A Quantitative Bio-economic Investigation of Inshore Fisheries

by

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Declaration

I, the undersigned, hereby declare that the work contained in this dissertation is my own original work and I have not previously in its entirety or in part submitted it at any university for a degree.

Abstract

The efficient management of renewable resources may ensure sustainable income to communities and countries. In the past the mathematical modelling used in the management decisions, in South Africa, was based on biological considerations only. In this thesis we include economic factors in the models and aim to determine steady state harvesting levels such that a maximum present value of all future revenues may be reached. A bio-economical approach is followed throughout the study and applied to the South African Cape Rock Lobster (*Jasus lalandii*) resource. We first address the problem using the simplest surplus production models. The model is applied to the Cape Rock Lobster, finding that the economical factors do indeed influence the steady state results, emphasising that they should be incorporated in the modelling process. A more descriptive two-sex-delay-difference model is then applied, which includes delay times for juveniles to reach sexual maturity and distinguishes between sexes. Yet further involved stage-class models are also studied and we propose a solution to the non-linear programming problem reached. These models may assist decision makers in future as knowledge on, for example, the growth of the two sexes, proper size limits and the influence of price differences are gained. Finally, we propose a harvesting strategy where catch is taken from alternative spatial lanes and apply here results from reaction diffusion theory. This theoretical approach might provide guidelines to new and underdeveloped fisheries in future, but also influence current inshore fisheries towards new management strategies.

Opsomming

Die doeltreffende bestuur van hernubare hulpbronne kan 'n volhoubare ekonomiese opbrengs aan gemeenskappe en lande verseker. In die verlede is die wiskundige modelle wat in die besluitnemingsproses gebruik is, in Suid Afrika, gebaseer op biologiese oorwegings alleen. In hierdie studie word ook ekonomiese faktore in die modelle ingesluit en word ewewigstoestande bepaal vir vangste, sodanig dat 'n maksimum huidige waarde van toekomstige inkomste uit 'n vissery bereik word. 'n Bio-ekonomiese benadering word deurgaans gevolg en modelle word toegepas op die Suid-Afrikaanse Weskus Kreefbron (*Jasus lalandii*). Die studie begin deur basiese surplus produksie modelle te gebruik. Die resultate van die toepassing op die Weskus Kreefbron toon dat die ekonomiese faktore 'n groot invloed op die voorgestelde ewewigstoestand van die populasie het. Dit benadruk dus die feit dat hierdie faktore in die modelleringsproses ingesluit behoort te word. Meer beskrywende twee-geslag-vertragings-verskil modelle word daarna toegepas, en sluit in 'n vertragings periode vir vis om 'n volwasse stadium te bereik. Hierdie tydfaktor verskil dikwels vir mannetjies en wyfies en daarom word hier 'n twee-geslag model gebruik. Meer gevorderde klasse modelle word ook bespreek. Ons stel 'n oplossing vir hierdie nie-lineêre programmeringsprobleem voor. Hierdie gevorderde modelle mag in die toekoms handige hulpmiddels wees wanneer inligting rakende 'n spesie gesoek word. Sulke inligting mag insluit die groeitempos van mannetjies en wyfies, geskikte grootte beperkings vir vangste en die invloed van prysverskille vir verskillende groottes vis. 'n Nuwe vangste strategie word ook voorgestel waar vangste slegs geneem word uit alternatiewe ruimtelike bane en pas ons hier resultate uit die reaksie-diffusie teorie toe. Hierdie teoretiese oplossings mag riglyne bied wanneer nuwe visserye in die toekoms ontgin word, maar ook huidige visserye beïnvloed in die rigting van 'n nuwe bestuur strategie.

Acknowledgement

"To my parents"

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Chapter 1

Introduction

Already since 1910 conservationists have been concerned about the rate at which resources essential for civilization are extracted from nature (Fisher, 1981). Man's basic needs are met by the exploitation of natural resources such as wood, water, coal, oil, as well as agricultural and marine resources (Schumann *et al.*, 1964). Resource and environmental economics is concerned with the theories and issues regarding extractable resources in supporting life and other services.

The efficient utilization of these resources contributes largely to the material and social wellfare of nations. To exploit these resources, multibillion dollar industries have developed around the world, for example, the oil industry in the Middle-East and certain fisheries in the United States and Japan (Getz *et al.*, 1989).

Fisher (1981) distinguished between exhaustible and renewable resources. Contrary to the millions of years that are required for the formation of exhaustible resources, such as oil, renewable resources, such as timber, are regenerated every few decades. In the case of animal populations, continuous recruitment may regenerate a population within a few years. Different economic theories pertain to renewable resources than to exhaustible ones.

All resources are, however, limited. The total production of any mine or oil refinery is fixed by limited supply, for example, in the Witwatersrand in South Africa most gold

mines have stopped production (Schumann *et al.*, 1964). Even a renewable resource can be depleted, if the rate of utilization exceeds the limit within which the resource is able to regenerate, as has happened to many endangered species, such as the Antarctic Blue Whale (Clark, 1990). The danger that these resources might be overexploited, which could lead to a collapse of all relevant industries and ultimately countries and nations, never ceases. Another example of such a collapse is the highly productive Peruvian Anchoveta (*Engraulis ringens*) fishery which has been fished to exhaustion (Hilborn *et al.*, 1992). The status of many fisheries world-wide is bleak with an estimated 30% overexploitation of major fish stocks (Cochrane *et al.*, 1995). Most fisheries have reached their full capacity and access to these fisheries should be controlled to ensure future social and economic benefits (Waicent, 1999).

The scarcity of resources should be emphasized and concerns the wealth of future generations. Proper management of resources therefore has become increasingly important. Two important questions are asked by Fisher (1981). Firstly, how does the current exploitation affect the resource in the future, and secondly at what rate should the resource be utilized.

Research projects on the management of resource systems emphasize the necessity that management procedures should effectively restrict overexploitation as the global economy puts ever more pressure on the earth's resources (Fisher, 1981). However, these issues are complex. Short term survival of some very poor communities depends completely and exclusively upon specific resources (Waicent, 1999). When a resource is public property, it implies that it is owned by everyone who wishes to exploit it (Folmer *et al.*, 1995).

Competition puts pressure on the resource and may result in a dramatic reduction in exploitable levels in the long run. For example, when a new fishery is discovered, management procedures are usually lacking and fishers enter the fishery as long as the total sustainable revenue is greater than the total cost. This so-called *open access fishery* is open to any vessel at any time and the resource may be heavily exploited. As more fishers enter the fishery the individual income of each fisher drops and the

competition increases with an increase in effort (Folmer *et al.*, 1995). This is not beneficial to the fishers or the communities and for the fish populations it could be fatal. Thus, without well designed management procedures the misuse of a resource may result in the extinction thereof (Folmer *et al.*, 1995).

The fisheries sector in South Africa is of great economic importance for coastal communities. By 1995 South Africa's fishing industry was one of the ten largest fishing industries in the world and worth an estimated value of R1.9 billion in real terms (Cochrane *et al.*, 1995). The total commercial fishing sector employs up to 27 000 people and creates another 60 000 opportunities in related sectors (Mantel, 1999). The coastline of some 3 000 km stretches from the highly productive western coastal shelf towards the east coast where a high diversity of species are found. The major fisheries are the *demersal fishery*, which is South Africa's most valuable commercial fishery and is dominated by the Cape Hake species, the *pelagic fishery* which consists mainly of Anchovy and Sardines, the *rock lobster fishery* based on three species, one along the west coast and two along the east coast, the *abalone fishery* and the *line fishery* with the three components of squid, tuna and general recreation (Mantel, 1999). Since 1960 new initiatives, to improve management procedures, were followed after the escalation of the major fisheries. Again, in 1997, a new marine fisheries policy was implemented with the long-term vision to manage and develop this national asset for the benefit of current and future generations.

The decisions made on management strategies are to be taken carefully. In this decision making process managers should make use of proper analytical tools when necessary. A real data time series is an indication of a particular trend in the harvest (Hilborn *et al.*, 1992). A sustained harvest level may indicate that the resource is not in danger, whether it is at the optimal harvest level or not. In general a decrease in catch, however, must be associated with a decrease in harvesting effort, otherwise the resource may be subject to overexploitation. Extrapolations of these series, such as the catch per unit effort (CPUE) series of a fishery, may predict future production. The effect that changes in external parameters might have on the population and harvest levels are

however, unpredictable. It is clear that little knowledge of the status of a resource can be gained from these series alone.

Mathematical models though, serve as reliable tools to reflect the relationship between the resource and the environment (Murray, 1989). These models clarify our understanding of the physical laws and the dynamics of the resource. The relationship between survival, recruitment and mortality would describe the population dynamics.

Commercial fisheries, in particular, were traditionally managed for biological conservation (Clark, 1990) as quota systems were introduced to restrict catches. Stock assessment is an essential part of management when the desired quotas for the season are to be determined (Hilborn *et al.*, 1992). The determination of a total allowable catch (TAC) is based on the "surplus" production of a resource which can be harvested. Hilborn *et al.* (1992) warn that to accomplish a sustainable harvest this analysis should be done accurately. Uncertainties in the production function can be one of the key problems of the management process. Popular fishery models which have been developed by scientists include surplus production models, delay difference models and stage structured models.

Surplus production models are the simplest stock assessment models used in practice (Hilborn *et al.*, 1992). These models, for example, the Schaefer model, refer to population size in terms of biomass instead of numbers and is sometimes also called biomass dynamic models. The dynamics of the population is modelled in terms of biomass recruited to the resource, where recruitment is defined in terms of biomass and the gain in weight of the already present population. Losses are due to natural mortality and catches. Surplus production refers to the increase in total biomass, when there is no harvesting.

Delay difference models are sometimes implemented when generations overlap and recruitment is dependent on the population size of previous years.

When the different maturity stages of a species become important in the demographic processes, *stage structured models* are used. These models are based on age- or size classes and are much more complex to implement than the aforementioned.

However, it has become apparent that to model fisheries only on the basis of conservation is insufficient. Many other economic objectives have been proposed. For example, are decision makers aware of the socio-economic implications of their decisions? Such questions are not yet addressed by scientific modellers in South Africa, although some attempts have been made.

It has become worthwhile for policy makers to address the biological and economic aspects simultaneously. Each one of forestry, fisheries and wildlife has its own unique set of problems, but the principles of the management of these resources are based on similar economic notions (Getz *et al.*, 1989). In our study here, all harvesting options discussed, aim at optimizing economic yield subject to the limiting production potential of the fish population. Thus optimal management in mathematical terms is the maximization of the social benefits and/or the minimization of the biological and economic costs.

The outline of the rest of the thesis is as follows.

Chapter 2 will give a background discussion of fisheries management strategies worldwide. In this chapter different management options are discussed that will eventually have an effect on the socio-economics of communities. These effects are not specifically addressed in more detail in the rest of the thesis, although some factor could be incorporated in the cost factors in the models.

Chapter 3 will give a complete background on the South African Cape Rock Lobster *Jasus lalandii* fishing industry. In that chapter we discuss the biological facts, the industry and the available data sets. We shall apply the models discussed in Chapters 4 to 7 to this species.

Our first objective will be to provide a detailed description of surplus models in Chapter 4 and to extend these biological models so as to include economic values in the case of the South African Cape Rock Lobster resource (*Jasus lalandii*).

Our second objective will be to further generalize the bio-economic surplus production models of Chapter 4 so as to incorporate delay parameters. Thus in Chapter 5 we

will discuss the delay difference models firstly for species without gender and secondly, for species where the young develop into males or females. Here two-sex models are important especially when male and female delay times differ.

Our third objective will be to broaden the previous modelling approaches so as to accommodate age structure. This will be done in Chapter 6, where we shall also seek to establish an optimal harvesting strategy for the Cape Rock Lobster (*Jasus lalandii*) using the maximum sustainable economic yield. That is, here we will take into account age structure and its effects on species recruitment.

Our final objective will be to reconsider the problem of determining optimal harvesting strategies, but this time by including the spatial movement of a species. Using travelling wave solutions, we propose a harvesting strategy in Chapter 7 where the fishing area is divided into lanes and only alternative lanes are harvested.

Chapter 2

Fisheries Management Strategies

In this chapter we shall concentrate on management strategies that are currently used in the fishing industry worldwide. Here the focus will be on the economic aspects of the strategies and the implications of such management decisions. We first give a brief discussion of management options that are based purely on biological considerations, in Section 2.1 and mention the economic shortcomings thereof. These shortcomings are addressed in Section 2.2 where we discuss bio-economic management strategies. A background discussion on access rights is given in Section 2.3 as being part of a complete management process in fisheries. This topic is included here as it has important socio-economic implications. However, decisions regarding access rights, are mostly made after total allowable quotas are set and are thus not included in the objectives of this thesis. Throughout this thesis we shall refer to some basic economic principles that are defined in Appendix 9.1.

2.1 Biological Management

Two biological management strategies, namely the maximum sustainable yield (MSY) and operational management procedure (OMP) are discussed in this section.

A biological equilibrium in the population level is reached when only the amount of surplus fish generated by natural growth is harvested (Clark, 1990). This equilibrium

is maintainable when the fishery is fished at this sustained yield level. For smaller stock sizes the growth rate is much higher than for larger populations and when the population grows to the environmental carrying capacity the growth rate will tend to zero. Let x be the population size at time t. For some population size, say x^*, between zero and the carrying capacity, K, the growth rate, $\dot{x}$, will be at a maximum and the surplus generated maximized (see Figure 2.1.1).
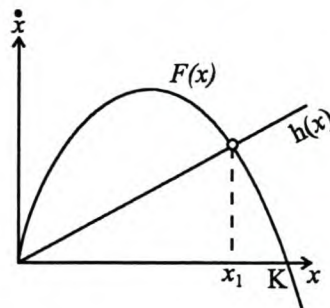
Figure 2.1.1: *The logistic population growth function. A sustainable yield, x_1, is reached where the harvest function, $h(x)$, equals the growth function, $F(x)$.*

In the past some fisheries were managed towards a maximum sustained yield (MSY) (Clark, 1990). Such a management policy is based on a model of biological growth, but it has become apparent that the MSY-concept is, in many respects, too simplistic for the optimal utilization of a resource (Clark, 1990). For example, when interdependent species are harvested, it is impossible to fish at the separate MSY levels for each species. Some weighting system should be employed in terms of either gross weight, protein contents or economic value. The MSY-concept is also insufficient when it becomes impossible to sustain a certain yield level. For example, there may occur occasional fluctuations in the stock size due to changes in the environmental conditions (Hannesson, 1993).

In South Africa long-term management plans are being developed. Some fisheries, like Hake, Anchovy and Sardines, and the Rock Lobster are managed by an *operational management procedure* (OMP). This procedure will

- develop a cooperative process involving all interested parties,

- be binding, though with procedures that allow amendments,

- include appropriate and cost-effective monitoring and control programmes and strict enforcement of fishing regulations,

- consider the socio-economic implications of altered levels of utilization (Mantel, 1999).

If the participation and cooperation of all stakeholders are required, then it is of great importance that their objectives are clarified and known. Since 1997 this OMP procedure has been applied to the Cape Rock Lobster fishery. Three data sets are used, namely

- somatic growth rates,

- commercial catch per unit effort (CPUE) and

- CPUE of independent monitoring surveys (Johnston *et al.*, 1997).

Currently no economic parameters are included in the models that are used, but a bio-economic modelling process could easily be adopted once clear objectives are formulated.

2.2 Bio-economic Management

Perhaps the most important shortcoming of the biological management strategies is that no cost factors are considered. Surely the managers wish to weigh all costs against the benefits to determine at which level to fish so as to be socio-economically optimal. Thus, socio-economic aspects should be incorporated into the models upon which management policies are based (Sandberg *et al.*, 1998). These more descriptive bio-economic models must include the revenue and cost functions attached to a fishery, as well as the cost for a company undertaking fishing, rather than an alternative profitable activity (see *opportunity cost* in Appendix 9.1). Fishing will be the optimal

choice when it is the more profitable activity, above any other. The optimal yield level, normally differs from the stock level at the maximum sustainable yield (Hannesson, 1993). Bio-economic mathematical and computer models have been used in various countries and a good theoretical background exists (Clark, 1990). Optimal management of resources includes the maximization of the discounted flow of net returns, maximization of social welfare, maximization of average sustainable yield and minimization of bycatch. Relevant articles appear regularly in journals such as *Marine Resource Economics*. Unfortunately, the economic principles underlying fisheries management are often not well understood by policy makers (Cochrane *et al.*, 1995).

One country that uses bio-economic models successfully in the decision making process is Norway (Sandberg *et al.*, 1998). An over-capacity of boats (and fishers) occurs in most fisheries, and Norwegian decision makers are also faced with the multi-objective task where the stock must be conserved while employment is secured.

Some fisheries even operate at a loss only to create employment. Such a fishery is the multi-fishery of the English Channel (Pascoe *et al.*, 1999). Operations research methods, namely goal programming, incorporating bio-economic models, were used to create a tool with which decision makers and administrators should be able to see the effect their decision will have on the fleet and the profit. Pascoe *et al.* showed that, with a relatively low reduction in fleet size with respect to certain vessel types, it is possible to operate at a profit, even though it is not at the maximum profit possible for the fishery.

A bio-economic analysis of the Greenland Shrimp (*Pandalus borealis*) fishery by Christensen *et al.* (1993) gave insight into the overfishing of the resource. Note that shrimp is the most important species in the Greenland fisheries industry. The importance of this analysis is recognised in the fact that the fishing industry forms the basis of the economy of the country.

To invest in future harvesting possibilities, is to manage fish stock such that it is allowed to grow and establish future wealth. On the other hand, if there is a continuous decrease in stock, it is to disinvest such future assets (Folmer *et al.*, 1995). The value

of the natural resource is the present value of the net future revenues expected from exploitation. It is clear that an understanding of resource economics has become essential in resource management (Fisher, 1981) and countries have moved towards a bio-economic management strategy. In the following chapters the total present value of all future income from the fish stock is maximized in terms of net revenue, while detailed biological models are used to describe the population dynamics.

Munro (1992) stated that the bio-economic theory that was first used by Clark (1990) (first edition in 1976) will in the future influence the analysis of fisheries management problems as yet unrecognized. In our study we aim to submit such mathematical tools, using Clark's theory as basis, in assisting future fisheries managers in South Africa.

2.3 Access Rights

In this section we discuss access rights, namely the allocation of fishing rights, as part of the broad bio-economic strategy. This important topic is included here to emphasize the complexity thereof in the socio-economic context. These socio-economic factors, could be included in the analytical process, but we refrain from such attempts in this thesis. Our objective is to determine an optimal economic yield level rather than to address these sensitive political issues.

