Chapter 8: Summary

The purpose of this research report was to explore biological population behaviour. Such behaviour was studied using a variety of population models; both deterministic and stochastic. The investigation was universal in scope: instead of creating models tailored to specific populations, all the models within this research report identified and incorporated principles that governed the behaviour of all, or alternatively a considerable proportion of, populations. (One such aspect of population behaviour that was incorporated in all but one of the population models was the fact that in any instant of time only one of three things can occur: a member of the population gives birth, a member of the population dies, or the population remains unchanged.) By focusing on the fundamental principles governing population behaviour, one is not only acknowledging the similarities shared by all populations, one is also able to uncover relationships that are more universal – and in a sense, more profound – in nature.

Accordingly, the primary aim of this research report is to introduce and study various models that incorporate the dynamics of a population; though Chapter 7 is dedicated to fitting a population model to data.

Chapter 2 studied deterministic population models. Most of the deterministic models were based on the rate at which the population size changed. Accordingly, both difference and differential equations were used to model the populations. The rate at which a population changes is equal to the difference between the population’s birth and the population’s death rate. Thus, if one knows what the birth and death rates are, one can come up with the appropriate differential equation to model the population. Initially, the independent birth and death rates were considered to be nonlinear functions of the current population size alone. This resulted in nonlinear differential equations. Nonlinear differential equations are notoriously difficult to solve. We thus needed to use locally linear approximations to make such equations tractable. Locally linear approximations will – by using first-order Taylor series expansions – give an approximate, analytical solution to nonlinear differential equations. The locally linear approximation is universal in its application: it can be applied to both deterministic and stochastic differential equations.

The latter models in Chapter 2 relaxed the assumption that the transition rates were functions of the current population size alone. The second set of models assumed that, in addition to the transition rates being functions of the current population size, that the
transition rates were also dependent on the population history. This enabled the model
to (under certain conditions) decay cyclically towards equilibrium. By studying a
population model that included the population’s history, we made an interesting
observation: it seems that the greater the influence the past history of the population
has on the current transition rates, the longer it takes for the population to decay
towards equilibrium after a perturbation. The final model within this chapter assumed
that the transition rates were also dependent on the current population size of a
competing species. This seemed to have a similar effect as the delayed regulation had
within the second set of models: under certain parameter conditions, both types of
models decayed cyclically towards equilibrium.

In the third chapter we studied traditional, stochastic birth-and-death models. A
population’s evolution was encapsulated by a set of Kolmogorov equations. The
Kolmogorov equations were directly solved for both a linear, births-only process and a
linear, deaths-only process. In both cases, the derivation of an analytical solution was
awkward – this despite the fact that the transition rates were linear. Consequently, three
alternatives to the Kolmogorov equations were looked at:

- The continuous approximation – though not amenable to analytical solution –
  enabled us to derive an approximate expression for the quasi-equilibrium
distribution. The distribution was shown to be Normal.

- The stochastic differential equations assumed that the change in population size
  over any time increment is Normal. The stochastic differential equations are
  amenable to Fourier analysis thus allowing one to derive approximate, analytical
  expressions for the mean, the variance and the autocovariance function of the
  population.

- Bailey (1964) derived a differential equation that characterized the evolution of
  the population’s moment generating function through time. The cumulant
  truncation procedure could be applied to the differential equation for the moment
  generating function thus allowing one to generate approximate solutions for the
  cumulants.

Renshaw (1998) gave a saddle-point approximation to the population’s probability
distribution that used the values of the first three cumulants. It was discovered that the
saddle-point approximation was not always applicable: in the example considered in this
research report, the saddle-point approximation made the probability density function

complex over certain ranges. Analytical expressions were also presented for the quasi-equilibrium distribution and for the gross fluctuation characteristics. In addition, an analytical expression for the expected time to extinction of a “deaths-only” process was derived.

In Chapter 4, Discrete Branching Processes were studied. This represented a significant break from the rest of the models in this research report as, unlike the other models studied, branching processes are not based on transition rates. Empirically, it seemed that the variance of the population increments decreased proportionately as the population got larger. Attention was drawn in this Chapter to the fact that the models in preceding chapters assume that the individual members of the population have identical birth and death rates. It was noted that this simplifying assumption caused the extinction risk arising from demographic stochasticity to be overestimated.

