_{\mathcal{A}} f^{\gamma}(x)dx}, \\ &= \frac{2z_\alpha}{(1-\alpha)\sqrt{2\pi}} \frac{1-2\Phi(-z_\alpha\sqrt{\gamma+1})}{1-2\Phi(-z_\alpha\sqrt{\gamma})} \sqrt{\frac{\gamma}{\gamma+1}}, \end{aligned}$$

in which z_α is the $100(1-\alpha/2)$ percentile value for a standard normal distribution. For example, $z_{.05} = 1.96$, and $\mathcal{A}$ becomes the highest abundance region containing 95% of the population.

Fig. 5.2 shows how the catchability changes with the knowledge parameter γ. In Fig. 5.2(A) we plot the ratio of catchability q_γ to q for two different aggregation models (spread=1 and 2) and four different effort models (X=1, 10, ∞ and $z_{.05}\sigma$). The last case means that fishing is restricted to the most abundant region containing 95% of the population. In all cases catchability increases with knowledge up to an asymptote that depends on spread but not on fishing area. This asymptotic value corresponds to fishing at the point of maximum abundance. Catchability decreases as the spatial limits widen. The case $\gamma = 0$ corresponds to uniform fishing within $(-X, X)$. Note that for an infinite area $q_0 = 0$; you have to have a finite area to get a non-zero catchability for uniform fishing.

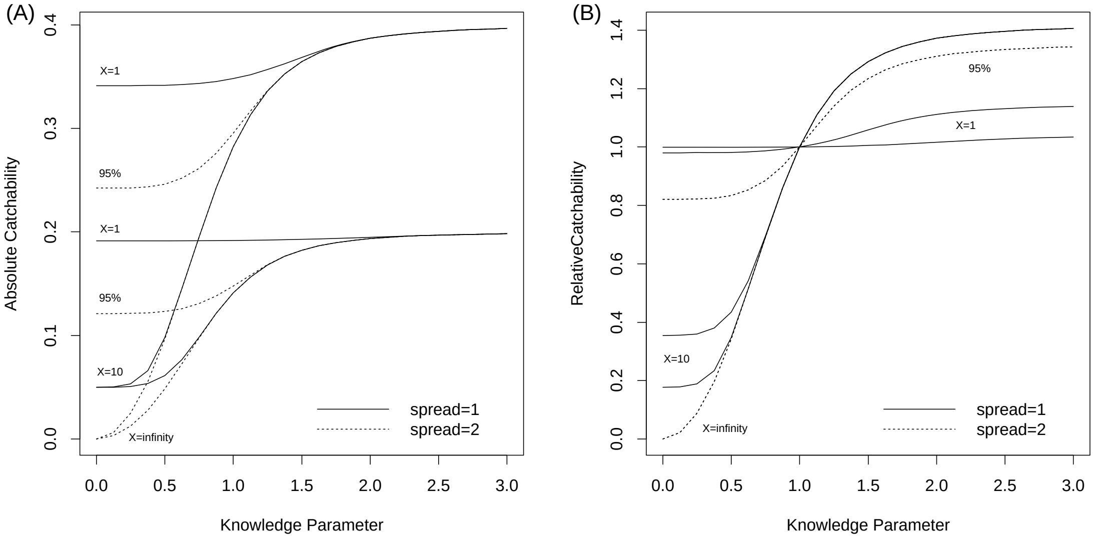
Fig. 5.2(B) shows the ratio q_γ/q_1 as a function of γ for the same cases as Fig. 5.2(A). Note that for the case where a fixed 95% of the population is covered, the catchability ratio is independent of the spread. The same is true for any fixed proportion, including 100% which is the case $X = \infty$. For high knowledge, the relative increase in catchability is greater for the more aggregated abundance.

5.5 Analysis of Catch-effort Data

Let $(c_{i,t}, e_{i,t})$ be the catch and effort data collected at time t and in grid (subarea) i of a unit area. If the abundance in the grid i is $n_{i,t}$, we have $\mathrm{E}(c_{i,t}) = q n_{i,t} e_{i,t}$. From (5.1), we have

$$\begin{aligned} q_e &= \frac{\sum_i \mathrm{E}(c_{i,t})}{\sum_i n_{i,t} \sum_i e_{i,t}}, \\ &= \frac{q \sum_i \mathrm{E}(c_{i,t})}{\sum_i \mathrm{E}(u_{i,t}) \sum_i e_{i,t}}, \end{aligned}$$

Fig. 5.2. (A) ratio of catchability q_γ to q vs γ for two different aggregation models (spread=1 and 2) and four different effort models (X=1, 10, ∞ and $z_{.05}\sigma$). (B) ratio q_γ/q_1 for the same models as (A).



in which $u_{i,t}$ is the catch-per-unit-effort (CPUE) in grid i at time t. This suggests that the ratio, $\kappa = \hat{u}_t/\bar{u}_t$, can be used as an index of catchability up to a scale parameter. Here $\hat{u}_t$ is the overall catch-per-unit-effort, $\sum_i \mathrm{E}(c_{i,t})/\sum_i(e_{i,t})$, and $\bar{u}_t$ is the mean of $\mathrm{E}(u_{i,t})$. Note that $\hat{u}_t$ can be thought of as the estimated CPUE under a sampling scheme that is weighted by effort (since $\hat{u} = \sum ue/\sum e$), whereas $\bar{u}_t$ is the estimated CPUE under a uniform sampling scheme.