Communities can benefit from these decisions when access to resources are fair and equally distributed. The trend world-wide is to move towards an access and property rights management system (Cochrane *et al.*, 1995). Through the centuries fishing nations have experimented with different approaches to access rights. One of the lessons learned, is that management of a fishery is only feasible and effective when accepted by the users and the general public. Management strategies should not be developed by the users of the resource as these strategies and access rights are inter-linked.

Most of this section is from the report by Cochrane *et al.* (1995). He defines access rights for fishing as follows: "to be the exclusive right to participate in a defined fishery

at a specific level and in accordance with stipulated regulations, for a specific period of time". The four regimes of property rights are open access, private property, state property and common property:

- The definition of an *open access fishery* has been given earlier. It allows free entrance to anyone, but controls on effort and fishing season may still be in place. Even with these minimum restrictions such fisheries will almost certainly be overexploited and over-capitalized. Competition will lead to investment in more efficient technology and ultimately profits will disappear and the national resource will be wasted.

- A fishery is defined as a *private property fishery* when exclusive rights to the fishery are allocated to individuals or companies. These rights to catch are tradable and the owners have control over the catch and effort levels of the fishery. The role of government is limited to the allocation and enforcement of property rights.

- When the government has sole ownership of the resource it is referred to as *state property*. Management decisions are then made by government on behalf of the users.

- When the resource is managed and controlled by an identifiable community of users it is called a *common property* system (Folmer *et al.*, 1995).

These are four extreme definitions and many fisheries fall somewhere between these boundaries. Specific management policies are effective when applied to a specific fishery.

The three parts of fisheries management are stock assessment, regulation and enforcement. Stock assessment is a mathematical and computational process where a quantitative prediction of the response of the stock to various management options is made.

Regulations are necessary to sustain utilization of the resource at an optimal level, by

(1) regulating the rate of fish being caught. A closed season is a suitable way to allow a fish population to recover.

(2) Regulating the size at which it is caught. For example, a larger mesh size of the fishing nets enables the smaller fish to escape.

(3) Effort limitation. This involves a limit on the number of boats, traps, rods, etc. used in harvesting the stock.

(4) Technology limitation. Limits could be placed on fishing gear and boats.

(5) Limiting the catch sizes of fishing by way of a quota system.

One disadvantage with a multi-species fishery is, what is applicable to one species is not necessarily to the others. Although in some cases effort control is favoured over catch limitations, fishers have found ways to bypass these limits and the aim to reduce the mortality rate of the stock is not obtained. One fishery where multi-gear on different vessels are used is the multi-fishery of the English Channel (Pascoe *et al.*, 1999).

The most popular method of resource control is to set a *total allowable catch* (TAC) on a fishery, as is done by fisheries in Canada, the United States of America, South Africa, Australia, New Zealand and others. Portions of this TAC are allocated to different owners. This method overcomes the major problems associated with effort control. However, fishers tend to cheat on reporting their catches. Problems also arise in multi-species fisheries when quotas for some species are filled quicker than others. Some systems allow "under-catches" to be transferred to the following season, thereby incorporating some flexibility.

Additionally, decisions need to be made to whom fishing rights are to be granted, whether or not these rights are transferable, the time period and the process of allocation. Whether the access rights are to be granted to individual vessels, companies or a group (community) are related to the transferability thereof. For example, rights

which are granted to vessels and which are non-transferable may be as effective as allocating transferable rights to individuals.

Access rights, by way of a quota system, permits entrance to a fishery to individuals, companies or communities. Japan and Turkey have successfully implemented the community based co-operative system. The *territorial user rights in fisheries* (TURF) within the broader communal based concept can give exclusive rights to a group to stocks which occur in limited areas. This allows zoning to avoid conflict between users.

Once the decision of "ownership" is made the question of transferability should be answered. In New Zealand an *individual transferable quota* system (ITQ) has been adopted. Within this system the owner may trade his rights. Transferability, however, can be adopted in a variety of ways. The effect will be that quota rights will be in the possession of the most efficient users with a possible reduction of price to consumers. In order to protect the industry from domination by only the strongest, a maximum quota limit may be set on individuals or companies. Norway is one country that has not moved towards an ITQ system to avoid a concentration of ownership. In Iceland quotas can be transferred, but only with the approval of the fishers' union or local authorities. Thus, transferability allows for greater economic efficiency and opens up opportunities for new fishers to enter a fishery. The rationalization may, however, result in job losses and smaller crews.

The duration of rights may vary from one season to in perpetuity. Long-term rights hold more security for fishers and encourages investment, while short-term rights give rise to some of the same problems of an open access system. New entrants will only enter with some long-term assurance. Allocating long-term rights, however, reduces the opportunity to correct errors made in the initial allocation.

Governments may solve the sensitive issue of allocating rights to potential fishers by taking the options to

- delegate ownership of the resource to a public enterprise,

- hiring contractors to do the fishing,

- granting fishing rights,

- renting or selling exclusive rights at a predetermined price, or

- auctioning out rights.

Each option or combination thereof holds unique advantages, but allocation is usually done on historical performance.

In South Africa the new (1997) policy on Marine Fisheries outlines a restructuring process in creating equity, effectiveness and sustainability in the fishing industry. The commercial fishing industry has quota (control of catch) and non-quota (control of effort) sectors (Mantel, 1999).

In the 1997 policy, the right of access is to be puchased through public tender and companies and fishers will be invited to submit bids. Fishers who bid will be required to pay for their right to fish. This right is transferable, inheritable and divisible, and is to catch a proportion of the TAC, or to exercise a certain amount of effort determined annually by the authority (Mantel, 1999).

However, perhaps the most important part of management is enforcement of policies. The best scientifically developed management strategy is only successful with an effective enforcement system. In marine fishing this is a difficult task when the vast fishing areas to be covered are considered. Enforcement is easier, though, when the management objectives are supported by those involved. However, there will always be those who transgress regulations, and the failure to enforce regulations can be fatal to any fish population.

The South African Cape Rock Lobster industry is managed by a closed season between 1 May and 22 November, a 75 mm carapace length minimum size limit for commercial fishers, closed areas and a limited mesh size for traps. The commercial fishery is controlled by company-allocated quotas within a TAC. The Quota Board, who is appointed by the responsible minister, allocates quotas to persons or companies according to certain guidelines (Mantel, 1999). Recreational divers must buy permits

and are not allowed to catch lobsters that are in berry, sell lobsters or to catch more than four lobsters a day. For recreational fishers the size limit is 80 mm carapace length.

It is thus clear from this discussion on access rights that the management of fisheries regarding long term strategies and control are complex and decisions should be carefully implemented.

Although we have briefly discussed access rights here, the rest of the thesis will focus on bio-economic models as tools. We first discuss the lobster fishery in South Africa in the next chapter.

Chapter 3

Cape Rock Lobster Fishery in South Africa

In the rest of this thesis we shall apply theoretical bio-economic models to the Cape Rock Lobster fishery in order to suggest optimal harvesting strategies. Here, this lobster fishery is discussed. In Section 3.1 we give a brief outline of the biological background of the species so as to be able to understand its population dynamics. Then we review the lobster fishing industry in Section 3.2 and discuss the data sets available, in Section 3.3, which are used in the chapters that follow.

Three species of the spiny lobsters support the South African fisheries. The most popular among the commercial fishers is the Cape Rock Lobster, *Jasus lalandii* (Pollock, 1986). It is one of eight cool water species in the southern hemisphere and can be found along the African west coast in the Atlantic coastal waters. During the seventeenth century *Jasus lalandii* were abundant, even in shallow pools, before serious harvesting commenced (Pollock, 1986). A dramatic decline in the population levels alarmed biologists and proper management policies became necessary to protect the species from extinction.

3.1   Biological Background

The following information is from the work of Pollock (1986) and personal communication with Marine and Coastal management of South Africa. See also the references in Pollock (1986) for more detail.

Observational studies have shown that adults stay in a certain area and alongshore movement from one area to another is minimal. On and offshore migration occur as seasonal changes in oxygen levels occur.

The adult lobster moults once a year. The female lobster moults annually between April and June (see Figure 3.1.1), and the male lobster six months earlier during spring or early summer. An interesting fact is that the growth rate of adults differs along the coastal areas with the slower rates along the most northern areas closer to the Namibian waters. This could be ascribed to changes in the habitat and the sensitivity of the species to oxygen concentration. Temperature variability does not seem to play a role. After larvae settlement the female and male growth rates differ. The female growth rate is slower than that of the male and, in general, it takes 5-6 years for the female to reach a carapace length of 60 mm. The male lobster reaches the same length in 4-5 years. Thus maturity is reached first by the males at about 60 - 65 mm. The average female attains a carapace length of 89 mm after approximately 20 years of normal growth conditions. The males grow much faster and reach this length in 7–11 years (Pollock *et al.*, 1981).

Mating occurs during June when the female's carapace is soft. Most mature females are in berry from July until late October. The eggs are fertilized internally and the larvae are released closely inshore. Females with carapace length ranging from 60 to 80 mm are responsible for 54% of the egg production. Only 9% of the total egg production originates from the 89+ mm group. During her lifetime a female can release about 1 million larvae.

The following theory is accepted by most scientist and also here, namely that the south easterly winds of the Cape play an important role in the early stages of the larvae. Peak

April	June	July	October	November	December	April

females mating females   peak hatching   larvae return

moult   in berry   male moulting
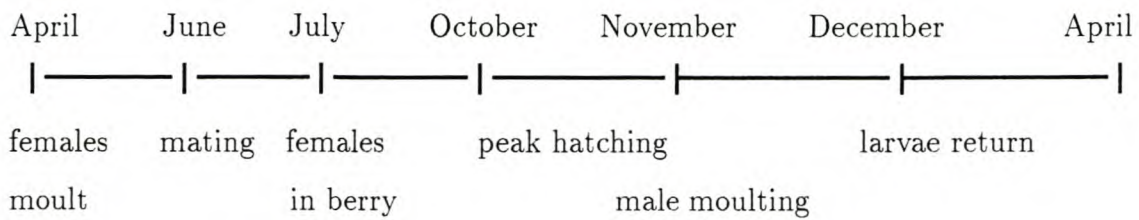
Figure 3.1.1: *Life cycle of* **Jasus lalandii.**

hatching occurs during October and November when strong winds activate upwelling in the surface layers and the larvae are rapidly driven northwards and offshore. The larvae, known as phyllosomata, have a drifting existence and the Atlantic ocean current system transports the larvae anticlockwise to the Brazilian coastline and back to South African waters. This could take 1 to 2.5 years. During this period larvae are mainly found in the upper 10 m layer of the sea. The phyllosoma larvae moult through 11 stages. The final puerulus larvae stage is reached when the larvae approach the edge of the continental shelf. It now metamorphoses into the swimming stage.

Depending on its age the juvenile lobster moults several times a year until it reaches maturity.

Spiny lobsters, in general, have strong jaws which are adapted for crushing hard-shelled organisms. The Cape Rock Lobster feeds mainly on black mussels, but also on echinoderms, gastropods, bryozoams and polychaetes. The species is preyed upon by seal pups and inkfish. The natural mortality rate for the species is high among juveniles, with cannibalism occurring in overcrowded habitats. The natural mortality rate decreases with size and age and was calculated to be 0.1, for male adults, from studies done at the Robben Island sanctuary (Pollock, 1986).

More information on the biological properties of this species could be found in the articles by Cockcroft (1995), Goosen (1995) and Pollock (1997).

3.2   The Fishery as Industry

The Cape Rock Lobster fishery has developed into a highly competitive industry, while recreational fishing has become more and more popular lately. Pollock (1986) reports the following historical development.

Commercial exploitation exploded since 1900. Average annual landings (whole mass) of 10 000 mt to 11 000 mt were recorded for 1950 -1965. As the fishing effort increased it became necessary for the government to introduce management policies. In 1933 a minimum size limit of 89 mm carapace length was enforced, and in 1946 a tail-mass allowable level was introduced for export markets. Although a TAC for 1966 was a high 10 400 mt, this limit was not reached. Statistics show that it was the most northern fishing areas, Port Nolloth and Hondeklip Bay, that suffered the most in those years. This was an almost uncontrolled fishing ground where the smaller limit of 76 mm was valid. In 1970 the TAC was dropped to 5513 mt (whole mass) and divided amongst 34 companies. The size limits in all areas were set to 89 mm. The quota levels were revised each year and increased slightly to 6297 mt in 1976 but then decreased again to 3700 mt in 1980. Catching areas were zoned into nine areas and the catch of lobster is the sum of TAC's of these areas. (The nine fishing areas are shown in Figure 3.3.1.) Other limits which have been enforced, include a closed fishing season between 1 July and 14 November, a bag limit of 4 animals per day for amateurs, limits on the number of traps per boat, deck-grid sorters and closed areas.

Recently a lower animal growth rate has prompted a reduction in legal minimum size. Since the 1993 season the maximum size of 89 mm was reduced to 75 mm for commercial fisherman and 80 mm for recreational fishermen, but the TAC dropped to 2200 mt (Cruywagen *et al.*, 1994). An even more strict quota was introduced since the 1995 season. As a result of the recent dramatic drop in catches of this fishery, the falling income is of increasing concern to the communities whose livelihood and income depend on this resource while, at the same time, there is an increasing threat to the species' biological well-being.

Without neglecting the biological relevance, the economic aspects of the fishery are modelled in future chapters, in conjunction with the biological dynamics of the stock. An optimal equilibrium population level is estimated by maximizing the present value of the discounted net economic revenue.

3.3   Data

This section will discuss the available data sets for the Cape rock lobster species. These data sets will be used in the chapters that follow.

Data sets that are available are the total commercial catch data, catch per unit effort data, tagging growth data, experimental sampling of egg production and results on survival. These data sets are listed in Appendix 9.8 as it is used in the thesis.

The total landed commercial catch data are known for each year since 1900 (see Figure 3.3.2). Each commercial catch that is landed is inspected by an appointed inspector and weighed in kilograms to evetually determine the total catch of the season. A record catch of 18 900 mt (whole mass) was landed in 1951, while for several years catches exceeded 10 400 mt, which is well above the current (1999) catch of 1 700 mt. The total allowed catch (TAC) had often been greater than what was actually caught (Pollock, 1986). For example, the TAC for 1967 and 1968 had been 10 400 mt while only 7 100 mt and 6 200 mt were landed respectively. As a result, since 1970, quotas have been drastically reduced and revised on an annual basis. Cruywagen (1995b) gave the percentage males in the catch per year, although it is interpolated over some years. See Table 9.8.1 for the male and female catch data that was used in this tesis.

Note that there was a change to the recording period in 1969. From 1900 to 1968 catches were recorded per calendar year even though fishing occurs from November until May. The recorded 1969 catch was taken from the 1st of January 1969 until the 31st of October 1970, while the catch for the 1970 season is the total catch taken from the 1st of November 1970 until the 31st of October 1971 and so on.
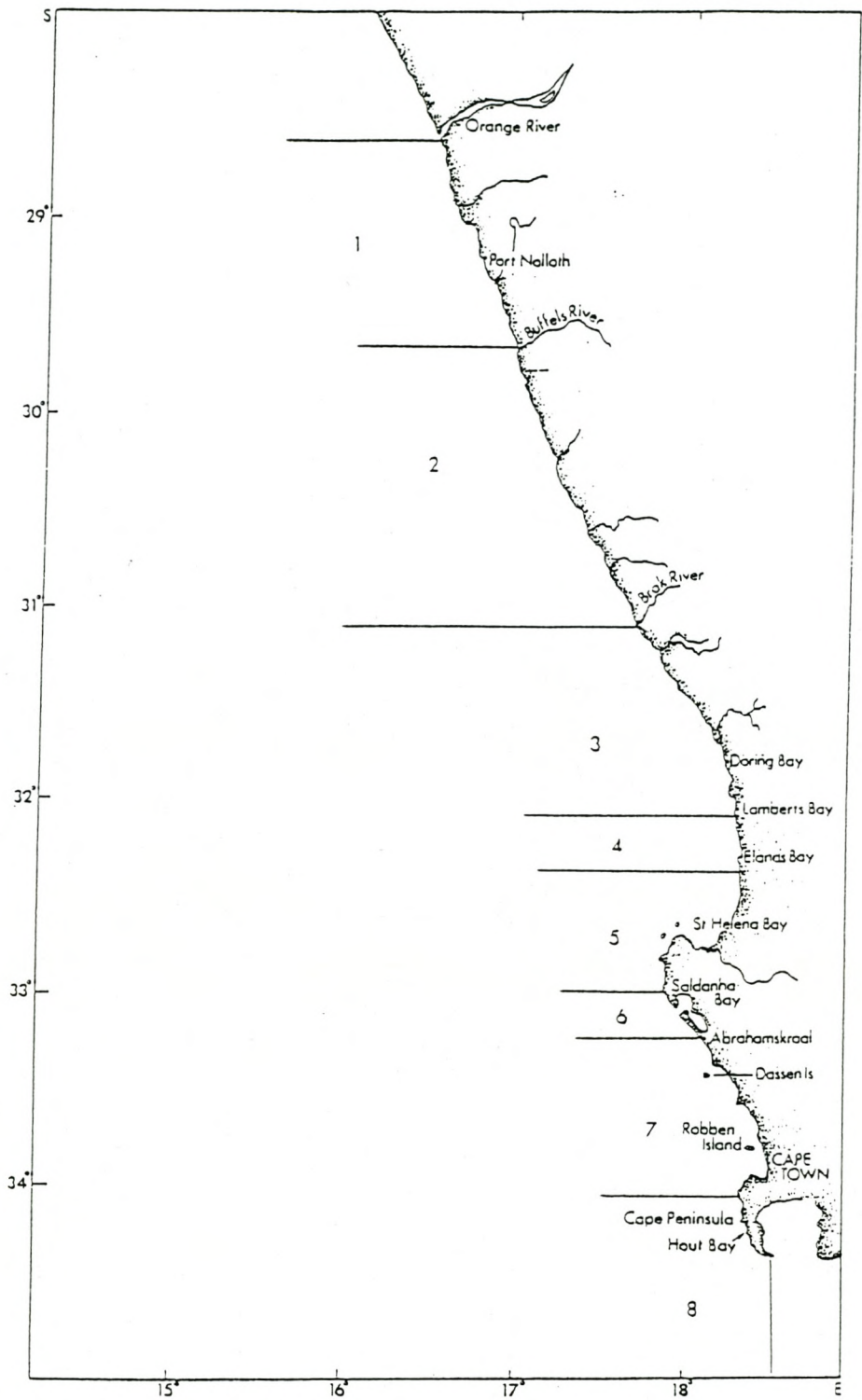
Figure 3.3.1: *Fishing grounds for the Cape Rock Lobster,* **Jasus lalandii**.
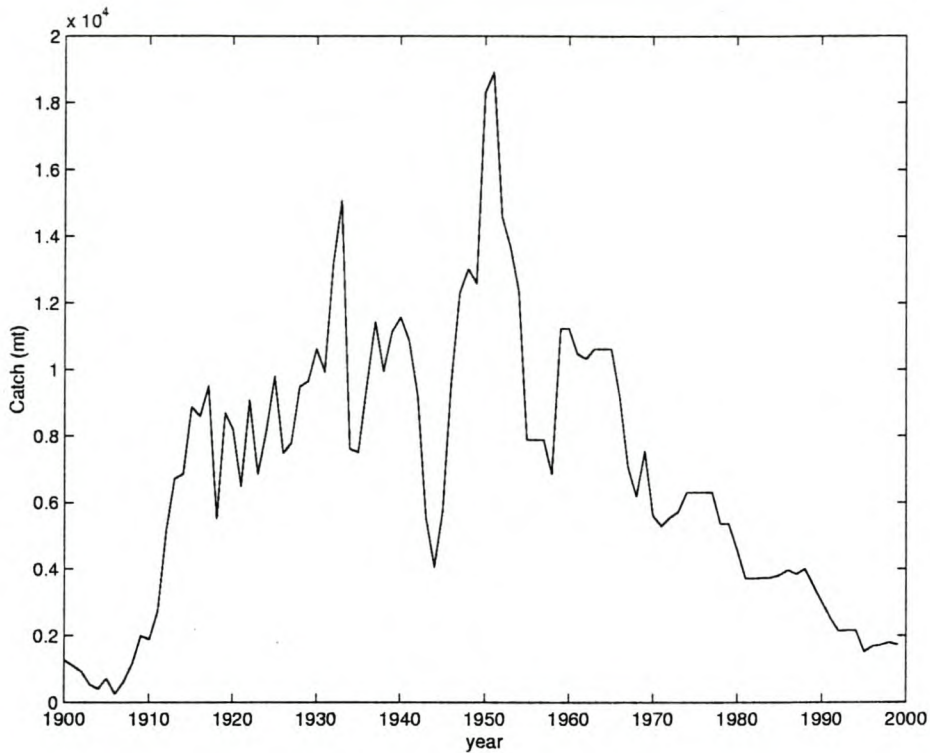
Figure 3.3.2: *Total landed catch per season for the Cape Rock Lobster, Jasus lalandii, since 1900 (see Appendix 9.6), as logged by commercial fishers and used by Marine and Coastal management of South Africa.*