The environment has a significant impact on the behaviour of a population. In Chapter 5, variability in the environment was incorporated within the population models. The transition rates were assumed to be both functions of the environmental condition as well as functions of the current population size. In the first instance, we considered the population’s response to sinusoidal fluctuations in the environment. A number of the methods used in Chapter 3 to approximate the population are also valid for transition rates that are functions of both the population size, \( N \) and the environment, \( \phi \). In particular, one can approximate the population’s probability density using both stochastic differential equations and the cumulant truncation procedure. By performing a Fourier analysis on the linearized form of the stochastic differential equation, we derived analytical equations for the long-term mean and variance of the population as well as for the population’s autocorrelation function. We obtained empirical evidence that the linear estimates of the gross fluctuation characteristics (i.e. the mean and variance) become more inaccurate as one increases the amplitude of the environment’s seasonal variation. This is expected as larger environmental fluctuations will take the population away from \( N^* \), the point around which the stochastic differential equation is linearized.

Chapter 5 also examined stochastic environmental fluctuations. Marion et al. (2000) gave the equivalent differential equations to the Kolmogorov equations for a population subject to random, Markov fluctuations in the environment. Unfortunately the equations presented by Marion et al. (2000) are incorrect (and a proof of these equations was not given). This research report presented the probability differential equations in their
correct form and gave a heuristic proof. Analytical equations for the mean, variance and the autocorrelation function of the population were again derived using the linearized version of the corresponding stochastic differential equations. We considered in detail an environment, \( \phi \) that followed an Ornstein-Uhlenbeck process and which affected the population. The transition rates were assumed to have the following form:

\[
B(N, \phi) = a_1 N - b_1 N^2 + c_1 N \phi \\
D(N, \phi) = a_2 N + b_2 N^2 - c_2 N \phi
\]

The general cumulant truncation equations, to both the second and third order, were derived. We obtained empirical evidence to Marion et al.’s (2000) assertion that higher order cumulant truncation does not necessarily result in more accurate values for the cumulants. Finally, approximate analytical formulas for the mean time to extinction were derived.

Chapter 5 looked at an environment that only changed gradually over time. This is not realistic for some populations: often the environment experiences drastic changes e.g. an epidemic breaks out, an earthquake occurs. Chapter 6 studied how the population responded to drastic changes in the environment. One way of modelling extreme changes in the environment is to use Levy processes. This was not pursued. A second way of modelling extreme changes in the environment is by using transition rates. The problem with this method is in ensuring that the transition rates remain positive for any value that the environment and the population can take. From this latter model, it was observed that the greater the likelihood of an environmental disaster, the greater the population’s extinction risk. Furthermore, the extinction risk will increase if the magnitude of the environmental disaster increases. The results of this section are new.

In Chapter 7, we looked at how one would fit a population model to available data. A framework for deriving the likelihood function (developed by De Valpine et al. (2002)) was studied. This framework was applied to a stochastic differential equation population model. The population transition rates were assumed to be quadratic. It was noted that one could derive approximate parameter estimates by linearizing the stochastic differential equation. An expression for the log-likelihood function of the linearized stochastic differential equation was derived. Such an expression can be used to estimate the parameter values for a quadratic Stochastic Differential Equation. In order to test the validity of this log-likelihood procedure, the log-likelihood function was
calculated for a simulated set of population data that had measurement errors. The maximum of this log-likelihood function could not be found. However, the conditional log-likelihoods were observed to be close to the true parameter values.

This research report has studied a number of aspects that must be considered when modelling populations. However, there is scope for further research in a number of areas including:

- Studying the effect that population heterogeneity will have on gross population behaviour.
- Modelling a population within a spatial environment. Also to allow for spatial environmental heterogeneity.
- Ensuring that transition rates are always positive when transition rates are used to model both the population and the environment. A possible approach to this problem would be to use transformations.
- Develop methods of fitting population models to data that can follow many related processes (e.g. the environment, competing species) simultaneously. It would also be advantageous to develop a method that can deal with correlations between observation errors from one time to the next.
- Explore the impact that the environment will have on a population if it follows a Levy process.

Perhaps the area in which research is most urgently required is in parameter estimation. Little work has been done in this area. Any progress in this field will surely make existing population models far more practical.