The empirical density distribution of R at time t takes the value of $u_{i,t}/\sum_i u_{i,t}$ at $\mu u_{i,t}$, and 0 elsewhere. Here μ is the constant of proportionality linking CPUE with abundance. Therefore, $\mathrm{E}(R^\gamma)$ can be estimated by

$$\frac{\sum_i u_{i,t}^{\gamma+1}}{\sum_i u_{i,t}}\mu^\gamma,$$

which, using equation (5.6), leads to

$$l(\gamma) = \frac{A\sum_i u_{i,t}^{\gamma+1}}{N\sum_i u_{i,t}^{\gamma}}\mu.$$

The scale parameter μ is given by the equation $l(0) = A\bar{u}_t\mu/N = 1$, and is simply the ratio of the mean abundance to mean CPUE. The $l(\gamma)$ measures the effect of aggregation on catchability when the knowledge parameter about the stock is fixed as γ. Substituting for μ in the previous expression gives

$$l(\gamma) = \frac{\sum_i u_{i,t}^{\gamma+1}}{\bar{u}_t \sum_i u_{i,t}^{\gamma}}. \tag{5.7}$$

In particular, when $\gamma = 1$, the ratio becomes

$$\frac{n_t \sum_i u_{i,t}^2}{(\sum_i u_{i,t})^2} = 1 + \rho^2(t),$$

in which $\rho(t)$ is the coefficient of variation of u.

We may use the first and second moment estimates of R to estimate the aggregation index λ thus:

$$\hat{\lambda} = \frac{1}{\bar{u}_t^2} \left[\frac{\sum_i u_{i,t}^3}{\sum_i u_{i,t}} - \left(\frac{\sum_i u_{i,t}^2}{\sum_i u_{i,t}} \right)^2 \right], \tag{5.8}$$

since $\mathrm{var}(R) = \mathrm{E}R^2 - (\mathrm{E}R)^2$.

The knowledge parameter is estimated essentially by regressing log effort against log CPUE. Actually we use a generalized linear model in which effort e_{ijk} follows a Poisson distribution with extra-variation, and CPUE u_{ijk} is used as a covariate and therefore is assumed to be known. (It might seem more appropriate to treat effort as the covariate, and CPUE as the response. However then the coefficient to be estimated would be $1/\gamma$, which is unbounded around $\gamma = 0$, the expected range of γ.)