Catches are taken by both traps and hoopnets. As catches before 1900 are believed to be limited, we assume that the population biomass was at a pristine level prior to 1900.

Other data available is the catch per unit effort (CPUE) data. A complete CPUE series for all the fishing areas is only available since the 1975 season. The skipper of each boat log the number of traps that is lifted and the number of traps that is set in the sea. The CPUE is now calculated by taking the trap catches only and is measured in terms of the catch in kg per number of traps carried per vessel per fishing day.

Until the 1991 season a legal minimum carapace length of 89 mm was enforced. In the 1992 season the legal minimum carapace length was dropped from 89 mm to 80 mm. Since the 1993 season it has been dropped even further to 75 mm, mainly due to the
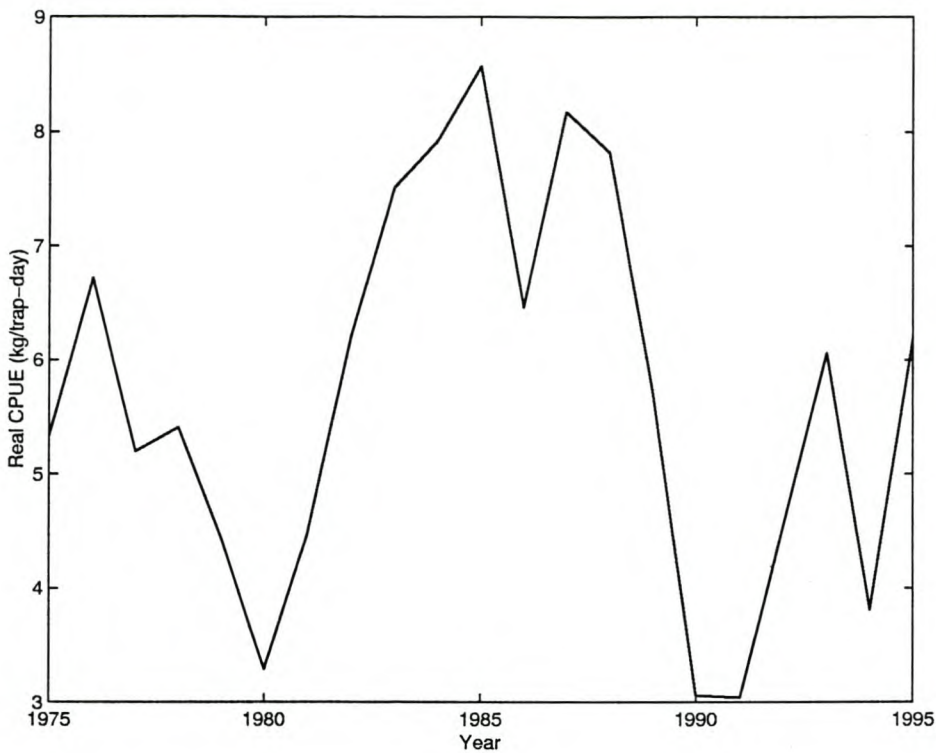
Figure 3.3.3: *The real data CPUE (see Appendix 9.6), as logged by commercial fishers and used by Marine and Coastal management of South Africa.*

unavailability of the larger lobsters and the market preference for smaller lobsters. As a result, with the same effort as before, larger catches were taken which thus lead to an increased CPUE (see Figure 3.3.3).

Growth parameters were also used. Cruywagen (1997) uses a Ford-Walford growth model in terms of lengths successfully. As the data for the Cape Rock Lobster is available in terms of weight we describe this model in terms of weight. In Appendix 9.3 we theoretically describe the Ford-Walford growth model in terms of weight in detail. This model is used in Chapter 5 when the delay difference model is applied to the Cape Rock Lobster resource.

Tagging data was used to determine the growth parameters. That is the growth increments in the carapace lengths of once-moulted males that were systematically selected over areas and years were recorded. Eight different fishing areas are considered

separately because quotas are allocated on an area basis (Cruywagen, 1997). The following conversion from length (cm) to weight (g) has been used by Cruywagen (1995b)

$$w = 0.8799l^{2.7663}$$

where w is the weight and l is the carapace length (Beyers, 1979).

The male and female intercept parameters, α_m and α_f, given in Table 9.8.4 was determined by Cruywagen (1995b), using the length-weight conversion of Beyers (1979), with the slope parameters set at $\rho_m = 0.9643$ and $\rho_f = 0.9829$.

Heydron (1969) also reports the length-weight conversion for males and females separately as

$$w_m(\text{kg}) = 0.822445l_m^{2.89} \ (\text{mm})$$
$$w_f(\text{kg}) = 0.624689l_f^{2.97} \ (\text{mm})$$

where the subscript m indicates males and f indicates females.

Other useful data that became available from diving experiments are the egg production per area at a specific date. Table 9.8.6 illustrates the 1987 data sample from the records of Marine and Coastal Management of South Africa. The total weight of eggs produced per individual (or sample) of a certain length was recorded and multiplied by a constant factor to determine the total number of eggs produced per female. A linear relation was fit through the data for each year. See Figure 9.8.1 for some of these. Table 9.8.7 lists all the intercept and slope parameters for all years.

Several work has also been done on the survival rate of the species. Pollock (1986) described natural mortality for the Cape Rock Lobster to be 0.1. Natural mortality, M, and natural survival, s, relate as follows:

$$s = e^{-M}.$$

That means that a natural mortality of 0.1 indicates a natural survival rate of 0.9. Johnston *et al.* (1993) reported a conservative region for the natural survival parameter between 0.82 and 0.95. Here different data sets were used.

Johnston *et al.* (1992) also used the following relation for the size-structured model that was applied to the Cape Rock Lobster:

$$s_i^m = s_i^f = 0.9 \quad \text{for all } i \geq 70$$

$$s_i^m = s_i^f = (i-1)\frac{(0.9 - 0.01)}{69} + 0.01 \quad \text{for all } i < 70,$$

where s_i^m indicates the survival rate of a male lobster of size i and s_i^f the survival rate for a female lobster of size i.

Cruywagen (1999) used the Ford-Walford model and performed a general linear modelling analysis to confirm that for both sexes the range $0.88 < s < 0.95$ is plausible. These survival rates are used in Chapter 6.

The data sets listed here are used in the applications of the bio-economic models that are discussed in the rest of the thesis.

Chapter 4

Surplus Production Models

In this chapter we shall study the properties of surplus production models from a bio-economic perspective. Clark's (1990) bio-economic Schaefer based fisheries model is well known in the literature. We generalize Clark's model to the Pella-Tomlinson model (Hilborn *et al.*, 1992) for application to the South African Cape Rock Lobster (*Jasus lalandii*) fishery. Hilborn *et al.* (1992) reason that although age structured models (see Chapter 6) may describe the population more fully than surplus production models, similar data failures may occur in the applications of these more detailed models. Furthermore, conclusions drawn from age structured- and surplus production models are often the same. Thus although simplistic, surplus production models are valuable tools in fisheries management.

In Section 4.1 we discuss, in general, the production function and harvesting function of the surplus production model. Then we discuss specific control policies. Depending on the management strategy followed by the authorities controlling the resource, a range of bio-economically stable situations could follow. Three different approaches are discussed in detail. The first option that we discuss in Section 4.2 is the open access fishery which is a fishery of no, or very limited management. Then in Sections 4.3 and 4.4 we consider two sole owner management options. The maximum sustainable yield (MSY) option where the fishery is managed towards the biological optimum is discussed in Section 4.3. Thirdly we discuss the sole owner maximum economic yield

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(MEY) option in Section 4.4 where the bio-economic optimum is discussed.

A maximum economic yield strategy, where we wish to maximize the total present value of all future income, is a control problem where the harvesting function is the control variable. A detailed discussion of the general optimal control solution is given in Appendix 9.2. The theory is applied to the general fishing problem in Section 4.4. Section 4.5 considers the case where a fixed number of owners operate successfully in a fishery. It becomes a social optimization problem as the present value of the entire industry is maximized where in the private optimization problem each owner maximizes his or her own profit. Control theory is applied to find the general equilibrium solution for both the social and private optimization problems. In Section 4.6 we apply the three management options that were theoretically compared in Sections 4.2, 4.3 and 4.4 to the South African Cape Rock Lobster fishery.

4.1   Population Dynamics

The most basic model that can easily be used for a bio-economic analysis is the surplus production model. This model for a single species is described by the ordinary differential equation

$$\frac{dx}{dt} = F(x,t) - h(x,t) \qquad (4.1.1)$$

where $x(t)$ is the biomass of the population at time t, F is a function representing the population's growth rate and h is a function representing the harvesting rate (Clark, 1990).

The growth function represents the natural biological dynamics of the species; hence, $F(x,t)$ should reflect both the natural mortality rate and recruitment of the species. The choice of an appropriate production function for a certain stock is often determined by a good fit to available data, but this does not necessarily guarantee that the biological dynamics is best described. Data sets are often incomplete and are collected at discrete time intervals with no knowledge of the population in between data points.

Thus all available data and information should be used in the stock assessment prosess (Hilborn *et al.*, 1992).

Examples of the production functions, that have been used for fishing modelling, in equation (4.1.1) are

- Logistic: $F(x,t) = rx(1 - \frac{x}{K})$ (Schaefer, 1954),

- Fox: $F(x,t) = rx(1 - \frac{\ln x}{\ln K})$ (Fox, 1975) and

- Pella-Tomlinson: $F(x,t) = rx\left(1 - \left(\frac{x}{K}\right)^{\alpha}\right)$ (Pella *et al.*, 1969),

where r is the intrinsic growth rate of the species and is assumed to be constant. K is the carrying capacity or saturation level and α the shape parameter of the function (Punt, 1988).

The growth functions can be classified into three groups. When the proportional growth rate, $F(x)/x$, is a decreasing function of x, we have a *pure compensation* model (see Figure 4.1.1(a)). However, contrariwise, when $F(x)/x$ is an increasing function of x, for certain values of x, we have, *local depensation.* In Figure 4.1.1(b) we have depensation for $0 < x < K^*$, but compensation for $x > K^*$. When $F(x) < 0$ for certain values of x, near $x = 0$, we have *critical* depensation (see Figure 4.1.1(c)) (Clark, 1990).

Note that the critical depensation models predict total extinction of the population when the population size, x, is reduced below a certain critical level K_0. That is

$$\lim_{t \to \infty} x(t) = 0 \quad \text{when } x(T) < K_0 \quad \text{for any } T.$$

Next we discuss the harvesting function. The function h is usually described in terms of the fishing effort. The measurement of effort is usually taken in terms of vessel-days, nets, traps or lines used (Clark, 1990). In most cases the actual catch and effort used are the only data available and the catch per unit effort (CPUE) is often assumed to be proportional to the biomass level. In such cases the catch is linear in the stock size,
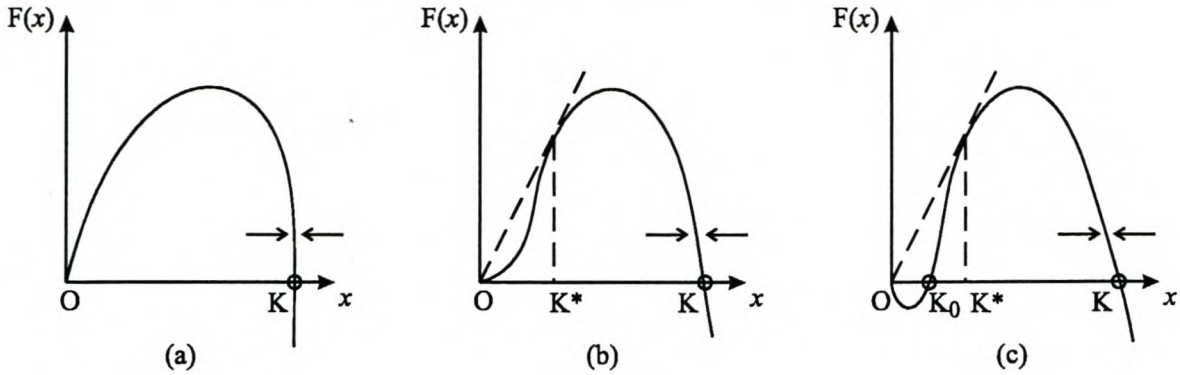
Figure 4.1.1: *Growth functions with (a) pure compensation, (b) depensation and (c) critical depensation.*

namely

$$h = qEx,$$

where q is defined as the catchability coefficient and E represents the fishing effort. The surplus production model that uses the logistic growth function and the linear catch dependence is called the Schaefer model (Schaefer, 1954). That is

$$\frac{dx}{dt} = rx(1 - \frac{x}{K}) - qEx.$$
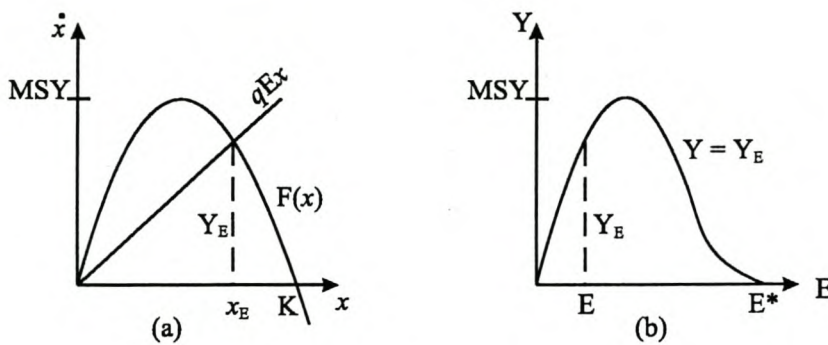
Figure 4.1.2: *Stable equilibrium, x_E, at a yield level, Y_E, occurs with compensation (see Clark, 1990). The critical effort level for overexploitation is E^*.*

A sustainable harvest is attained when there is no change in the population size. Mathematically this occurs when $\frac{dx}{dt} = 0$, or $F(x,t) = h(x,t)$ (see Figure 4.1.2). In

the past resource management has primarily revolved around the idea of a maximum sustainable harvest (see Chapter 2). Thus the aim is to harvest the *total surplus production* of the species. When the effort level is higher than a critical effort, E^*, the population is overexploited. On the other hand, if the effort is lower than E^*, or if there is even no harvest at all, the population will grow to its environmental carrying capacity, K. When the population has reached its carrying capacity, (that is $x = K$), the surplus production will be zero.

When depensation occurs for certain values of x, more than one equilibrium solution exists. For the example in Figure 4.1.3 (a) stable solutions are found at $x = 0$ and $x = x_1$ while an unstable solution is found at $x = x_2$.
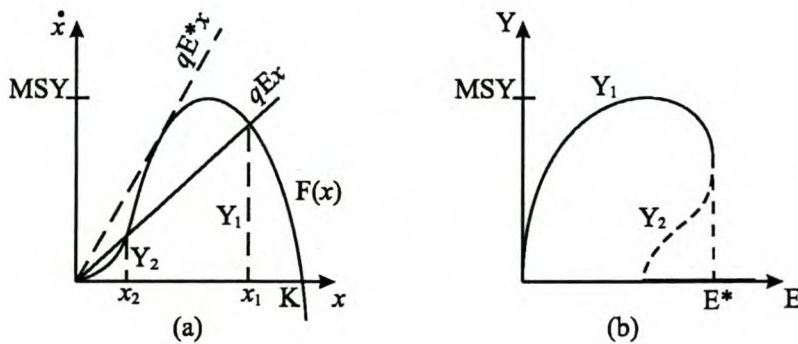
Figure 4.1.3: *(a) Stable and unstable equilibrium at x_1 and x_2 respectively, occurs when there is depensation. (b) Yield- effort curve for a depensation model (see Clark, 1990). The critical effort level is at E^*.*

The unstable solution for the yield Y_2 for each effort level indicates that when the initial biomass level $x(0)$ is such that $x(0) > x_2$ then the ultimate equilibrium for the biomass is x_1, but if we have $x(0) < x_2$ total extinction of the population will occur because $x \to 0$ as $t \to \infty$.

A critical effort level E^* exists in all cases, such that when $E > E^*$ equilibrium is established at $x = 0$ (see Figure 4.1.3 (b)). When, in the case of critical depensation, the effort level is higher than E^* and the population level is reduced to a level below K_0 (see 4.1.1), irreversibility occurs: no matter how low the effort is dropped, the

ultimate extinction of the population is unavoidable at the stable equilibrium level $x = 0$.

The simplicity of the surplus production model must be emphasized and all predictions should always be compared with real phenomena.

4.2   Open Access Fishery

In an open access fishery neither consumers nor the fishers enjoy full potential benefit from the resource as costs are too high and competition for fish necessitates long working hours (see Chapter 1). Since total revenue equals total costs for the fishery as a whole, the net economic revenue is always zero. In this section we shall determine the equilibrium population and harvesting levels that will be reached in an open access fishery, in the long run. Here, the harvest function is assumed linear in the population level, x, namely

$$h(x,t) = qEx \qquad (4.2.1)$$

where q represents the catchability coefficient and E the fishing effort (see Section 4.1). We also define the net economic revenue derived from the fishery as

$$P = pqEx - cE, \qquad (4.2.2)$$

where p is the unit price, and c, the operational cost per unit effort. Assume that the price p and cost c are constants. The primary objective of any company is to ensure that its total economic net present revenue is as high as possible. Here we work in real terms, where real economic rate is the nominal rate plus the inflation rate. This approach is followed in general in fisheries management. If δ (>0) is the discount rate (See Appendix 9.1) of future cash flows starting in year $t = T$, the expression

$$PV(T) = \int_T^\infty e^{-\delta t} P(t, x, E) dt \qquad (4.2.3)$$

calculates the present value of a continuous time-stream of future revenues.

Within the open access fishery a biological and economical equilibrium is reached at (x_{OAF}, E_{OAF}) when

$$\frac{dx}{dt} = F(x) - h(t) = 0$$

and

$$P_{OAF}(t, x, E) = 0.$$

Then

$$E_{OAF} = \frac{r}{q}\left(1 - \left(\frac{c}{pqK}\right)^{\alpha}\right)$$

and

$$x_{OAF} = \frac{c}{pq}, \qquad (4.2.4)$$

for the Pella-Tomlinson model. Suppose the biological parameters r, K and q are known, then the effort level E_{OAF} is dependent on only p and c.

4.3   Sole Owner Maximum Sustainable Yield

On the opposite end of the scale to the open access management strategy is the *sole owner* management strategy. In this case the sole owner (which could be either the government or a private company) owns complete rights to exploitation.

In this section we investigate the sole owner maximum sustainable yield management option. The maximum sustainable yield (MSY) is achieved at the population level where the population growth is at its highest. For the Pella-Tomlinson function, using the conditions (4.2.1) and (4.2.2) this is when

$$\text{MSY} = \frac{rK\alpha}{(1+\alpha)^{\frac{\alpha+1}{\alpha}}},$$

at a biomass level

$$x_{MSY} = \frac{K}{(1+\alpha)^{1/\alpha}}, \qquad (4.3.1)$$

with effort

$$E_{MSY} = \frac{r}{q}\left[1 - \left(\frac{x_{MSY}}{K}\right)^{\alpha}\right].$$

The only time when the open access fishery can have a yield equal to maximum sustainable yield (MSY) is when

$$x_{MSY} = x_{OAF}$$

thus

$$\frac{qK}{(1+\alpha)^{1/\alpha}} = \frac{c}{p}.$$

It is, however, highly unlikely that the cost-price ratio takes exactly the value that is required for MSY, especially in an unregulated fishery.

Usually in an open access fishery, price is much larger than cost, so that E_{MSY} will be well below E_{OAF}. For this reason some external control should be imposed on a fishery to reduce fishing effort to the MSY-level and to force the net economic revenue, P, to be positive. At the MSY-level the net economic revenue is

$$P_{MSY} = r \left[px_{MSY} - \frac{c}{q} \right] \left[1 - \left(\frac{x_{MSY}}{K} \right)^{\alpha} \right].$$

Note that when $x_{\text{MSY}} = x_{\text{OAF}}$ this expression reduces to zero.

Given a stock level of x_{MSY} and a MSY management strategy the present value of all future revenue is

$$
\begin{aligned}
\text{PV}(0) &= \int_0^\infty e^{-\delta t} P_{MSY}\, dt \\
&= \frac{1}{\delta} P_{MSY},
\end{aligned}
$$

(see Appendix 9.1). Suppose, however, the current level of biomass, x_C, is not at its MSY-level, $x_C \neq x_{MSY}$, then the quickest way of attaining $x_C = x_{MSY}$ is by the so called *bang-bang* approach, namely,

$$
h(t) = \begin{cases}
h_{\max} & \text{when} & x_C > x_{MSY} \\
F(x_{MSY}) & \text{when} & x_C = x_{MSY} \\
0 & \text{when} & x_C < x_{MSY},
\end{cases}
$$

where $h_{\max}$ is the maximum feasible harvest rate. (We assume this can be achieved in one season.)

Now we define the net depletion revenue, NDR, as the income during this time of maximum harvesting. That is

$$\text{NDR} = p(x_C - x_{MSY}) - c \int_{x_{MSY}}^{x_C} \frac{1}{q\,x} dx,$$

and the total present value is therefore

$$\text{TPV}(P_{MSY}) = \text{PV}(1) + \text{NDR}.$$

However, suppose that $x_C < x_{MSY}$, then the approach would be to have zero harvesting to allow the population to recover towards the required equilibrium level. The necessary duration, T^*, during which no harvesting should be enforced, is calculated from equation (4.1.1), as,

$$T^* = \int_{x_C}^{x_{MSY}} \frac{dx}{r x \left[1 - \left(\frac{x}{K}\right)^{\alpha}\right]}.$$

Here it is clear that NDR= 0, and so TPV(P_{MSY}) =PV(T^*).

Suppose the level E_{OAF} is less than E_{MSY}, then the effort is still below the maximum sustainable biological yield. But when E_{OAF} is such that $E_{OAF} > E_{MSY}$, biological overfishing occurs. In this situation it is necessary to reduce the effort with the obvious results of an increase in revenues (a higher yield level can be expected with an increase in stock level) and a reduction in costs. That is, the stock level will increase after a reduction in effort, with an ultimate increase in yield. But the immediate effect will be a decrease in yield (see Figure 4.3.1).

4.4   Sole Owner Maximum Economic Yield

A third strategy that we discuss in this chapter is when the sole owner aims to reach an optimal economic yield from the fishery. In this section we first discuss the sole owner maximum economic yield strategy, in general, considering a non-linear harvesting strategy. Then the specific linear harvesting strategy is compared to the strategies of Sections 4.2 and 4.3.
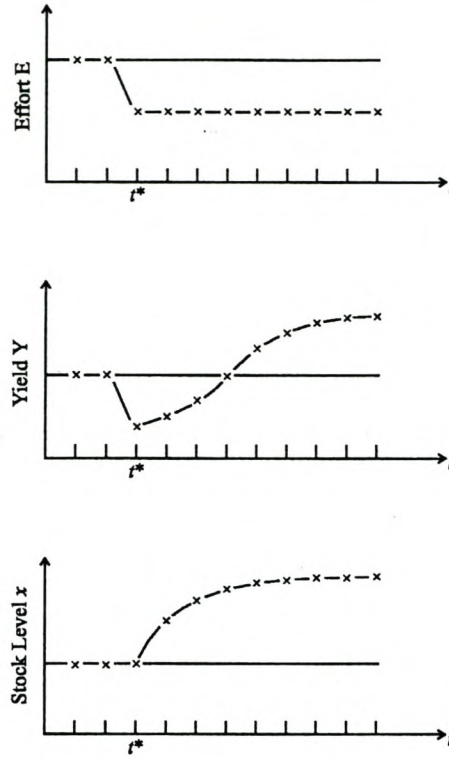
Figure 4.3.1: *Effect on yield and stock levels with a reduced effort (Clark, 1990).*

For the general non-linear fishery problem we apply the control theory for optimization, that is described in Appendix 9.2.

Consider the sole owner fishery (see Chapter 2) where the state equation for the non-linear optimization fishery problem is

$$\frac{dx}{dt} = F(x,t) - h(t) \qquad (4.4.1)$$

with the initial and terminal conditions

$$x(0) = x_0, \qquad x(T) = x^*,$$

where T is the time horizon, x^* the optimal stock level and $h(t)$ the control function. Let $\Pi(x,h,t)$ be the net revenue function, then the problem is to maximize the total present value

$$J = \int_0^\infty \Pi(x,h,t)\,dt$$

subject to the state equation. Using the control theory described in Appendix 9.2 we are able to define the Hamiltonian as

$$H(x, h, t) = \Pi(x, h, t) + \lambda(t)[F(x, t) - h(t)],$$

where the canonical equation is given by

$$\frac{d\lambda}{dt} = -\frac{\partial \Pi}{\partial x} - \frac{\partial F}{\partial x}, \qquad (4.4.2)$$

with λ a real function of t. The necessary condition to maximize J is now

$$\frac{\partial H}{\partial h} = \frac{\partial \Pi}{\partial h} - \lambda = 0$$

or

$$\lambda(t) = \frac{\partial \Pi}{\partial h}. \qquad (4.4.3)$$

The function $\lambda(t)$ can be interpreted as the change in net income for every change of one unit in the harvest. Alternatively $\lambda(t)$ is the marginal value of the capital stock, x, at time t. It is often referred to as the *shadow price* (Clark, 1990).

The term $\frac{dJ}{dt} = \Pi(x, h, t)$ may be interpreted as the flow of the net return and the rate $\frac{dx}{dt}$ in equation (4.4.1) as the flow of "investment" in the stock. Multiplying the right hand side of equation (4.4.1) by the shadow price $\lambda(t)$ renders the value of this "investment". In other words, the Hamiltonian represents the total rate of increase in the value of assets (Clark, 1990).

In principle it is possible to find the three functions $x(t)$, $\lambda(t)$ and $h(t)$ from equations (4.4.1), (4.4.2) and (4.4.3). Depending on the complexity of the functions F and Π this solution may not be trivial.

Suppose the total revenue function $R(h)$ is nonlinear in h, with $R(h)$ smooth, convex and nonnegative when $h \geq 0$ and let $C(x, h)$ denote the total harvesting cost function. With a constant discount rate, δ, on future income, the objective functional is

$$J(h) = \int_0^\infty e^{-\delta t}[R(h) - C(x, h)]dt.$$

The Hamiltonian therefore becomes

$$H(x, h, t) = e^{-\delta t}[R(h) - C(x, h)] + \lambda(t)[F(x) - h(t)]$$

with the canonical equation

$$\frac{d\lambda}{dt} = -\frac{dH}{dx} = e^{-\delta t}\frac{\partial C}{\partial x} - \lambda(t)F'(x), \qquad (4.4.4)$$

where we use the notation F' for $\frac{dF}{dx}$. Also use R' for $\frac{dR}{dh}$, then the necessary condition for the maximum is

$$\frac{\partial H}{\partial h} = e^{-\delta t}\left[R'(h) - \frac{\partial C}{\partial h}\right] - \lambda(t) = 0$$

or

$$\lambda(t) = e^{-\delta t}\left[R'(h) - \frac{\partial C}{\partial h}\right],$$

and

$$\frac{d\lambda}{dt} = e^{-\delta t}\left\{R''\frac{dh}{dt} - \frac{\partial^2 C}{\partial h^2}\frac{dh}{dt} - \frac{\partial^2 C}{\partial x \partial h}[F(x) - h(t)] - \delta\left(R' - \frac{\partial C}{\partial h}\right)\right\}.$$

Substitution in equation (4.4.4) leaves

$$\left(R'' - \frac{\partial^2 C}{\partial h^2}\right)\frac{dh}{dt} = \frac{\partial C}{\partial x} + \left(R' - \frac{\partial C}{\partial h}\right)(\delta - F'(x)) + \frac{\partial^2 C}{\partial x \partial h}\dot{x}.$$

When $C(x, h) = c(x)h$ the expression reduces to

$$R''\frac{dh}{dt} = \left(\delta - F'(x)\right)\left(R' - c(x)\right) + c'(x)F(x).$$

We obtain the dynamical system

$$\begin{aligned}
\frac{dx}{dt} &= F(x) - h(t) \\
\frac{dh}{dt} &= \frac{1}{R''}\left\{\left(\delta - F'(x)\right)\left(R' - c(x)\right) + c'(x)F(x)\right\}.
\end{aligned}$$

Thus, an optimal solution, $x(t) = x^*$, for the non-linear problem is

$$F'(x^*) - \frac{c'(x^*)F(x^*)}{R' - c(x^*)} = \delta, \qquad (4.4.5)$$

and

$$h = F(x^*).$$

Now we use phase-plane theory to determine the optimal harvest strategy (Clark 1990). The x-isocline where $\dot{x} = 0$ is the line $h = F(x_{MEY})$ while the h-isocline is where $\dot{h} = 0$ or the line $x = x_{MEY}$ that satisfies equation (4.4.5).
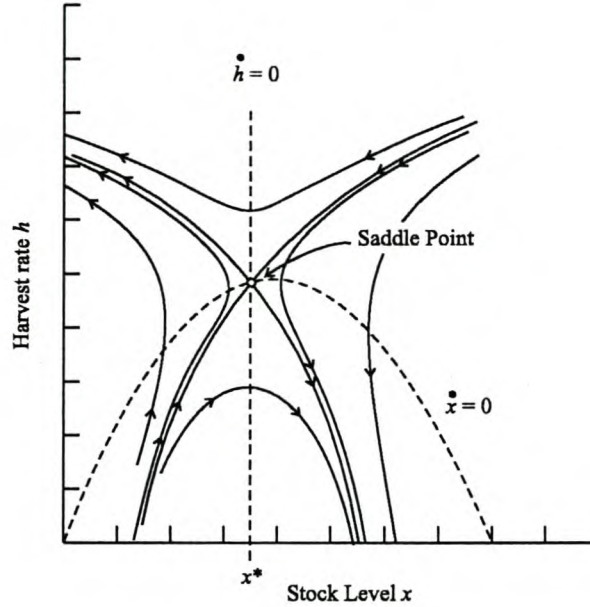
Figure 4.4.1: *Isoclines and trajectories system defined by the nonlinear fishery model (Clark, 1990).*

We know from phase-plane theory that any trajectory with initial condition (x_0, h_0) intersects the line $\dot{x} = 0$ vertically and the line $\dot{h} = 0$ horizontally. The directions as indicated in Figure 4.4.1 are determined from the signs of $\dot{h}$ and $\dot{x}$ in the different sectors and denote increasing time.

It is now easy to see that the equilibrium solution is a saddle point with the associated separatrices through the point (x^*, h^*) (see Figure 4.4.1). All trajectories begin at infinity and converge towards (x^*, h^*) but then diverge again away from it towards infinity. The optimal trajectory to select will depend on the initial condition $x(0)$ and the terminal condition $x(T)$. The time, T, to traverse a chosen trajectory increases as it passes closer to the equilibrium and the solution may spend most of its time close to the equilibrium when T is large. With an infinite time horizon $T \to \infty$ the trajectory will converge towards the separatrix and the solution will approach the point $x = x^*$

asymptotically (see Figure 4.4.2).
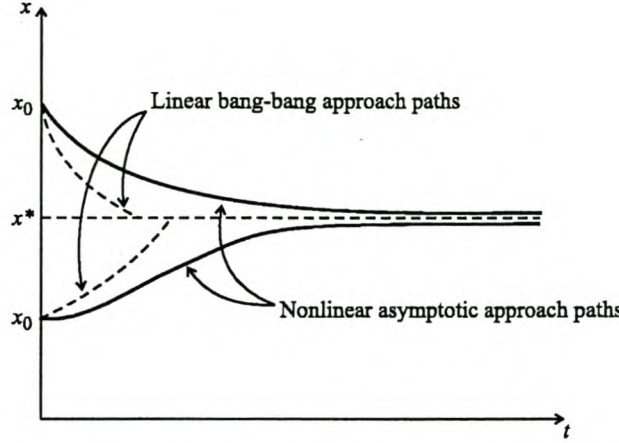
Figure 4.4.2: *Optimal population path for the non-linear fishery compared to the linear fishery (Clark, 1990).*

The optimal approach path for the non-linear fishery is a more gradual attempt than the bang-bang approach of the linear fishery with less drastic implications to the industry (Clark, 1990).

Let us now investigate the linear harvesting model as in Sections 4.1 and 4.2. For the linear harvesting model we can define the revenue function as

$$P(t, x, E) = \left(p - \frac{c}{qx}\right) h(t),$$

using equation (4.2.1).

To find the optimal stock level, we can use equation (4.4.5). The Hamiltonian for the Pella-Tomlinson model is

$$H = e^{-\delta t} \left(p - \frac{c}{qx}\right) qEx + \rho \left[rx \left(1 - \left(\frac{x}{K}\right)^{\alpha}\right) - qEx\right],$$

where ρ is the adjoint variable. By applying the maximum principle and the necessary condition for a maximum, we derive the expression

$$\frac{-(1+\alpha)}{K^{\alpha}} x_{MEY}^{\alpha+1} + \left(\frac{c\alpha}{pqK^{\alpha}}\right) x_{MEY}^{\alpha} + \left(1 - \frac{\delta}{r}\right) x_{MEY} = \frac{-c\delta}{pqr}, \qquad (4.4.6)$$

where x_{MEY} is the optimal stock level.

For the Schaefer model, that is when $\alpha = 1$, this expression reduces to

$$x_{MEY} = \frac{K}{4}\left(\lambda + \sqrt{\lambda^2 + \mu}\right),$$

where

$$\lambda = \frac{c}{p}\left(\frac{1}{qK}\right) + 1 - \frac{\delta}{r}, \qquad \mu = \frac{c}{p}\left(\frac{8\delta}{qKr}\right),$$

(Clark, 1990).

The negative root of x_{MEY} is ignored, because it is biologically unrealistic. Note that the cost-price (c/p) ratio, rather than the absolute values determine the optimal equilibrium population level, x_{MEY}.

From the above we see that the optimal harvesting level is then

$$h(t) = F(x_{MEY})$$

for all t. More specifically, for the Pella-Tomlinson model, the net sustainable revenue is

$$P_{MEY} = r\left[px_{MEY} - \frac{c}{q}\right]\left[1 - \left(\frac{x_{MEY}}{K}\right)^\alpha\right].$$

If the current stock level is not at x_{MEY}, then again the quickest way of attaining it is by the *bang-bang* approach (see Section 4.3). The simplicity of the bang-bang approach is based on the linearity of the model, but we must emphasize that this approach, that is to close down an entire fishery, is rather unrealistic. Here a more gradual approach will be more feasible.