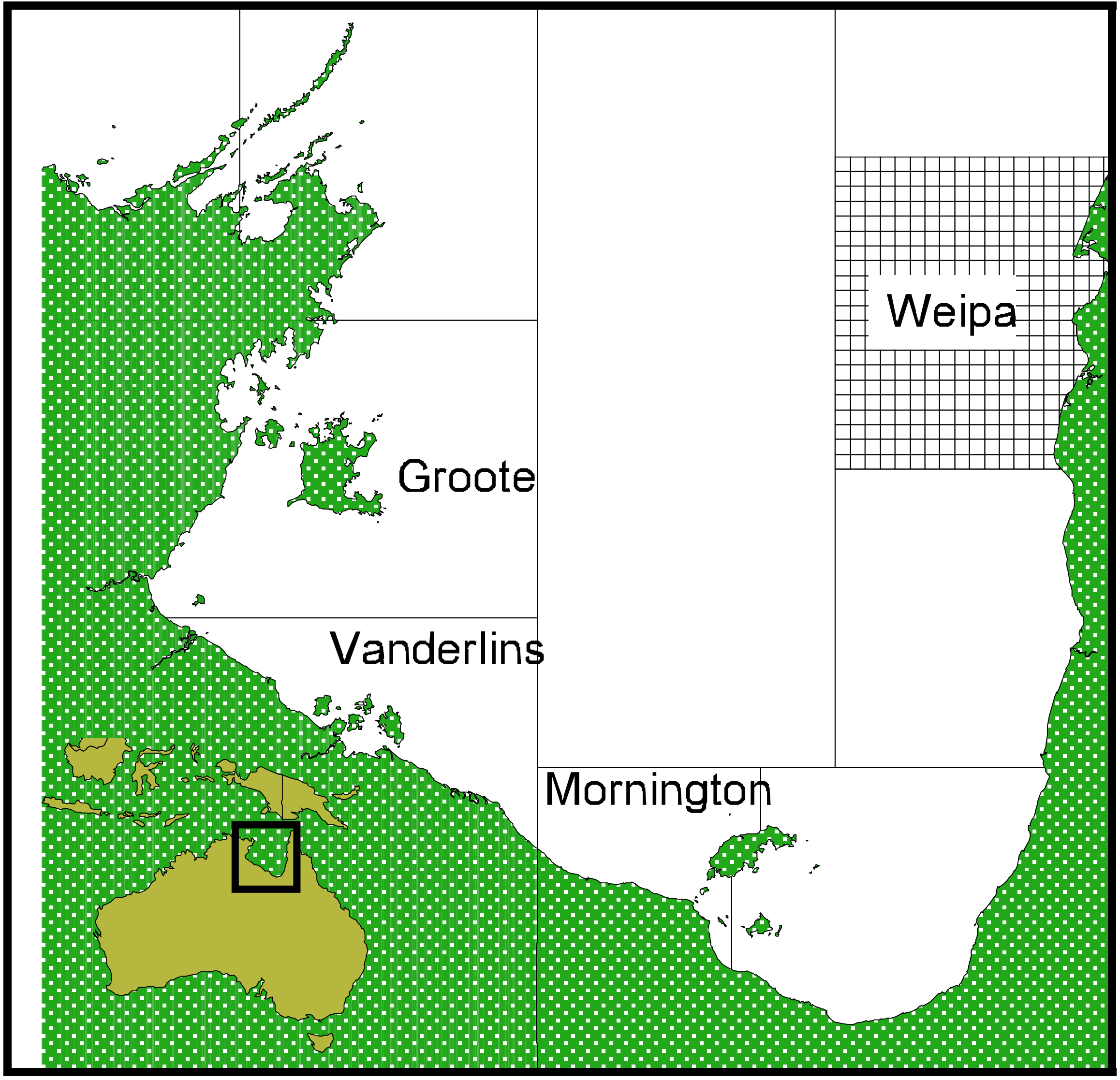
The details of the model are

$$\begin{aligned} \mathrm{E}(e_{ijk}) &= e^{\mu_{ijk}}, \\ \mathrm{var}(e_{ijk}) &= \phi \mu_{ijk}^{\xi}, \\ \mu_{ijk} &= (\alpha_j^1 + \beta_k^1 + \delta_{jk}^1) \log u_{ijk} + (\alpha_j^0 + \beta_k^0 + \delta_{jk}^0), \end{aligned} \tag{5.9}$$

where e_{ijk} is the effort in grid i for year j and month k, u_{ijk} is the CPUE, ϕ is the dispersion parameter and ξ is an exponent to be estimated by inspection of the residuals. The dispersion parameter is estimated from the Pearson χ^2 statistic.

Estimates $\hat{\gamma}$ of the knowledge parameter can be plugged into the expression (5.7) to give a second estimate, $l(\hat{\gamma})$, for the catchability ratio.

Fig. 5.3. The Gulf of Carpentaria, Australia, showing large-scale management areas and small-scale 6-nautical-mile grids.



5.6 Analysis of Commercial Catch-Effort Data from the Northern Prawn Fishery

We now apply the theory of density-dependent catchability to the tiger prawn fisheries of the Gulf of Carpentaria, using commercial catch and effort data from 1970 to 1996. The Gulf is divided into large-scale management areas as shown in Fig. 5.3. We focus on the four most important tiger fishery areas: Groote, Vanderlins, Mornington and Weipa.

To detect density-dependent effects we must have differential effort and density distribution within the area of the stock. The finest practical scale on which to estimate density is the grid level (6 nautical mile squares), which are the small squares in Fig. 5.3. For the temporal scale, we use the month (i.e. we sum catch and effort within each month). This is because prawn distribution (and so effort) can change markedly from one month to the next.

We also need to decide on the scale of the stock. Although the large-scale areas are in fact sub-divided into smaller management areas, such areas are probably too small to contain a stock, and have too few grids for reliable estimation. We therefore work on the large-scale areas (or amalgamations thereof): we assume that these areas completely contain the prawn stock whose catchability we are estimating.

The pattern of effort in Mornington shows a marked decline in September and October, which suggests that the fleet moves to neighboring Vanderlins. We therefore carry out catchability analysis on amalgamated regions as well as on the basic areas. Such regions are: SW Gulf (Mornington and Vanderlins), W Gulf (Groote, Mornington and Vanderlins) and all four areas combined.

In 1980–81 there was a major expansion of the fishery, so that many new 6 nautical mile grids were visited. We restrict attention to the most important months for the tiger fishery, namely August, September and October. Before the seasonal closures were introduced in 1988 there was year-round tiger effort; however, this effort was still concentrated in the months August to November when the prawns are at their largest.

5.6.1 Catchability-ratio index κ

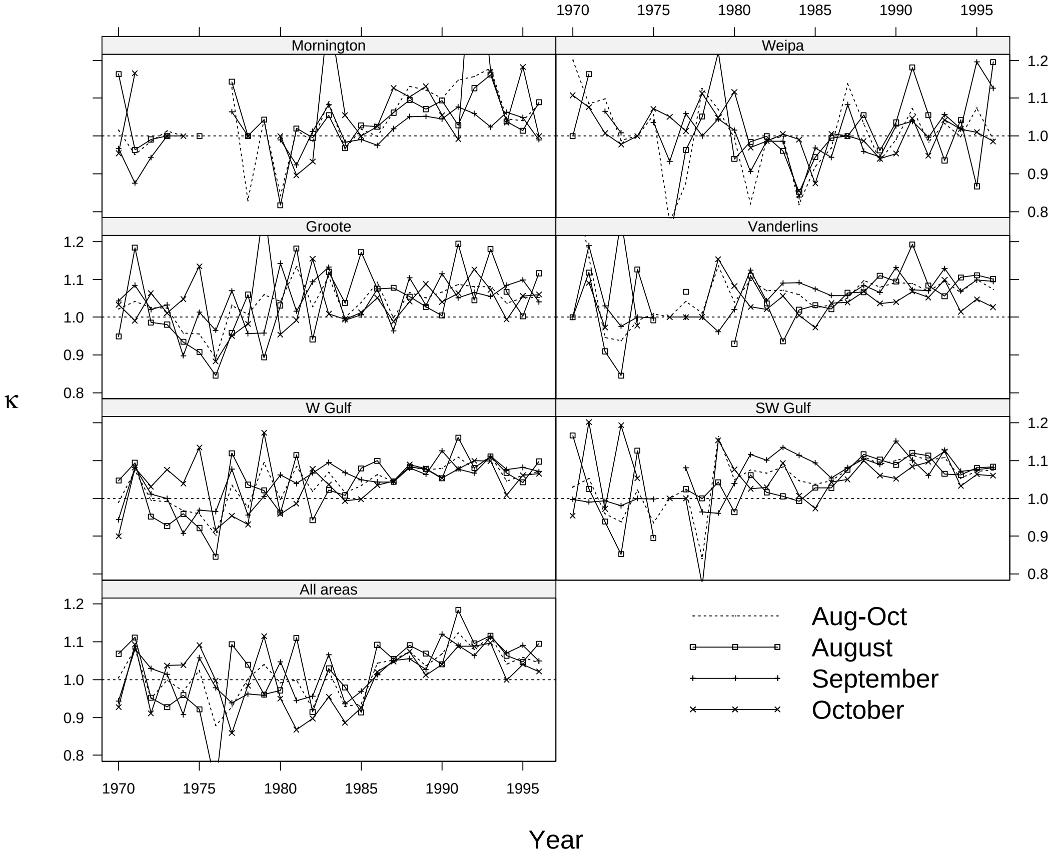
We have computed the catchability index, $\kappa = \hat{u}_t/\bar{u}_t$, for all three months within each year for each region. Grids with only a single day's effort have been excluded. Table 5.1 shows how many grids are included for each region, month and year. The results are shown in Fig. 5.4. The dotted horizontal line at $\kappa = 1$ corresponds to no density-dependent effect.