The total net present value is calculated by determining the net revenue obtained in approaching the sole owner equilibrium and adding the net present value obtained from being at the equilibrium level. As in Section 4.3 if $x_C > x_{MEY}$ then

$$\text{NDR} = p(x_C - x_{MEY}) - c\int_{x_{MEY}}^{x_C} \frac{1}{qx}dx,$$

else NDR= 0. The total present value is then

$$\text{TPV}(P_{MEY}) = \int_{T^*}^{\infty} e^{-\delta t} P_{MEY} dt + \text{NDR}.$$

We determine T^* in the same manner as in Section 4.3.

In addition to the three management strategies discussed above, many more exist. Typically these could involve various constraints on individual vessels or companies (Arnason, 1989). When biological overfishing exists the management policy should be to reduce effort. By increasing the cost (with restrictions on gear etc.) the effort should be effectively reduced.

The optimal harvesting path for the linear and non-linear models should be implemented by way of the different access rights strategies discussed in Chapter 2. The optimal solution (x^*, h^*) should be the objective when deciding on limited entries and TAC's.

4.5 Maximum Economic Yield for a Fixed Number of Owners

Let us consider the case in which individual vessels or companies can operate at different operating costs due to the differences in technology and locations (Arnason, 1989).

Assume that vessel i operates at effort $E_i(t)$, with E_i independent of other vessels and $0 \leq E_i(t) \leq E_{i,MAX}$, where $E_{i,MAX}$ is the maximum allowable effort level. Then the catch of this vessel will be

$$h_i = q(x)E_i,$$

where q again denotes the catchability function. Assume that $\frac{dq}{dx} > 0$ and that $q(x)$ is the same across the whole fishery as the gear is specified.

Consider the case of pure competition (where no one company is dominating the market) and assume there is no crowding of vessels. The managers of the individual companies ignore the effect that their harvesting will have on future stock as each

company wishes to maximize the profit function

$$P_i = pq(x)E_i - C_i(E_i),$$

where p is the price per unit of fish, E_i is the control function, and $C_i(E_i)$ the cost function. The average cost function is $\overline{C}_i(E_i) = \frac{C_i(E_i)}{E_i}$.

Now suppose the marginal cost $\frac{\partial C_i}{\partial E_i} = C_i'(E_i)$ equals the average cost at effort level E_{r_i} (Clark, 1990) (see Figure 4.5.1), then
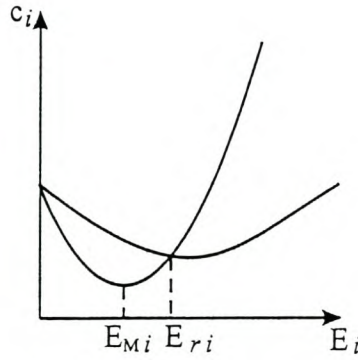
Figure 4.5.1: *Marginal cost and average cost of effort curves (Clark, 1990).*

$$C_i'(E_{r_i}) = \frac{C_i(E_{r_i})}{E_{r_i}} = r_i.$$

To maximize profit, $P_i > 0$, the company will operate at an effort such that

$$\left. \begin{array}{ll} C_i'(E_i) = pq(x) & , \quad pq(x) > r_i \\ E_i = 0 & , \quad pq(x) < r_i \end{array} \right\}$$

That is, when vessel i has a negative profit function P_i, it will withdraw, or $E_i = 0$. This occurs when the biomass level x is such that $x < x_i$ where

$$x_i = q^{-1}\left(\frac{r_i}{p}\right).$$

If companies are enumerated in increasing order in accordance with the x_i's, then

$$x_1 \leq x_2 \leq x_3 \leq \ldots \leq x_N.$$

The total effort of N companies is

$$E_T = \sum_{i=1}^{N} E_i$$

and the total catch of the industry is

$$h_T = q(x)E_T,$$

such that

$$\frac{dx}{dt} = F(x) - h_T.$$

The fish population will be at a stable equilibrium when $\dot{x} = 0$. Suppose this steady state is at level $\bar{x}$, then

$$F(\bar{x}) = q(\bar{x})E_T.$$

At the equilibrium state the inefficient vessels, that is vessels for which $\bar{x} < x_i$, have withdrawn. Suppose the marginal vessel, j, is the least efficient vessel that is still fishing, then

$$E_T = \sum_{i=1}^{j} E_i,$$

and

$$P_j(\bar{x}, E_j) \simeq 0$$

or

$$\overline{C}_j(E_j) \simeq pq(\bar{x}).$$

When j is known we can specify how many vessels are operating in the fishery (Clark, 1990).

4.5.1   Social Optimization Problem

Consider the optimal fishing problem where the centralized authority must find the time path of fishing effort that will maximize

$$J = \int_0^{\infty} e^{-\delta t} \sum_{i=1}^{N} P_i(x, E_i)dt$$

subject to

$$\frac{dx}{dt} = F(x) - q(x) \sum_{i=1}^{N} E_i,$$

with

$$x, E_i \geq 0, \qquad i = 1 \text{ to } N$$

(Arnason, 1989). The Hamiltonian for this optimization problem is

$$H = \sum_{i=1}^{N} e^{-\delta t} \left(pq(x)E_i - C_i(E_i) \right) + \mu(t) \left(F(x) - q(x) \sum_{i=1}^{N} E_i \right),$$

where E_i, is the control function, and μ is the adjoint variable (Clark, 1990). The maximum principle implies

$$\mu = e^{-\delta t} \left(p - \frac{C_i'(E_i)}{q(x)} \right), \tag{4.5.1}$$

and the adjoint equation states that

$$\frac{d\mu}{dt} = - \sum_{i=1}^{N} e^{-\delta t} pq'(x)E_i - \mu \left(F'(x) - q'(x) \sum_{i=1}^{N} E_i \right). \tag{4.5.2}$$

By using equations (4.5.1) and (4.5.2) we obtain

$$F'(x) + \frac{C_i'(E_i)q'(x)F(x)}{q^2(x)\left(p - \frac{C_i'(E_i)}{q(x)} \right)} = \delta.$$

The individual optimal effort from the maximum principle as indicated by equation (4.5.1) is therefore

$$C_i'(E_i) = \left(p - e^{\delta t}\mu \right) q(x), \quad \text{when } \left(p - e^{\delta t}\mu \right) q(x) > r_i$$
$$E_i = 0 \qquad \qquad \text{otherwise.}$$

The marginal vessel j, catches at a level such that

$$\overline{C_j}(E_j) = C_j'(E_j) = r_j.$$

Then the optimal equilibrium solution, (x^*, E_i^*), satisfies the equation

$$F'(x) + \frac{r_j q'(x)F(x)}{q^2(x)\left(p - \frac{r_j}{q(x)} \right)} = \delta \tag{4.5.3}$$

(Clark, 1990). If we consider the linear problem where $q(x) = qx$ and $C(E_i) = c_i E_i$, then, where $c_i = r_j$, or in the case of only one company, equation (4.5.3) reduces to the sole owner (MEY) problem(see equation (4.4.5)).

4.5.2 Private Optimization Problem

Consider now the optimization problem of Section 4.5 again, now from the viewpoint of the private company, i (Arnason, 1989). All the owners still operate under the specific fishing policies as described earlier. The private optimization problem is where each manager wishes to operate at a maximum profit level. This problem differs from the open access situation where everyone may fish without restrictions on effort or catch size.

The objective function is

$$J = \int_0^\infty e^{-\delta t} P_i(E_i, x) dx$$

subject to

$$\frac{dx}{dt} = F(x,t) - \sum_{i=1}^N h_i(E_i, x).$$

The Hamiltonian for this problem is

$$H = e^{-\delta t}\left(pq(x)E_i - C_i(E_i)\right) + \sigma_i\left(F(x) - q(x)\sum_{i=1}^N E_i\right)$$

with σ_i the adjoint variables. The maximum principle leads to

$$\sigma_i = e^{-\delta t}\left(p - \frac{C_i'(E_i)}{q(x)}\right).$$

When applying the adjoint equality the optimal solution satisfies

$$F'(x) + \left[\frac{C_i'(E_i)}{q^2(x)}q'(x)F(x) + pq'(x)\left(E_i - \sum_{i=1}^N E_i\right)\right]\frac{1}{\left(p - \frac{C_i'(E_i)}{q(x)}\right)} = \delta.$$

This again reduces to the original equation (4.4.5) when there is only one company, that is when $N = 1$.

Some other detailed bio-economic studies on surplus production models have been done. For example, Sandal *et al.* (1994) considered a feedback control solution of the problem where the revenue function is given as quadratic in the harvest level.

4.6 Application to Cape Rock Lobster

In this section the models that were discussed in Sections 4.2, 4.3 and 4.4 will be applied to the South African Cape Rock Lobster fishery (see Chapter 3). Equivalent modelling studies have, for example, been carried out by Kuronuma *et al.* (1994) on the Antarctic Minke Whale.

The required parameters in the biological model are the intrinsic growth rate of the resource, r, the carrying capacity, K, and the production function *shape* parameter, α. Kuronuma *et al.* (1994) assumed that these values have already been estimated. Here a major part of the investigation centres around the estimation of these parameters by fitting the model output to available data. The parameter estimation procedure that is used is discussed in Section 4.6.1.

Two data series that are used here is the total landed catch data from 1990 to 1995 and the CPUE data series since 1975. These sets are listed in Appendix 9.8 in Tables 9.8.1 and 9.8.2 and discussed in detail in Chapter 3. In Section 4.6.2 we explain the reason for various constraints that are used to ensure that the parameter estimation procedure is realistic.

In Section 4.6.3 the results of the estimation for the biological parameters are given for three different examples. The first example is for the case where no constraints are used in the parameter estimation procedure. In the second example bounds, as discussed in Section 4.6.2, are placed on the parameters. In the third example the specific Schaefer function along with the constraints as before, are used.

Also necessary are certain economical parameters, namely, the total unit price, p, the cost per unit effort, c, and the discount rate, δ. The average price attained per 10 kg of rock lobster, over a range of size classes, was R 488 during the years 1993, 1994, 1995 (unpublished information, South African Inshore Fishing Industry Association). For our purpose we therefore approximate price as a constant of R 50/kg for all times. A discount rate of 5% is assumed, reflecting a long term realistic real interest rate for South Africa. For reasons of confidentiality the cost per unit effort is not as readily

obtainable. We approximate it to R 40/trap-day and use sensitivity tests to investigate alternatives.

The Pella-Tomlinson production function is used throughout this section.

It is further assumed that the catch rate is linearly proportional to the biomass, so that

$$h(t) = h = qEx, \qquad (4.6.1)$$

where E denotes effort and q the catchability coefficient.

The catchability coefficient, q, will differ for the different enforced minimum legal sizes, since the subpopulation targeted in each case differs. If q_1 is the catchability coefficient for the period 1900 to 1991 a different q, say q_{1992}, is required for 1992 and again a different q, say q_2, is required for the seasons since 1993. Refer to Chapter 3 for more detail on how the minimum legal sizes varied over time.

Substitution of the production and harvest functions into the harvesting model gives

$$\frac{dx}{dt} = rx \left[1 - \left(\frac{x}{K} \right)^\alpha \right] - qEx.$$

To estimate the model parameters we use the discrete version of the model, because the recorded data are for discrete fishing years. For computational purposes we discretize the differential equation. If X_t represents the total biomass in year t, the discrete model is

$$X_{t+1} = X_t + rX_t \left[1 - \left(\frac{X_t}{K} \right)^\alpha \right] - qEX_t. \qquad (4.6.2)$$

In Section 4.6.4 we will determine the equilibrium population levels for the three management options for the three examples. In Sections 4.6.1 to 4.6.3 we first discuss the biological parameters to be used.

4.6.1   Biological Parameter Estimation Procedure

It is standard practice to assume that the observed catch per unit effort, CPUE_t, has a lognormal distribution (Hilborn *et al.*, 1992). The model predicted CPUE can then be

expressed as $\widehat{\text{CPUE}}_t = \text{CPUE}_t e^{\varepsilon}$, with $\varepsilon = \text{N}(0, \sigma^2)$, a normal distribution with mean, 0 and the standard deviation σ.

To estimate r, K and α, the CPUE series, as predicted by the model, is fitted to the data using the maximum likelihood function for the normal distribution. Due to the change in legal size the fit is done over two periods, each with a different q, q_1 and q_2, and σ, σ_1 and σ_2. Note that fitting to the 1992 CPUE datum value does not contribute towards the parameter estimation procedure, since only the value of q_{1992} can be gathered from this.

The likelihood function to be maximized is

$$L = L_1 \times L_2$$

where

$$L_1 = \left(\frac{1}{\sqrt{2\pi\sigma_1^2}}\right)^{17} \left[\exp\left(-\frac{1}{2\sigma_1^2}\sum_{t=1975}^{1991}(\ln\text{CPUE}_t - \ln\widehat{\text{CPUE}}_t)^2\right)\right],$$

$$L_2 = \left(\frac{1}{\sqrt{2\pi\sigma_2^2}}\right)^{3} \left[\exp\left(-\frac{1}{2\sigma_2^2}\sum_{t=1993}^{1995}(\ln\text{CPUE}_t - \ln\widehat{\text{CPUE}}_t)^2\right)\right],$$

and σ_1, σ_2, q_1, q_2, r, K and α are unknown parameters to be estimated. Taking natural logarithms and using the fact that, $\widehat{\text{CPUE}}_t = qX_t$, the likelihood function reduces to

$$\begin{aligned}
\ln L = {} & -\frac{17}{2}\ln(2\pi\sigma_1^2) - \frac{1}{2\sigma_1^2}\sum_{t=1975}^{1991}(\ln\text{CPUE}_t - \ln q_1 X_t)^2 \\
& -\frac{3}{2}\ln(2\pi\sigma_2^2) - \frac{1}{2\sigma_2^2}\sum_{t=1993}^{1995}(\ln\text{CPUE}_t - \ln q_2 X_t)^2.
\end{aligned} \qquad (4.6.3)$$

To maximize this function we differentiate with respect to σ_1^2, σ_2^2, q_1 and q_2, and set the resulting expressions to zero. After simplification

$$\sigma_1^2 = \frac{1}{17}\sum_{t=1975}^{1991}(\ln\text{CPUE}_t - \ln(q_1 X_t))^2,$$

$$\sigma_2^2 = \frac{1}{3}\sum_{t=1993}^{1995}(\ln\text{CPUE}_t - \ln(q_2 X_t))^2,$$

$$q_1 = \left[\prod_{t=1975}^{1991} \frac{\text{CPUE}_t}{X_t} \right]^{1/17},$$

$$q_2 = \left[\prod_{t=1993}^{1995} \frac{\text{CPUE}_t}{X_t} \right]^{1/3}.$$

The number of unknown parameters has now been reduced to three, namely r, K and α and we use the Powell minimization method (Press *et al.*, 1989) to estimate these parameters. Initial values are assigned to these unknown parameters. These values are then improved upon by using a method of steepest descent. To ensure that a global rather than local minimum is reached a range of initial parameter values are tested.

4.6.2   Biological Parameter Constraints

As reported by Cruywagen *et al.* (1994) initial estimates of, and bounds on the unknown parameters and the biomass, X, could be obtained from previous studies of the Cape and other rock lobster resources.

Additional information regarding the intrinsic growth rate parameter, r, is gathered from the study of McKoy *et al.* (1981) on *Jasus edwardsii* in New Zealand. *Jasus edwardsii* is of the same genus as the Cape Rock Lobster. Using the Schaefer model they estimated the intrinsic growth parameter as $r = 0.272$.

For the Pella-Tomlinson model Barkai *et al.* (1992) obtained a value of $r = 0.39$ for the Dassen Island area, which is one of the rock lobster fishing areas along the Cape west coast. Since Dassen Island is considered a "*good* growth area", (Cruywagen, 1997) an average value of less than 0.39 can be expected for the intrinsic growth parameter for the South African west coast as a whole. Based on these, the following upper and lower bounds are therefore placed on the value of the intrinsic growth parameter r,

$$0 < r \le 0.4. \tag{4.6.4}$$

Environmental observations indicate that the current population level is far from its pristine level (Barkai *et al.*, 1992). By 1995 the biomass level was estimated to be between 30000 to 50000 mt by the length-based stock assessment model (Johnston *et al.*, 1995). In the light of this we add a constraint to the maximum likelihood problem, (4.6.3), namely, that the biomass (at the date of calculation, namely 1996) lies within the reasonable boundaries of

$$20000 \leq X_{1996} \leq 90000. \tag{4.6.5}$$

The above constraints are included in the parameter estimation procedure. Using the Powell minimization method, the function, $-\ln L$, is set to a very large number, say 10^{10}, whenever these constraints are violated, and the estimation process continues until the minimum of the negative loglikelihood function is found.

4.6.3 Biological Model

The parameter estimation procedure as described in Section 4.6.1 was applied to solve for the parameters of the Pella-Tomlinson model (4.6.2). Initially it was assumed that α is known and the constraints (4.6.4) and (4.6.5) were not incorporated. The results obtained, for selected values of α, are shown in Table 4.6.1. Values for r, K and q for different Pella-Tomlinson functions (different choices of α) were estimated. Note the marked difference in estimates for r and K for different values of α.

One difficulty encountered with the parameter estimation procedure is that the negative log likelihood fuction, $-\ln L$, declines with increasing r, and so a simultaneous search for r, α, and K results in an unrealistic result where α is very small and r is unusually high. To overcome this the additional constraints (4.6.4) and (4.6.5), discussed in Section 4.6.2, had to be taken into account.

As expected, with $0.0 < r \leq 0.4$ and K, r and α the unknown parameters, the estimation procedure selects values equal to the bounds on r. Thus, for any initial set of values for K, r and α, either $r \simeq 0$ or $r \simeq 0.4$ was obtained.