Some years are missing because of lack of grids (see Table 5.1). The dotted line is the index for all months combined. Groote, Vanderlins and Mornington appear to have $\kappa > 1$ (i.e. a density dependent effect) since 1980–1985. This is quite clear when the regions are combined (W Gulf). For Mornington there is a reduction in effort in October, leading to a more variable κ across months. This becomes less variable across months and years when we combine Mornington with Vanderlins (SW Gulf); we consistently get $\kappa \approx 1.1$ since 1987. Groote has roughly the same mean, but a higher variation across years. The estimate from the three months combined tends to be more consistent. Weipa shows no consistent density-dependent effect.

Table 1. Number of grids in a region for which total effort is at least 2 days.

	All areas			W Gulf			SW Gulf			Groote			Vanderlins			Mornington			Weipa		
year	Aug	Sep	Oct	Aug	Sep	Oct	Aug	Sep	Oct	Aug	Sep	Oct	Aug	Sep	Oct	Aug	Sep	Oct	Aug	Sep	Oct
1970	41	40	44	40	40	37	15	21	17	25	19	20	1	1		14	20	17	1		7
1971	29	53	47	27	53	43	13	25	16	14	28	27	5	11	13	8	14	3	2		4
1972	53	52	52	53	50	43	27	18	20	26	32	23	15	8	20	12	10			2	9
1973	36	39	38	36	37	25	9	8	5	27	29	20	8	7	4	1	1	1		2	13
1974	13	21	23	13	21	22	3	1	5	10	20	17	3	1	4			1			1
1975	18	17	9	18	9	3	4	2		14	7	3	3	2		1				8	6
1976	13	12	13	8	10	10			1	8	10	9			1				5	2	3
1977	21	36	19	18	26	13	5	8	1	13	18	12	2	1	1	3	7		3	10	6
1978	15	21	25	13	20	19	1	2	4	12	18	15		1	3	1	1	1	2	1	6
1979	9	28	44	7	24	39	2	5	24	5	19	15		5	24	2			2	4	5
1980	76	131	146	69	119	135	15	52	59	54	67	76	10	50	58	5	2	1	7	12	11
1981	131	142	143	124	126	129	64	49	51	60	77	78	31	41	49	33	8	2	7	16	14
1982	184	164	156	158	140	124	84	81	59	74	59	65	38	53	55	46	28	4	26	24	32
1983	189	191	243	181	167	215	106	96	106	75	71	109	40	65	88	66	31	18	8	24	28
1984	237	225	209	217	197	189	127	104	91	90	93	98	63	80	82	64	24	9	20	28	20
1985	207	219	231	179	197	198	123	110	91	56	87	107	73	76	90	50	34	1	28	22	33
1986	194	234	244	183	207	223	88	95	110	95	112	113	50	88	93	38	7	17	11	27	21
1987	157	250	222	155	245	221	91	145	117	64	100	104	51	110	104	40	35	13	2	5	1
1988	219	212	228	208	185	203	127	95	94	81	90	109	52	62	85	75	33	9	11	27	25
1989	238	240	214	220	203	186	136	122	86	84	81	100	67	93	76	69	29	10	18	37	28
1990	173	185	178	156	172	155	107	100	85	49	72	70	57	74	73	50	26	12	17	13	23
1991	145	174	142	139	165	131	99	101	61	40	64	70	48	70	50	51	31	11	6	9	11
1992	167	165	149	161	159	130	89	92	48	72	67	82	49	66	43	40	26	5	6	6	19
1993	128	148	134	126	137	123	95	86	63	31	51	60	66	72	55	29	14	8	2	11	11
1994	129	127	141	118	114	127	63	67	48	55	47	79	40	56	45	23	11	3	11	13	14
1995	103	130	112	99	117	95	49	73	43	50	44	52	14	43	38	35	30	5	4	13	17
1996	120	144	120	110	121	98	87	74	35	23	47	63	54	50	33	33	24	2	10	23	22

Fig. 5.4. Catchability index, κ, for each month, year and region. Also shown (dotted) is κ for the whole tiger season.



5.6.2 Aggregation index λ

Estimates of the aggregation index λ from equation (5.8) are shown in Fig. 5.5 for each region and year. The estimates are on a logarithmic scale. Three curves are given per panel, one for each month. With the exception of Weipa, all regions show a steady decline in aggregation since 1980. As before for Mornington the estimates for October are highly variable.

5.6.3 Knowledge parameter γ

Using a range of values for ξ in the generalized linear model (5.9), we have found that $\xi = 2$ produces the flattest variance-mean relationship in the Pearson residuals. We have found that grids with a single day's effort can have high influence on the estimates (see also, Pollock, Hoenig, Jones, Robson and Greene (1997)); therefore we have restricted the analysis to grids with two or more days' effort. The analysis has been carried out using the SAS procedure GENMOD.

Fig. 5.5. Aggregation index, λ, for each month, year and region. Also shown (dotted) is λ for the whole tiger season.

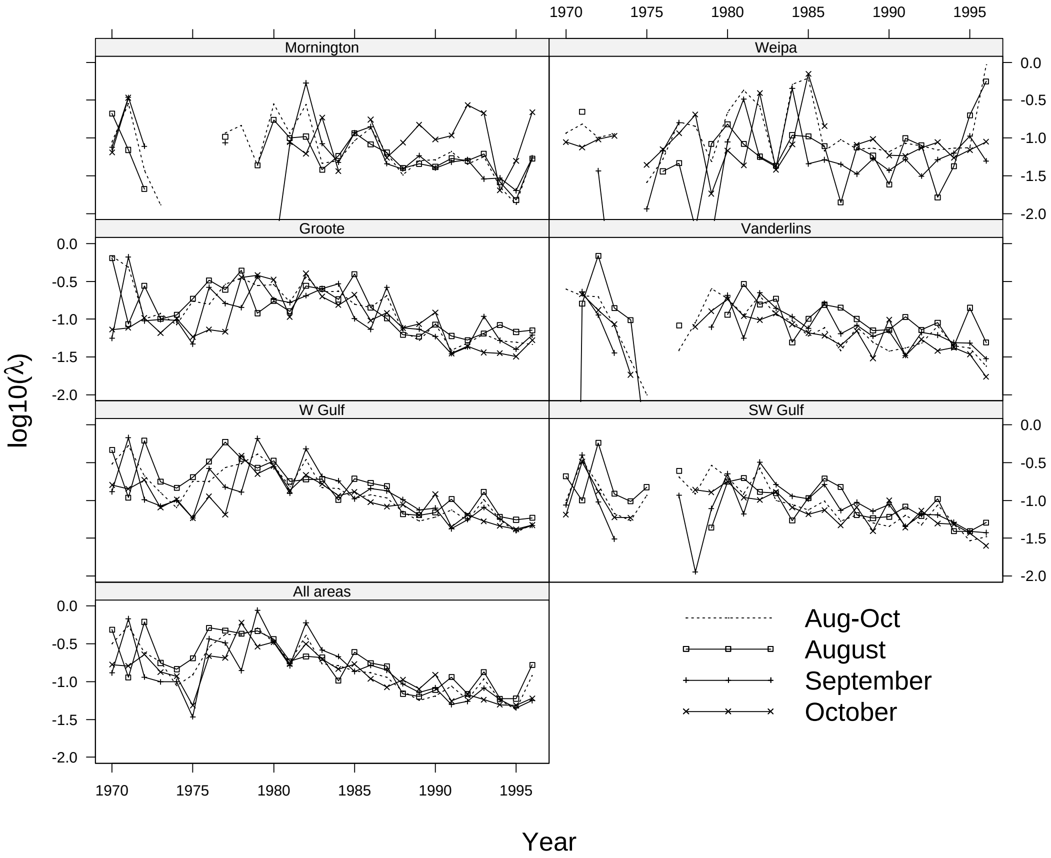
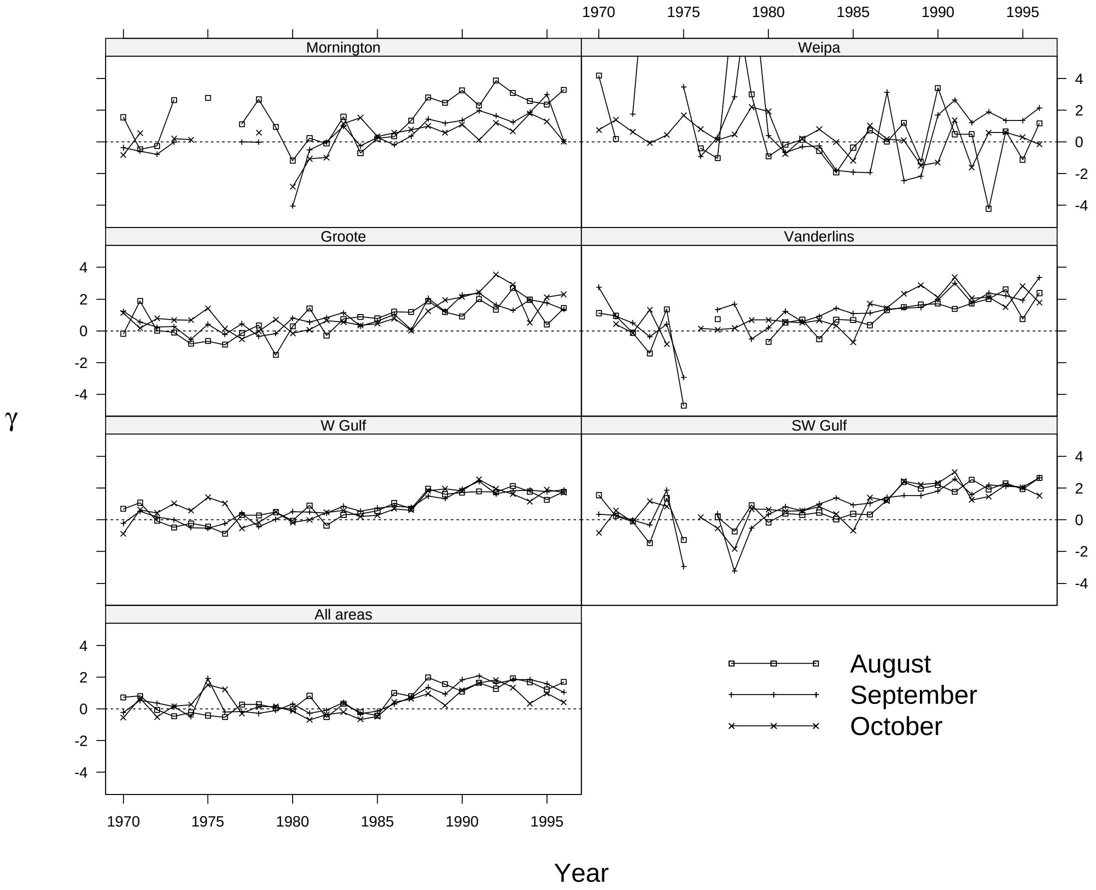