α	r	K (mt)	q_1	q_2	X_{1996}	$-\ln L$
0.2	2.82	62 809	1.0e-07	9.0e-08	59 409	4.77
0.3	1.9	64 539	1.0e-07	8.7e-08	61 177	4.77
0.7	0.84	71 287	8.9e-08	7.8e-08	68 049	4.78
1.0	0.6	76 194	8.3e-08	7.3e-08	73 031	4.79
1.5	0.41	84 188	7.4e-08	6.5e-08	81 122	4.81
2.0	0.32	92 022	6.7e-08	5.9e-08	89 028	4.82
2.5	0.26	99 790	6.1e-08	5.5e-08	96 851	4.83
3.0	0.22	107 535	5.6e-08	5.0e-08	104 635	4.84
4.0	0.17	123 204	4.9e-08	4.4e-08	120 347	4.86
10.0	0.06	235 792	2.5e-08	2.3e-08	232 364	4.89

Table 4.6.1: *Estimated values for the intrinsic growth rate, r, the carrying capacity, K, and the catchability coefficient, q, for a range of fixed values for α using the general Pella-Tomlinson model (see 4.6.2). The estimated 1996 biomass, X_{1996}, is also shown for each case.*

We now consider three specific examples.

Example 1:

The growth rate, r, was fixed at a realistic value of 0.1 and the parameter estimation method was used to estimate K and α. With initial values set to $K = 2.0 \times 10^5$ mt and $\alpha = 2$, the estimated carrying capacity is $K = 178003$ mt, the shape parameter $\alpha = 5.48$ and the 1996 biomass $X_{1996} = 174243$ mt, with $q_1 = 3.3 \times 10^{-8}$ and $q_2 = 3.0 \times 10^{-8}$.

Note that the estimated biomass for 1996, X_{1996}, is close to the estimated pristine biomass. Refer to Figures 4.6.1 and 4.6.2. This corresponds to the results found in Table 4.6.1. For example, when $\alpha = 1.5$, then $K = 84188$ mt and $X_{1996} = 81122$ mt.

Example 2:

Here we extended Example 1 by incorporating both the bounds (4.6.4) and (4.6.5).

We then estimated r, K and α simultaneously. An intrinsic growth parameter value of $r = 0.042$, a carrying capacity of $K = 309957$ mt, the shape parameter $\alpha = 5.00$ and the current biomass as $X_{1996} = 90000$ mt, with $q_1 = 6.5 \times 10^{-8}$ and $q_2 = 6.1 \times 10^{-8}$ were obtained.

Although the predicted value for X_{1996} is equal to its upper bound as expected, the intrinsic growth parameter, r, is not at its lower bound.
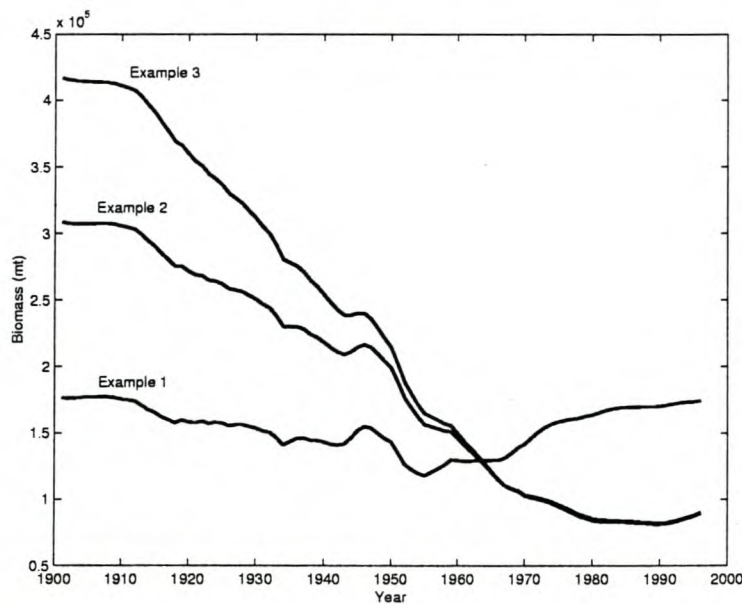
Figure 4.6.1: *Three biomass predictions of the Cape rock lobster using the initial values of (a) Example 1, (b) Example 2 or (c) Example 3.*

These results are illustrated and compared with those of Example 1 in Figures 4.6.1 and 4.6.2. The 1996 biomass level obtained in Example 2 is considerably lower than when there is no constraint on X_{1996} as in Example 1. In the case of Example 2, for the species to be able to "survive" the high catches of the 1950's (without total extinction), a relatively high carrying capacity and a low growth rate are required. Contrary to Example 1, Example 2 predicts that although the biomass was able to increase after 1992, due to the drastic decrease in catches, it still is not close to the estimated pristine level.

Figure 4.6.2 plots the estimated and actual CPUE's for Examples 1 and 2. There is no

substantial difference in the modelled CPUE series for the two examples even though there is a distinct difference in estimated values for q.
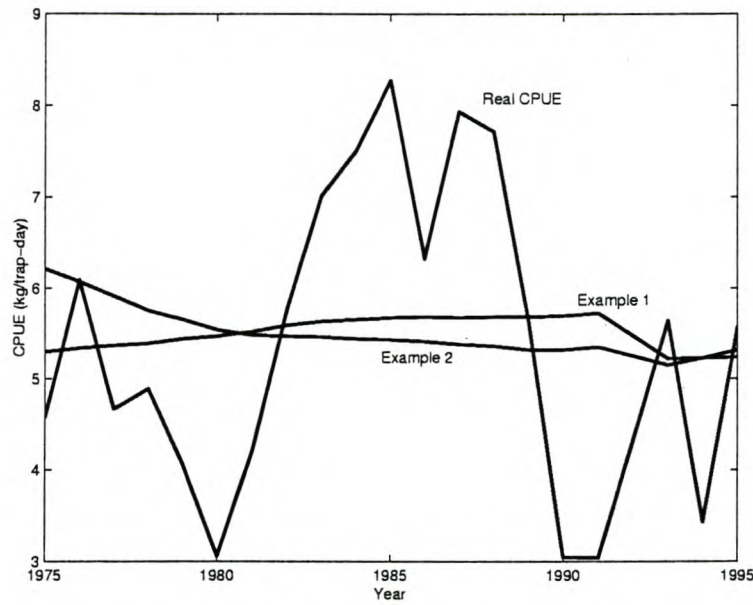
Figure 4.6.2: *The modelled and real data CPUE for (a) Examples 1 and (b) Example 2.*

Example 3:

Example 2 was repeated, but, instead of the Pella-Tomlinson production function the Schaefer production function was used, thus $\alpha = 1$. After running the model for a range of initial values it converged to a global minimum with a carrying capacity of $K = 418189$ mt, an intrinsic growth rate of $r = 0.054$ and a current biomass of $X_{1996} = 90000$ mt, with $q_1 = 6.6 \times 10^{-8}$ and $q_2 = 6.1 \times 10^{-8}$.

With the bounds placed on X_{1996} and r the estimated carrying capacity and growth rate for the Schaefer production function is higher than those for the Pella-Tomlinson function. This is an unexpected result, in the light of Table 4.6.1, where we saw that without bounds on X_{1996} and r the estimated carrying capacity increases with an increase in the shape parameter.

4.6.4   Management strategies

With the parameters as estimated above we are now able to compute the equilibrium biomass levels for the open access, MSY and MEY management strategies, using equations (4.2.4), (4.3.1) and (4.4.6). Table 4.6.2 lists the different yield and biomass levels for the three examples considered above. The yield level in each case is taken as $Y = qEX$. We used equations (4.2.4), (4.3.1) and (4.4.6) in the calculation.

	X_{OAF}	Y_{OAF}	X_{MSY}	Y_{MSY}	X_{MEY}	Y_{MEY}
Example 1	26 473	2 647	126 677	10 704	120 097	10 620
Example 2	13 208	555	216 606	7 581	80 050	3 358
Example 3	13 111	685	209 095	5 639	62 597	2 874

Table 4.6.2: *Estimated optimal biomass and yield levels (in mt) where X_{MSY} and Y_{MSY} are the biomass and yield levels for the MSY management strategy, X_{OAF} and Y_{OAF} are the equilibrium biomass and yield levels, respectively, for an open access fishery and X_{MEY} and Y_{MEY} the biomass and yield levels, respectively, for a MEY management strategy. The discount value is taken as $\delta = 5\%$, the constant price as $p = R \ 50/kg$ and the cost per unit effort as $c = R \ 40/trap\text{-}day$.*

The equilibrium biomass levels for each of the management strategies are remarkably different for each example. As expected, the equilibrium biomass level for the open-access fishery is much lower than for either a controlled MSY management strategy or for a controlled bio-economical managed fishery. *This is true for all 3 examples considered.* Also, in all three examples, the yield level of the open access fishery compares unfavourably with the yield levels of the MSY and MEY management strategy.

Note that the open access equilibrium biomass levels in all three examples are very low relative to the respective carrying capacities. For example, the biomass of 13 208 mt of Example 2 is much less than the carrying capacity of 309 957 mt. By definition the net revenue for an open access fishery is zero.

The biomass level at MSY differs considerably for the different examples. The MSY

levels are of $O(10^4)$ mt for Example 1 and $O(10^3)$ mt for Examples 2 and 3 (see Table 4.6.2). Note that for Examples 2 and 3 the MSY yield levels are less than the 10 400 mt TAC level of the 1960's (Pollock, 1986).

	R_c	C_c	NDR	R_s	C_s	P_s	TPV
Example 1	2 707	493	2 215	531	117	414	10 493
Example 2	498	77	420	168	28	140	3 224
Example 3	1 379	240	1 139	143	30	113	3 400

Table 4.6.3: *Economic values in $(R\,10^6)$ as determined by the bio-economic model (see Section 4.5). Examples 1, 2 and 3 are as in Section 4.6.3 where R_c and C_c are the revenue and cost respectively at the equilibrium biomass level, NDR the net depletion revenue, R_s the gross sustainable revenue, C_s the sustainable harvest cost, P_s the net sustainable revenue and TPV the total present value. The discount value is taken as $\delta = 5\%$, the constant price as $p =R\ 50/kg$ and the cost per unit effort as $c = R\ 40/trap\text{-}day$.*

For a fishery under sole control and MEY management the optimal yield is higher for the Pella-Tomlinson production function (Example 2) than for the Schaefer production function (Example 3) (see Table 4.6.2). The values of Clark's economic parameters for a MEY management strategy are given in Table 4.6.3. Note that the total present value is higher for Example 1 than for Example 2, because of the different yield levels.

Since we believe the results of Example 2 to be the most realistic (Johnston, 1996) we have used it to compare the economic outcome of the MSY and MEY managment options for a single owner. It is important to note that the total net present value is crucially dependent on the initial biomass, X_{1996}. The length of the time period during which no harvest is required, for the population to recover to the required biomass, that is X_{MSY} or X_{MEY}, has an important impact on the total net present value to be obtained from the fishery. Naturally the sole owner fishery with a maximum economic yield strategy, gives higher economic revenues than the MSY fishery.

Assuming a discount rate, $\delta = 5\%$, a constant price of $p =R\ 50/kg$ and a cost per unit

δ	c	p	X_{OA}	Y_{OA}	X_{MEY}	Y_{MEY}	TPV_{MEY}	TPV_{MSY}
0.03	40	50	13 208	555	176 734	6 975	6 656	6 132
0.05	**40**	**50**	**13 208**	**555**	**80 050**	**3 358**	**3 088**	**2 370**
0.1	40	50	13 208	555	22 772	956	2 636	394
0.05	38	50	12 547	527	76 514	3 211	3 126	2 377
0.05	47	50	15 519	652	91 460	3 833	3 182	2 343
0.05	50	50	16 510	693	95 866	4 015	3 007	2 331
0.05	52	50	17 170	721	98 642	4 129	3 086	2 324
0.05	40	55	12 007	504	73 540	3 086	3 474	2 622
0.06	80	100	13 208	555	80 050	3 358	6 175	4 739

Table 4.6.4: *Sensitivity of the equilibrium biomass and yield level for an open access fishery, X_{OA} and Y_{OA}, respectively, and for a MEY management strategy, X_{MEY} and Y_{MEY}, respectively. Also shown are the total present value, TPV (both for the sole owner fishery and the MSY fishery) in $R\,10^6$, associated with the different economical parameters, where δ is the discount value, c is the operating cost per unit effort and p is the unit price. Only one of δ, c and p is changed at a time and compared to the highlighted figures. In the last row both c and p is doubled.*

effort of $c = \text{R}\,40/\text{trap-day}$ the economic rent for the sole owner fishery is maximized at a biomass level of 80 050 mt with a net sustainable revenue, P_{MEY}, of $R\,140$ *million*, the net depletion value, NDR, of $R\,420$ *million* and a total present value of $R\,3$ 088 *million*. The biological optimum biomass level at MSY is 216 606 mt with a net sustainable revenue, P_{MSY}, of $R\,355,9$ *million* and a total present value of $R\,2\,370$ *million*. Table 4.6.4 compares the total present values for the MEY managed fishery with the MSY fishery for different values of the discount rate, δ, the price, p, and the cost, c. The total value for the MEY management strategy is always higher than that for the MSY management strategy irrespective of the initial biomass.

Since the economic parameters are market dependent, sensitivity tests are essential. The sensitivities of the equilibrium biomass and yield to the three economic parameters

are illustrated in Table 4.6.4. Recall that the MSY level depends only on the biological parameters. As the discount value, δ, only influences the present value of a sole owner's future income, the steady state biomass of an open access fishery is not affected by it.

As is evident from the theoretical formulation of Section 4.5, the optimal equilibrium solution depends on the cost-price ratio, c/p, rather than on their absolute values. An important conclusion is, that for certain c/p -ratios, the expected 1996 biomass, of 90 000 mt as calculated in Example 2, is less than both the MSY and MEY equilibrium levels (see Table 4.6.4). For example, for $p = R\,50/\text{kg}$ and $c = R\,47/\text{trap-day}$ the estimated value for X_{MEY} is 91 460 mt.

4.7   Conclusion

In this chapter we have studied the bio-economic principles using the basic surplus production models, describing the population dynamics. The control problem, that was formulated when the maximum economic yield is sought, was solved using the Hamiltonian theory. We compared different management strategies with respect to the sustainable population level, suitable harvest levels and the total present value earned from such fisheries. Three different management strategies, namely, an open access, a maximum sustainable yield given sole control, and a maximum economic yield management strategy given sole control, have been compared.

We have used the same surplus production functions as Kuronuma *et al.* (1994) and Cruywagen *et al.* (1994) for modelling the dynamics of the Cape Rock Lobster fishery. Rather than being concerned with actual results obtained, the relative behaviour of the models, regarding specific bio-economical objectives, were considered. Moreover, the results are also a useful indicator as to the present state of the Cape Rock Lobster resource.

A maximum likelihood parameter estimation method was used with biologically realistic restrictions on the intrinsic growth rate ($0.0 < r \leq 0.4$) and current total biomass ($20000 \leq X_{1996} \leq 90000$).

In Example 1 the unknown biological parameters, K and α were estimated while r was fixed at 0.1. No other restrictions were placed on the parameters. The results were compared with those in Example 2 where K, r and α were simultaneously estimated while restrictions were placed on both X_{1996} and r. The Pella-Tomlinson production function was used in both Examples 1 and 2.

The simpler Schaefer production function ($\alpha = 1$) was used in Example 3. Both the Pella-Tomlinson and Schaefer models, with X_{1996} and r constrained as in Examples 2 and 3, predict a very low intrinsic growth rate, namely $r = 0.042$ and $r = 0.054$ respectively. This low growth rate is consistent with the fact that the fishery has been very slow to recover since the overfishing of the 1950's.

The reliability of the parameter estimation procedure depends heavily on the accuracy of the data. According to Goosen (1995) the possibility of inaccuracies in the CPUE data should not be ignored; therefore to rely solely on the CPUE data could give misleading results.

We have reason to believe that the population did not recover from the high catches in the 1950's as indicated by Example 1. Our belief stems from the fact that fishers had been unable to land the total allowable catch (TAC) for several successive seasons. For example, the annual landings for 1968 and 1980 were 6 200 mt and 4 548 mt respectively, while the TAC's for these years were 10 400 mt and 4 796 mt, respectively (Pollock, 1986). We believe the predictions of Example 2 to be a reasonable indication of the real situation. Note, however, that most of our conclusions rest on the assumption that $20000 \leq X_{1996} \leq 90000$.

An alarming conclusion on the one hand, but encouraging on the other hand, is that, for some price-cost ratios, the optimal biomass level for the MEY fishery and the MSY fishery is higher than the current estimated biomass of 90 000 mt. According to Clark's (1990) bio-economical model (see Section 4.5) this implies that a zero harvest ($h = 0$) has to be applied for optimal recovery to the steady state optimal level. *Recall that the TPV is only attainable at an optimal biomass level and, in order to maximize profit, the fishery should be managed along the optimal biomass "path".*

Note that a MEY management strategy results in a higher total present value. The results of Kuronuma *et al.* (1994) bio-economic studies on the Antarctic minke whale were similar and lead to the conclusion that the MEY management option will be the better choice of the three discussed here.

However, it is important to note that our analysis is true only for constant values of price and cost. The supply-demand characteristics which influence price, p, and cost, c, have been ignored.

Another shortcoming of the model discussed here is the assumption of linear dependence between total economic revenue, P, and the price, p. Further work should be carried out to investigate non-linear relationships.

This chapter was an attempt to contribute towards the search for an optimal management strategy for the rock lobster fishery. An attempt was made to provide a framework for possible alternative management strategies. Moreover, our results confirm the conclusions of other modelling efforts that the Cape Rock Lobster resource has been overexploited (see Cruywagen *et al.* 1994 and Johnston 1996).

In further chapters we use more involved biological models to examine further.

Chapter 5

Delay Difference Models

The surplus production models of the previous chapter assume that the various factors affecting the population, such as harvesting or weather, can be accounted for instantaneously. In other words, no historic information that might have an impact has been incorporated. In reality however, the entire life history of the population is important as some events do have an immediate and homogeneous impact on a population's structure. A natural way to model these long term effects on the population dynamics is by using delay difference equations. The use of such discrete time population models is popular in fishery management strategies as is the case, for example, with the Pacific salmon fishery (Clark, 1990).

In many species there is no overlap of generations and population growth can therefore be modelled in discrete time intervals. Typically this is always the case for insect populations. The standard model reads,

$$N_{t+1} = F(N_t),$$

where N_t is the density of the population at time t and $F(N_t)$ is the recurrence function. Note that the population density at time $t + 1$ depends entirely on the population density at time t. Non-overlapping species require one time interval to reach sexual maturity. For simplicity we assume from here onwards that one time interval is equal to one year.

Even the simplest non-overlapping species, described by the above nonlinear difference equation, have remarkable and varying dynamical behaviour that depends on the functional form of F and on the biological parameters, such as the intrinsic growth rate, appearing within the function F. The difference equation may have a stable equilibrium solution which bifurcates into two, four or even eight point cyclical oscillations as the intrinsic growth rate increases. For even larger values of this parameter the system becomes chaotic. So, depending on the values of the biological parameters, solutions may fluctuate within some bounded area with different periodic or a-periodic cycles (May, 1974).