Fig. 5.6 shows point estimates of $\gamma_{jk} \equiv \alpha_j^1 + \beta_k^1 + \delta_{jk}^1$. The dotted line at $\gamma = 0$ corresponds to no targeting. There appears to have been definite targeting since the mid-80's in Groote, Mornington and Vanderlins, but not in Weipa. The pattern tends to be fairly consistent across months for Groote and Vanderlins, and the consistency is improved for Vanderlins and Mornington when they are combined (SW Gulf).

To assess the accuracy of the estimates, in Fig. 5.7 we show standard errors for one of the months (October in Weipa, August elsewhere). The choice of October for Weipa is based on there being more available grids. It is clear that before the mid-80's there is little evidence of targeting anywhere. Although the statistical power is low, this may actually be a real effect due to the absence of GPS technology. On the other hand the positive γ for areas in the western Gulf appears to be a significant effect. The dispersion parameter estimates range from 0.7 to 1.4, the larger values corresponding to 'All areas' and Weipa. This further confirms that the relationship between CPUE and effort differs between Weipa and the W Gulf.

The standard errors are governed by the number of grids that have been fished in

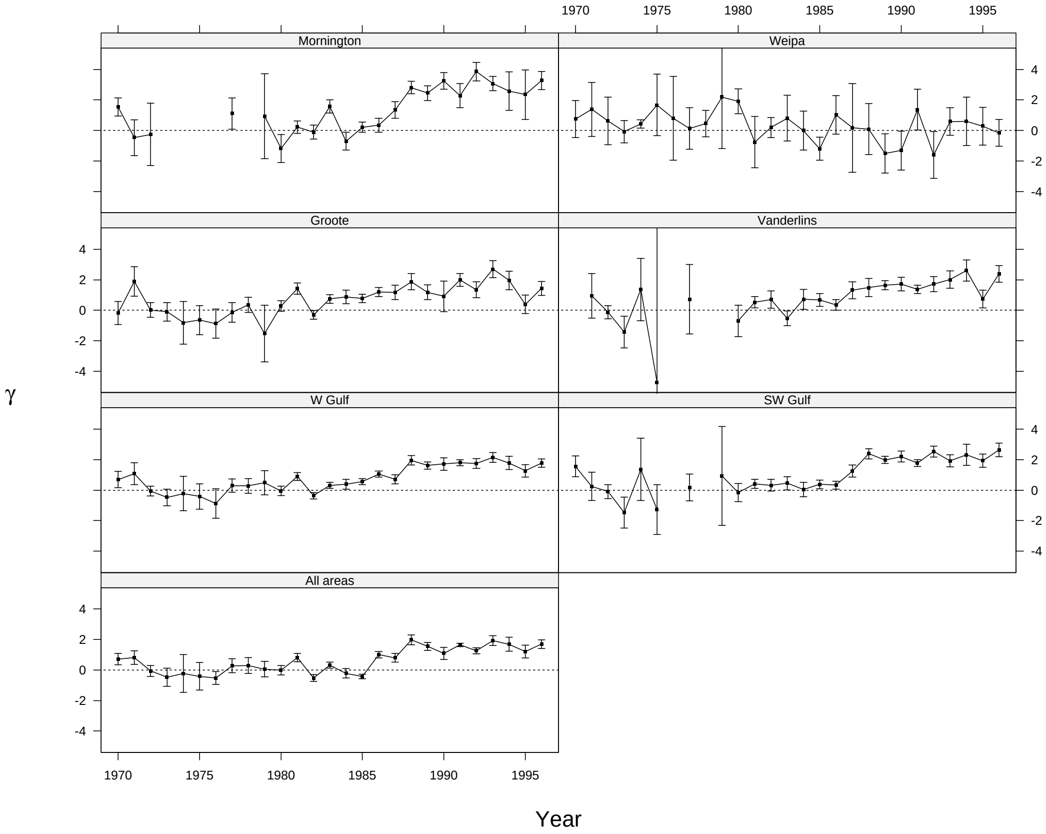
Fig. 5.6. Knowledge parameter, γ, point estimates for each month, year and region.



the region (see Table 5.1). There was a lull in effort in Mornington and Vanderlins around 1975; consequently fewer grids were visited. Also the level of effort in Weipa has been lower than in the other regions for most years. The smaller number of grids in earlier years may also be due to lack of reporting, because it was not yet compulsory to record grid-level position in the log books.

Using the estimated knowledge parameters for each month, year and region, we evaluated the alternative estimates of the catchability ratios, $l(\hat{\gamma})$ using (5.7). Fig. 5.8 shows the scatter plots of $l(\hat{\gamma})$ against κ for each month, year and region. They appear to agree well, indicating that the power law for the effort distribution is a reasonable approximation of the targeting in fishing.

Fig. 5.7. Estimates of γ in August for each region and each year, with standard errors shown by bars. For Weipa, the γ estimate is for October.

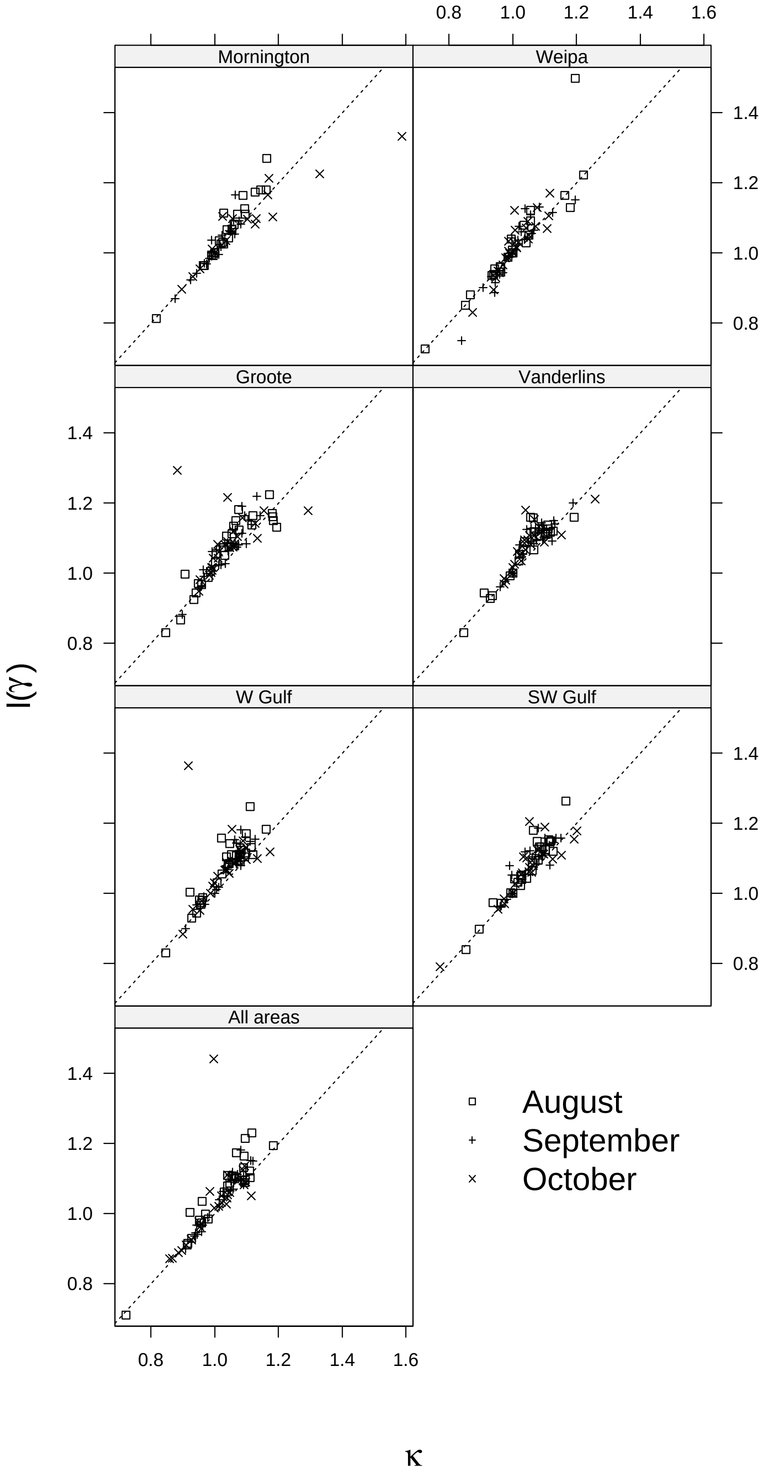


5.7 Discussion

We have further investigated the effect of aggregation and targeting on catchability following Swain and Sinclair (1994), and suggested three indices to measure the extent of aggregation, targeting and the changes in catchability. Simple estimation methods are also proposed. As catch-effort data is quite commonly collected in most fisheries, the proposed methods can be easily applied to these data to quantify possible effects on catchability.