In this chapter we wish to address two extensions to the surplus production models discussed in the previous chapter. The first is that, with many species, recruitment to the breeding population takes place only some years after birth and not instantaneously as assumed by the surplus production model. In other words, sexual maturity is reached only after a few years. In the management of species with a low fecundity, like whale and seal populations, the relationship between the spawning stock and recruitment is crucial and is therefore usually modelled by non-linear delay difference equations (Goh, 1980). Secondly, stock-recruitment functions are density dependent or density independent, referring to the relative mortality rate of the species. The relative mortality rate of juveniles can be written as:

$$\frac{1}{N}\frac{dN}{dt} = -(\mu_1 + \mu_2 N),$$

where N is the number of juveniles, μ_1 is the *density independent* mortality rate and μ_2 the *density dependent* mortality rate. Thus, a proper stock-recruitment relation should be determined carefully. Popular recruitment functions are discussed in Section 5.1.1.

In Section 5.1 we review various studies that have been carried out on delay difference models for *monoecious* species, that is, species where only one gender occurs. More specifically we discuss the recruitment functions, stability, harvesting and optimal strategies as studied by various scientists. Clark (1976) has studied the stability of the equilibria and the optimal harvesting conditions associated with the delay difference model. He applied this model to the Baleen whale populations. In Section 5.2 we next

investigate a two-sex delay difference model - a model in which the two genders are treated separately. Such species, where gender is distinguished, are called *dioecious* species. The model is analysed in detail and extended to include a bio-economic analysis. In Section 5.3 we apply the two-sex delay difference model to the Cape Rock Lobster species.

5.1   Monoecious Delay Difference Models

The population structure of any developed species, like birds or fish, includes both sexually mature and immature individuals, depending on their age. Thus, sexual maturity should be incorporated into the difference equation. A possible density dependent mechanism is

$$N_{t+1} = N_t F(N_{t-T}), \qquad (5.1.1)$$

where T represents the delay factor (Levin *et al.*, 1976). A delay of T years implies that it takes a newborn $T+1$ years to reach sexual maturity. In this case, competition might occur, where the current density affects the density of next year. Also note that the total number of individuals born to a certain year class is dependent on the size of the sexually mature population or spawning stock at that time.

In cases where recruitment (that is the number of newborns that reach spawning age) is assumed to be independent of the current population and a proportion of the current population survives to the next year, it is more convenient to use slightly modified delay difference models. These models could be used instead of the more complicated age-structured models, which will be discussed in Chapter 6. Assume also that the recruitment depends entirely on the density of the population $T+1$ years earlier. Now

$$N_{t+1} = \sigma N_t + F(N_{t-T}), \qquad (5.1.2)$$

where σ $(0 < \sigma < 1)$ is the survival coefficient and F the recruitment function (Botsford, 1992).

In Section 5.1.1 we discuss properties of the stock-recruitment relation with special reference to the Beverton-Holt function and the Ricker function. Then in Section 5.1.2 the stability of steady state solutions for these functions is investigated. The population size may oscillate between two steady states for certain parameter values; for even greater parameter values the behaviour may be described as chaotic. This dynamical behaviour is described in Section 5.1.3. In Section 5.1.4 the model is extended to include harvesting and a general bio-economic steady state population level is determined in Section 5.1.5.

5.1.1 The Recruitment Function

Stock-recruitment analysis concerns the empirical relationship between the spawning stock (or mature population) and the recruitment of individuals to the spawning stock. Usually it is the spawning stock that is controlled by the fishery management procedures. A thorough knowledge of all life stages prior to joining the mature population is thus necessary to be able to predict the effect that a possible change in the spawning stock might have on recruitment.

Observed data sets sometimes give a relatively clear relation between stock and recruitment. See for example studies on the Skeena River Sockeye salmon or the Icelandic Summer spawning herring (Hilborn *et al.*, 1992). The recruitment relationship is, however, not always as clear. Analysis of these data sets usually includes curve fitting procedures. As Hilborn *et al.* (1992) point out, one should not mistake the average curves for the real relationship; such a relationship is not totally predictable, since stochastic properties also exist. A stock-recruitment curve attempts to describe how the mean recruitment rate varies with stock size. Other observable relationships common to most stock-recruitment data sets, discussed by Hilborn *et al.* (1992), are:

(1) Large spawning stocks produce larger recruitment.

(2) The increase in recruitment starts dropping relative to the increase in spawning stock at large populations. Recruitment can sometimes decrease when the

spawning population becomes too large.

(3) Data points are usually scattered, and the stock-recruitment relationships may not be clear.

(4) The variability about the stock-recruitment curve is often higher for larger spawning stock sizes.

Thus, good techniques to measure stock size and the resulting recruitment are paramount for establishing a clear and reliable stock-recruitment relationship.

Four basic properties of stock-recruitment functions were listed by Ricker (1975).

(1) The graph of the function should intersect the origin, so that no parental stock implies no recruitment.

(2) The function should remain positive at high stock levels because reproduction should not be eliminated completely.

(3) The rate of recruitment (recruits-per-spawner) should decrease continuously with increasing parental stock. This sets a limit on population size.

(4) Recruitment must exceed parental stock over some subset of possible parental stocks. This ensures growth in population size at low stock levels.

Hilborn *et al.* (1992) added two additional properties, namely

(5) The average recruitment function should be continuous. There should be no discontinuities or rapid changes in recruitment for a very small change in spawning stock sizes. It is rather difficult to conceive that there could be a large difference in recruitment if the spawning stock were 101 000 instead of 100 000.

(6) The function should be time independent. Historical data may be used in future predictions, unless recruitment depends on external factors, such as the environment.

For obvious reasons we note that property (4) is mostly applicable to semelparous species (those who spawn only once), such as the Pacific salmon.
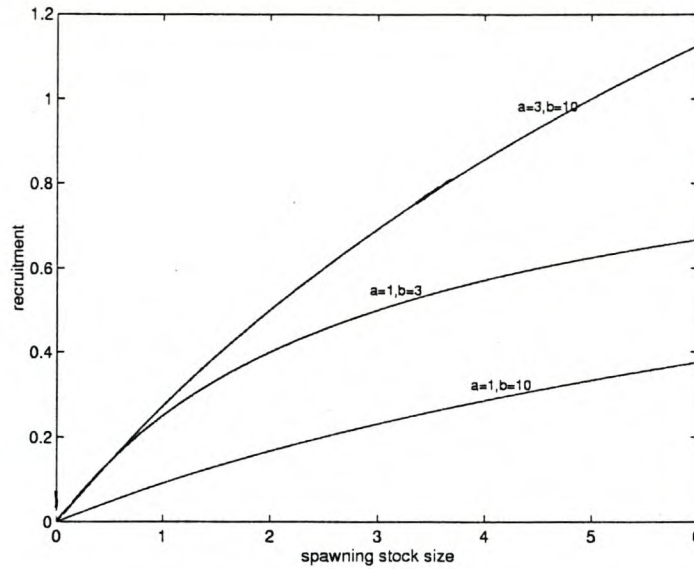
Figure 5.1.1: *The Beverton-Holt stock-recruitment function,* $F(S) = \frac{aS}{b+S}$. *Here the function is given for different values for a and b.*

Two curves that meet these requirements, namely, the Beverton-Holt (Beverton *et al.*, 1957) and Ricker (1954) stock-recruitment relations are widely used. With the Ricker model we make the biological assumption that the mortality rate of the eggs and juveniles is stock dependent rather than density dependent. The Ricker function therefore is applicable to cases of cannibalism, disease transmission, damage done by adults to spawning sites and density dependent growth coupled with size dependent predation.

The Beverton-Holt function, on the other hand, is usually applicable where competition for food and space occurs, where density dependent properties are modelled (Hilborn *et al.*, 1992).

The Beverton-Holt recruitment function is given by

$$F(S) = \frac{aS}{b+S},$$

where S represents the total number of spawning stock, a the maximum number of recruits produced and b the spawning stock needed to produce recruitment equal to $\frac{a}{2}$. Figure 5.1.1 is a graphical illustration of this function. It is bounded from above and approaches this upper bound as $S \to \infty$.
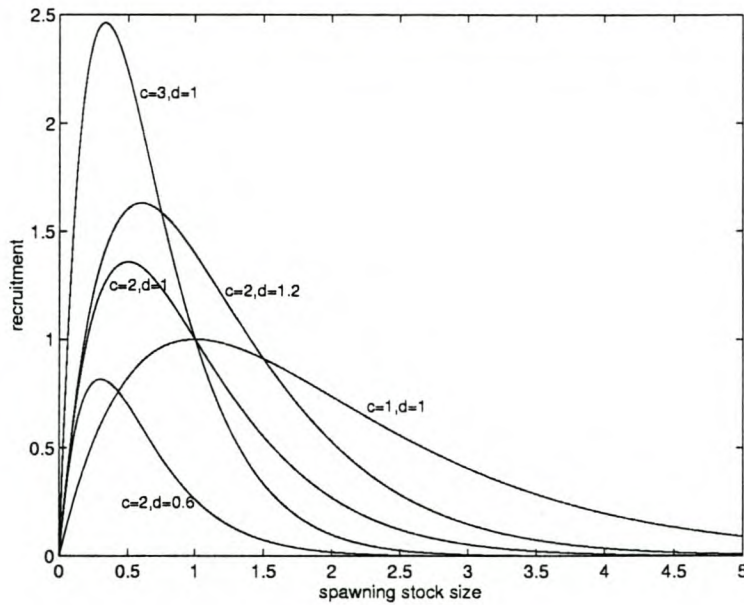
Figure 5.1.2: *The Ricker stock-recruitment function,* $F(S) = Se^{c\left(1-\frac{S}{d}\right)}$, *where the function is given for different values for c and d.*

The Ricker stock-recruitment function has the form

$$F(S) = Se^{c\left(1-\frac{S}{d}\right)}, \tag{5.1.3}$$

where c denotes the initial slope of the curve and d the value of S for which recruitment equals stock size. The function is illustrated in Figure 5.1.2. It differs from the Beverton-Holt function in that it declines with high stock sizes.

According to Hilborn *et al.* (1992) the "average" stock-recruitment relations of most species are captured by one of these two functions and it is seldom necessary to use more complex descriptions.

The Deriso function (1980), often mentioned along with the previous two functions, is

a generalization of them. This function is given by

$$F(S) = aS\left(1 - bcS\right)^{\frac{1}{c}},$$

where a, b and c are parameters determining the shape. It reduces to a Beverton-Holt function for $c = -1$, and to a Ricker function for $c = 0$.

5.1.2   Steady State Solutions

A necessary and sufficient condition for an equilibrium population size, N^*, of any discrete model

$$N_{t+1} = f(N_t)$$

to be locally stable is that the eigenvalue $\lambda = f'(N^*)$ should satisfy $|\lambda| < 1$ (see proof in Clark, 1990). We can apply this to the stock-recruitment functions discussed in the previous section. At the equilibrium population, N^*, the Ricker function satisfies

$$\begin{aligned}
N^* &= f(N^*) \\
&= N^* e^{c\left(1 - \frac{N^*}{d}\right)},
\end{aligned}$$

from which the eigenvalue $\lambda = \left(1 - \frac{c}{d}N^*\right) e^{c\left(1 - \frac{N^*}{d}\right)}$ may be calculated. When $N^* = d$ the condition for stability is $|1 - c| < 1$ or $0 < c < 2$. The population's behaviour outside this stability interval will be addressed in the next section.

Also for the Beverton-Holt function, at equilibrium $f(N^*) = \frac{aN^*}{b+N^*}$ (using property (3) of Ricker, listed in Section 5.1.1), satisfies the stability condition, as

$$f'(N^*) = \frac{a}{(b + N^*)^2} < 1.$$

Thus, any value of N^* will always represent a stable population density when applying the Beverton-Holt model.

Clark (1976) studied the stability of the delay difference model (5.1.2) at equilibrium, where

$$(1 - \sigma) N^* = F(N^*),$$

using a similar procedure as discussed above. The stability condition then becomes

$$\left| F'(N^*) \right| < 1 - \sigma.$$

To study the stability of the steady state solution, N^*, we linearize equation (5.1.2) about N^*. Let $N_t = N^* + v_t$ where $|v_t| \ll 1$ and assume that $v_t \propto z^t$. If we substitute this relation in equation (5.1.1), then

$$
\begin{aligned}
N^* + v_{t+1} &= \sigma(N^* + v_t) + F(N^* + v_{t-T}) & (5.1.4) \\
&= \sigma N^* + \sigma v_t + F(N^*) + F'(N^*)v_{t-T} + O\left(v_{t-T}^2\right). & (5.1.5)
\end{aligned}
$$

At the steady state we have

$$N^* = \sigma N^* + F(N^*),$$

therefore

$$v_{t+1} = \sigma v_t + F'(N^*)v_{t-T} + O\left(v_{t-T}^2\right),$$

or

$$z^{t+1} = \sigma z^t + F'(N^*)z^{t-T} + O\left(z^{2t-2T}\right).$$

The linearized relation is

$$z^{t+1} = \sigma z^t + z^{t-T} F'(N^*)$$

or

$$z^{T+1} - \sigma z^T - \lambda = 0. \qquad (5.1.6)$$

Thus, for stability, the linearized equation (5.1.6) should have roots with modulus $|z| < 1$. Clark (1976) studied the stability of different delay values. Clearly, when

$T = 0$ then $z = \sigma + \lambda$ and the roots of (5.1.6) satisfy the stability condition if and only if

$$-1 - \sigma < \lambda < 1 - \sigma.$$

The lower bound for stability for the quadratic equation, where $T = 1$, is determined using $-1 < z$. Then $\lambda = (z - \sigma)z > \sigma - 1 > -1$. To determine the upper bound we use the root $z_1 = \frac{\sigma + \sqrt{\sigma^2 + 4\lambda}}{2}$ and the condition $z < 1$. Thus we find

$$-1 < \lambda < 1 - \sigma.$$
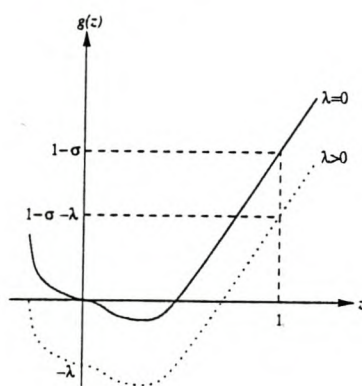
Figure 5.1.3: *The graphical representation of $g(z) = z^T(z - \sigma) - \lambda$ where T is even.*

In fact the upper bound, for any $T > 1$ is $1 - \sigma$. This result is easily found graphically as seen in Figure 5.1.3. (A similar graph could be given for the case were T is odd.) We say $g(z) = z^T(z - \sigma) - \lambda$, then it is clear that if $\lambda > 1 - \sigma$ the root of $g(z)$ is outside the stability interval for $z < 1$.

To find the lower stability bound, note that equation (5.1.6) must have a root $z = e^{i\theta} = \sin\theta + i\cos\theta$ of modulus one. Then equate the real and imaginary parts to be

$$\sin(T + 1)\theta - \sigma \sin T\theta = 0$$
$$\cos(T + 1)\theta - \sigma \cos T\theta = \lambda,$$

which can be solved numerically.

Various studies were also conducted on other recruitment functions. For example, Goh *et al.* (1977) investigated how the survival coefficient, α, and the delay time, T, influences stability using the model $F(N_t) = A\,N_t e^{-B\,N_t^2}$ in equation (5.1.2). They found that the survival coefficient, σ, has a stabilizing influence on the population size for a delay factor, $0 \leq T \ll 1$, but that for longer time delays, this is destabilizing. The time delay has a stronger effect on the population's stability than the survival factor, except for σ close to 1.

(i)

(ii)
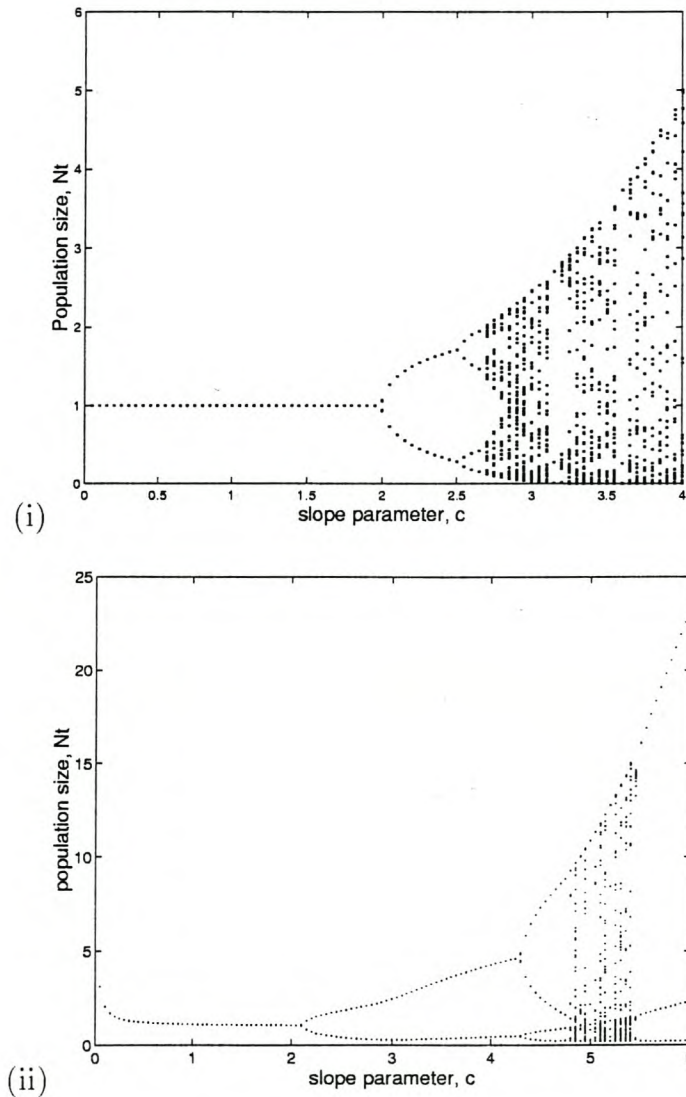
Figure 5.1.4: *The dynamical solution at equilibrium, using the Ricker function without any delay. Take survival, σ, as (i) 0.0, and (ii) 0.1.*

5.1.3   Bifurcation and Chaotic Solutions

Outside the stability region, that was discussed in Section 5.1.2, the steady state solution may bifurcate. This section studies the dynamic solution outside this reqion.