The various indices presented here are based only on grids that were fished, since CPUE information is not available for unfished grids. However, the population in reality extends over both fished and unfished grids. Therefore, the indices may be biased. To base indices on all grids requires assumptions about the CPUE in unfished grids. The estimate of κ is unbiased if mean CPUE for unfished grids equals $\bar{u}_t$, and the estimate of λ is unbiased if the abundance distribution is the same in both fished and unfished areas. Since the abundance is likely to be less in unfished areas, both κ and λ are therefore probably underestimated. The same

Fig. 5.8. Scatter plots of $l(\hat{\gamma})$ against κ for each month, year and region. Different months are denoted by a different symbol.



estimates of γ would be obtained if the unfished grids were included with CPUE set to zero. Since abundance is likely to be somewhat greater than zero in these grids, γ is also probably underestimated; the same applies to $l(\gamma)$. The effect of ignoring the unfished grids is therefore to underestimate all four indices.

It is therefore of great interest to further investigate the effect of these "missing" grids. One method is to impute CPUE values for the unfished grids. A simple form of imputation is to model CPUE thus (using SAS notation):

$$\text{CPUE} = \text{grid month(year)}. \tag{5.10}$$

Missing values can then be imputed by adding the grid effect to the month-within-year effect. Dropping the grid term leads to the simpler model where the imputed value is the mean CPUE over all grids for that time, which is the biased model assumed for estimating κ as already described.

Imputation with model (5.10) should be unbiased. However, more sophisticated approaches are possible: the categorical dependence on grid could be replaced by a spatially smooth dependence on position; and temporal correlation across months and spatial correlation between neighboring grids could be incorporated. Such approaches should impute the missing CPUE values more efficiently. The results presented here for tiger prawns should be regarded as preliminary, pending an unbiased analysis.

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Benefits

Uncertainty in the assessments of prawn stocks is costly to the fishing industry. These costs are the result of:

1 Adoption of precautionary management measures that seek to avoid unwanted impacts of fishing through suboptimal harvesting strategies.

2 Failure to identify changes in stock status and consequently failure to adjust harvesting and management strategies to such changes.

All Australian prawn fishing industries will benefit from this research. This includes the Northern Prawn Fishery, Torres Strait Prawn Fishery, the Western Australian fisheries in Shark Bay and Exmouth Gulf, the east coast fishery in Queensland, the NSW prawn fishery, and the South Australian prawn fishery. These fisheries have a combined estimated ex-vessel value of $250 million, and most are managed using stock assessment based techniques.

At present, research work on season closures and stock recruitment relationship in the NPF is impeded by the great uncertainties in the mortality rates and catchabilities. The optimal opening date can only be identified with a precision of one month because of the uncertainties in population parameters (Somers and Wang 1995). Better estimates of population parameters will lead to more precise estimates of stock status, more reliable advice on optimal opening date, more appropriate management and more efficient and sustainable harvesting of the fishery (Wang and Die, 1995; Wang and Somers 1995). Other prawn fisheries will directly benefit from applications of the new methods.

Any prawn stock reseeding project will also benefit from this study. The size-dependent mortality function will play an essential role in the cost-benefit analysis in determining the number and optimal size of the prawns to be released.

The actual benefits to each fishery will depend on the management strategies adopted and specific risk factors in that fishery. More accurate estimates of the parameters will increase the confidence when making decisions and minimise the risk of the decisions. From a long-term point of view, the benefits to each fishery will be in proportion to the landings. The flow of benefits assigned below was determined by the proportions of the landings and feasibility of applying the relevent data from each fishery in the life time of the project.

Further Development

We recommend that other researchers consider the implications of ignoring size-at-age variation in prawn growth. Our work clearly shows that ignoring this variation leads to biased parameters and we offer an alternative estimation procedure to overcome it. We suggest that our model should be used to review parameter estimates for other important prawn stocks in Australia.

We expected to obtain changes in natural mortality with size for juvenile prawns. Although difficult, it would be useful to extend this work to sub-adult, adult prawns and to other prawn species. These changes in natural mortality are especially relevant to projects on the enhancement of prawn fisheries through re-stocking of juveniles.

Our work on the relationship between catchability and aggregation at large and small scales has only scratched the surface of what is a very difficult problem. There are considerable benefits to be obtained by extending this work into more detailed modelling of the spatial dynamics of biomass. This work may be crucial in explaining why current NPF tiger prawn stock trends suggest that recent increases in fishing power in the NPF fleet are much larger than those that we can measure by analysing changes in fishery inputs.

Conclusion

This project has successfully developed new methods to estimate some of the most basic but critical population parameters for tropical prawn stocks. By systematically reviewing and developing new methods and by applying both new and old methods to real fishery data we have established a framework for the development of models of prawn stock dynamics. The new estimates of population parameters obtained through this work have also helped in improving the basic information used in the assessment of Australian prawn stocks, especially those in the Northern Prawn Fishery.

Appendix I: Intellectual property

There is substantial intellectual property associated with this project in the form of statistical procedures and software. However, these procedures have no prospects for commercial development.

Appendix II: Staff

The staff involved with this project were as follows:

You-Gan Wang, Principal Investigator, Statistician (CSIRO Mathematical and Information Sciences)

Nick Ellis, Statistician/Programmer (CSIRO Marine Research)

David Die, Population Modeller (CSIRO Marine Research)

M. D. E. Haywood, Marine Ecologist (CSIRO Marine Research)

Mervyn R. Thomas, Statistician (CSIRO Mathematical and Information Sciences)