In nature population sizes may fluctuate quite dramatically. Such fluctuations could arise because of random external factors, or alternatively as a result of chaotic population dynamics. In practice it is difficult to distinguish whether such fluctuating behaviour is the result of either *random* environmental events or *chaotic* dynamics. Studying the general, non-linear behaviour of a population model can provide insight into possible chaotic behaviour. In other words the non-linear population model might admit chaotic solutions under reasonable parameter choices. This may well be the explanation for observed fluctuations in a population. Botsford (1992) addressed the question of what the effect of an added age structure on the behaviour of the biological system (5.1.2) is. That is, how does the biological process change when a fraction of the parental stock survives to the next year.

May (1974) showed that, by using the general Ricker function (5.1.3) in equation (5.1.2) (where no survival, or delay factors are included), the steady state population size becomes unstable to give oscillating solutions once the bounds of stability have been overstepped. For $N^* = d$ in the Ricker function the stability interval is $0 < c < 2$. Figure 5.1.4(i) illustrates the dynamic solution of the Ricker stock-recruitment function. There occur a sequence of periodic doublings as the parameter c increases. The values for c where bifurcation occurs, are listed in Table 5.1.1.

The behaviour becomes chaotic (in the sense that no pattern could be recognized) for larger values, that is greater than the critical value $c^* = 2.692$ (May, 1974).

We also investigate the stability intervals when a survival factor is included. Such information could not be found in the literature and is done here for the first time, to the knowledge of the author. Table 5.1.2 lists approximate values for the parameter c where bifurcation occurs, given that a survival factor is introduced. Here the factor is taken as $\sigma = 0.1$. (See also Figure (5.1.4 ii)). Note the increase in the stability interval

Behaviour	Value of the parameter, c
stable steady state	$0 < c < 2$
2-point cycle	$2 < c < 2.526$
4-point cycle	$2.526 < c < 2.656$
chaos	$c > 2.692$

Table 5.1.1: *Dynamical behaviour of equation (5.1.2), with survival $\sigma = 0.0$, using the Ricker function $F(N_t) = N_t e^{c\left(1 - \frac{N_t}{d}\right)}$.*

with the addition of the survival factor compared to the results of Table (5.1.1).

Behaviour	Value of the parameter, c
stable steady state	$0 < c < 2.084$
2-point cycle	$2.084 < c < 4.225$
4-point cycle	$4.225 < c < 4.739$
chaos	$c > 4.81$

Table 5.1.2: *Dynamical behaviour of equation (5.1.2), with survival, $\sigma = 0.1$, using the Ricker function $F(N_t) = N_t e^{c\left(1 - \frac{N_t}{d}\right)}$.*

Botsford (1992) studied the discrete delayed-difference Ricker model where

$$N_{t+1} = \sigma N_t + N_{t-T} \exp\left(c \left(1 - \frac{N_{t-T}}{d} \right) \right), \qquad (5.1.7)$$

with σ the survival parameter and T the delay period. He found that with the addition of age (that is, the inclusion of the survival factor) to the model, the interval on the factor c, where stability occurs, increased compared to the model without survival. Figures 5.1.4, 5.1.5 and 5.1.6 compare the stable, periodic and chaotic interval for various values of σ and T. Figures 5.1.4 and 5.1.5 show that while T is kept fixed, the stability interval increases, while the critical values for chaos also increase for c. Practically this means that a much steeper stock-recruitment relation (larger c) is necessary to model chaos in a population with overlapping generations than in the case where the life expectancy of an individual is one year. The results of Figure 5.1.6,
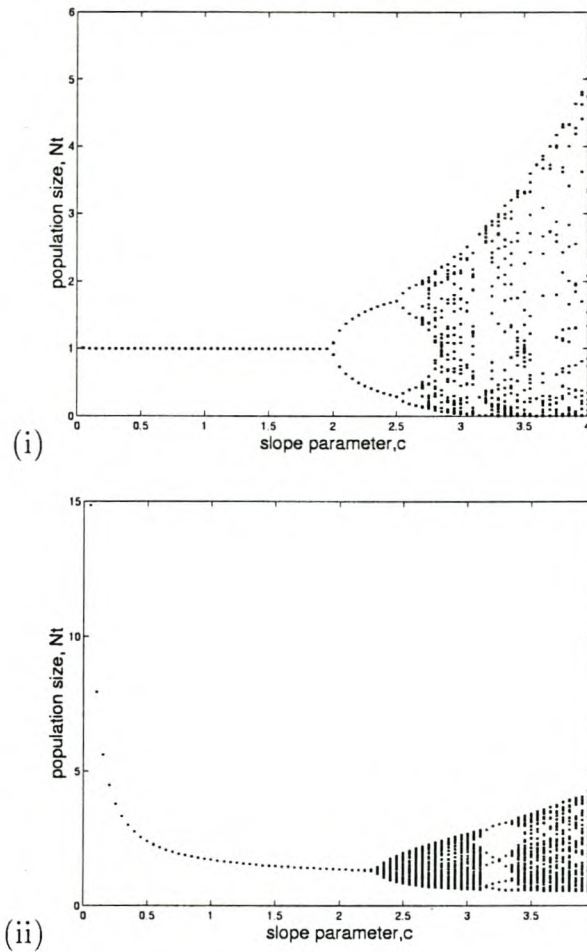
Figure 5.1.5: *The dynamical solution at equilibrium, using the Ricker function with the delay taken as 1. Take survival, σ, as (i) 0.0, and (ii) 0.5.*

are not exactly the same. Here the effect of the time delay, T, dominates the outcome and a high survival factor, σ does not increase the range over which c gives a stable solution.

Another conclusion may be drawn from these results. Contrary to the addition of age, the addition of the delay factor is destabilizing to the outcome. We have already stated that the time delay dominates the effect of the survival factor and therefore investigate only the case where $\sigma = 0$. Figure 5.1.7 illustrates that the stability interval decreases with increasing delay, T. This result was proven by Botsford (1992) for the case where $\sigma = 0$. Although not proven here we have illistrate his results for a more general case.

(i)

(ii)
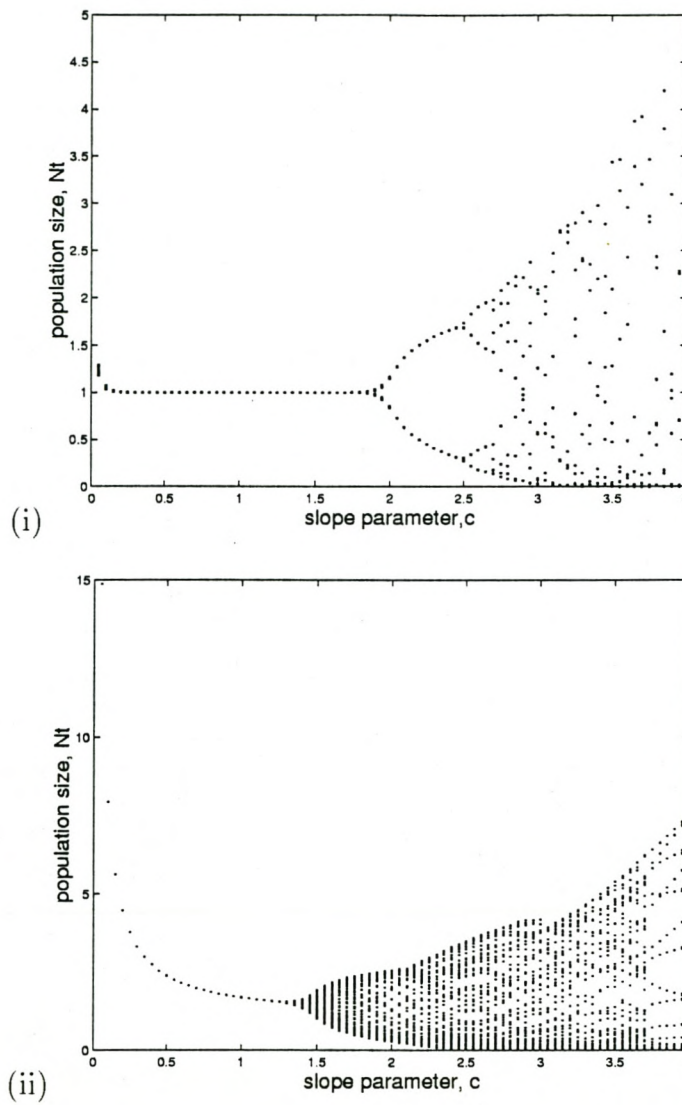
Figure 5.1.6: *The dynamical solution at equilibrium, using the Ricker function with the delay taken as 6. Take survival, σ as (i) 0.0, and (ii) 0.5.*
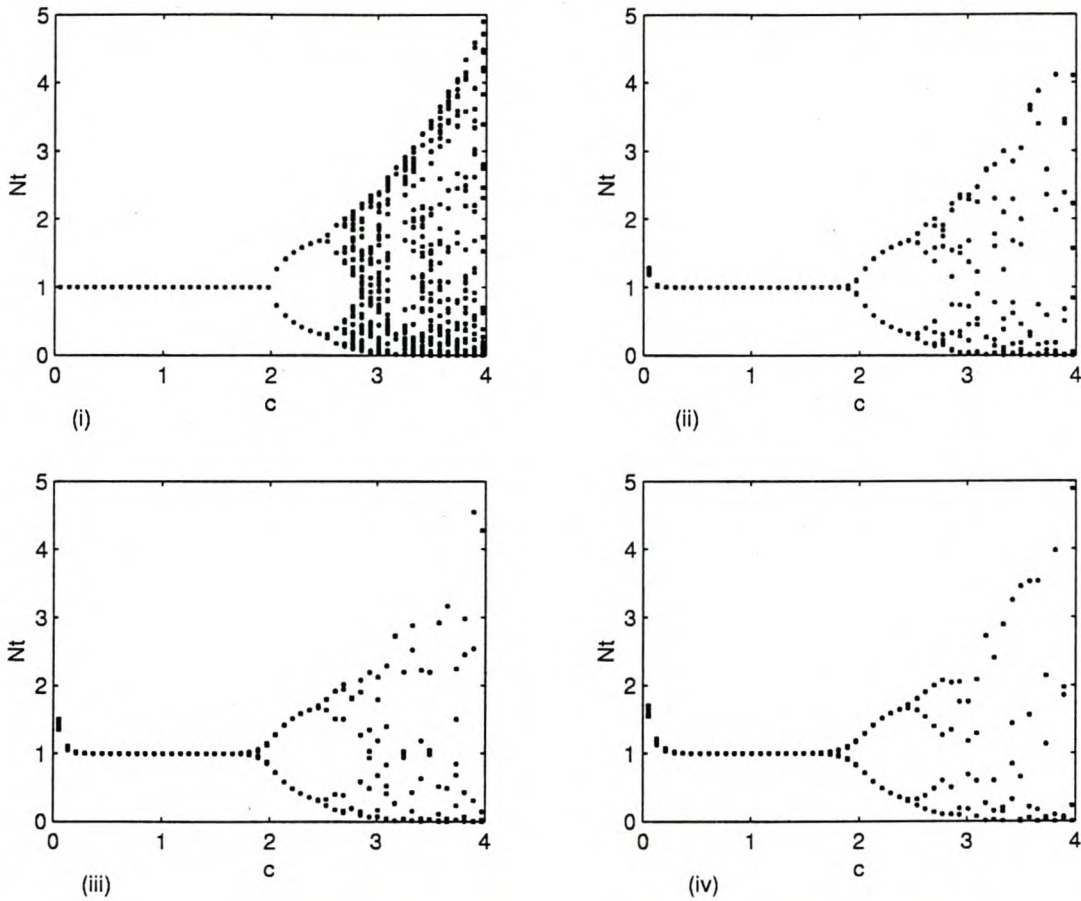
Figure 5.1.7: *The dynamical solution at equilibrium of the Ricker function with parameters (i)* $\sigma = 0$, $T = 0$, *(ii)* $\sigma = 0$, $T = 6$, *(iii)* $\sigma = 0$, $T = 10$, *(iv)* $\sigma = 0$, $T = 15$.

These results, namely that time delay is destabilizing and survival is stabilizing, confirm the results of Section 5.1.2. We have shown in Section 5.1.2 that no bifurcation will occur for the Beverton-Holt stock-recruitment function as any equilibrium value will be stable. This could easily be described graphically in the manner above.

5.1.4 Harvesting

As a next step harvesting is added to the basic delay difference model (5.1.2). Suppose the population is subject to harvesting and h_t indicates the number of individuals

harvested every year. Let the population at time t, remaining after harvesting, be $S_t = N_t - h_t$. Assume that the harvesting takes place during the time interval $[t, t + \Delta t]$, where Δt is small. Assume further that reproduction takes place during the interval $[t + \Delta t, t + 1 - \Delta t]$ and that recruitment occurs during the time interval $[t + 1 - \Delta t, t + 1]$. This implies that recruitment occurs after harvesting and so $F(N_{t-T})$ is replaced by $F(N_{t-T} - h_{t-T})$ in equation (5.1.2). Furthermore, survival is measured as a proportion of the remaining population, after harvesting. Thus the first term in equation (5.1.2) is replaced by $\sigma(N_t - h_t)$. So,

$$N_{t+1} = \sigma S_t + F(S_{t-T}). \tag{5.1.8}$$

Here, σS_t represents the numbers of adults at year t surviving to the next year and $F(S_{t-T})$ denotes the numbers of juveniles from the spawning stock of year $t - T$, which have survived to become members of the breeding population.

Goh *et al.* (1977) have demonstrated that a maximum sustainable yield can be achieved under constant effort harvesting. We prefer a bio-economic approach, as described in the following section.

5.1.5 Bio-economic Model

Finally we introduce the bio-economic aspects to the model. As in Chapter 4 we determined a harvesting level for which economic wealth is maximized. The following model is taken from the work of Clark (1990). Denote the effort at time, τ, by $E(\tau)$, where τ falls in the fishing season so, $t \leq \tau \leq t + \Delta t$. Assume the stock size at time τ is denoted by $n(\tau)$, then $n(t) = N_t$ and $n(t + \Delta t) = N_t - h_t$ with

$$\frac{dn}{d\tau} = -qE(\tau)\rho(n), \tag{5.1.9}$$

as Δt tends to 0. As in Chapter 4, q is the catchability constant and $\rho(n)$ the concentration profile of the species.

As in the previous chapter take c as the cost per unit effort. We suppose that the cost, C, at time τ, is proportional to the effort, E, so that

$$
\begin{aligned}
C(\tau)d\tau &= \frac{-c}{q\rho(n)}dn \\
&= -c'(n)dn.
\end{aligned}
$$

The total seasonal cost is

$$
C_t = \int_t^{t+\Delta t} C(\tau)d\tau = \int_{N_t-h_t}^{N_t} c'(n)dn.
$$

The net revenue for period k will be equal to

$$
\pi(N_k, h_k) = ph_k - C_k = \int_{N_k-h_k}^{N_k} \left[p - c'(n)\right]dn,
$$

where p is a constant price. The total value of all future net revenue, namely the present value, is then

$$
PV = \sum_{k=1}^{\infty} \pi(N_k, h_k)\alpha^{k-1},
$$

where $\alpha = \frac{1}{1+i}$ and i is the discount rate. The equilibrium population, S^*, for this problem that maximizes the present value subject to equation (5.1.8), satisfies the equation

$$
F'(S^*)\frac{p - C\left(F\left(S^*\right)\right)}{p - C(S^*)} = \frac{1}{\alpha}
$$

(Clark, 1990).

5.2   Sex-structured Delay Difference Models

In some species one distinguishes between gender at certain stages in their lifetime. Such species are called dioecious species. Important considerations in the life cycles of sexes are mortality, growth and development, and fecundity. As discussed by Caswell *et al.* (1986) the male mortality of humans almost always exceeds female mortality. They have addressed some other significant differences among sexes in nature. Often females reach maturity later than males. For example the mature female turtle

Pseudemys scripta is 2.7 - 3.2 times the age of the males while in some freshwater fish species females are about 1.3 times the age of males at maturity (Bell, 1980). Other experiments showed that sex-specific predation rates of freshwater copepods (*Diaptomus*) occur (Maly, 1970).

Sexual dimorphism in fish species is of significance in population dynamics, as for instance the growth rate of the two sexes may differ. It has therefore become important to extend the delay model (5.1.2) to a two-sex model as was done by Cruywagen (1996a). He investigated the effect of the delay time on the stability and also the effect of a constant effort harvesting strategy on a population's stability. We discuss some of these results here. In Section 5.2.1 we discuss the recruitment model that was proposed by Cruywagen (1996a). As was the case for the monoecious species a periodic solution results for specific parameter values. These bifurcations to two-, four- or eight-cyclic solutions is discussed in Section 5.2.2. We include harvesting in the model in Section 5.2.3 and discuss the stability of the steady state solutions in Section 5.2.4. A general bio-economical steady state solution is determined in Section 5.2.5.

5.2.1 The Recruitment Model

First extend the model (5.1.2) that was investigated in the previous section, so that males and females are incorporated. Let N_t^m represent the number of males at time t, while N_t^f represents the number of females at time t. Assume the survival factors for male and females to be σ_m and σ_f respectively and the time delay factors u and v respectively of the male and female population. Define the non-harvested population model with a sex-structure as

$$
\begin{aligned}
N_{t+1}^m &= \sigma_m N_t^m + H(N_{t-u}^m, N_{t-u}^f) \\
N_{t+1}^f &= \sigma_f N_t^f + G(N_{t-v}^m, N_{t-v}^f),
\end{aligned}
\tag{5.2.1}
$$

where $H(N^m, N^f)$ is the number of recruits that will develop into males and $G(N^m, N^f)$ is the number of recruits that will develop into females (Cruywagen, 1996a).

The recruitment functions in Section 5.1.1 are valid for monoecious populations. For dioecious populations the relative proportions between males and females become important and will be modelled here.

First we wish to define the recruitment function. Let the function $\psi(N^m, N^f)$ represent the number of zygotes produced as a proportion of the number produced when an unlimited number of males are available. Then the number of zygotes, $n(t)$, produced by the mature population in year t is

$$n(t) = N_t^f \psi(N_t^m, N_t^f)$$

According to Bergh (1991), for the function $\psi(N^m, N^f)$ to be biologically realistic it should satisfy the following assumptions:

(1) $\lim_{N^m \to \infty} \psi(N^m, N^f) = 1$, that is, all female gametes are fertilized when there is an unlimited abundance of males.

(2) $\lim_{N^f \to \infty} \psi(N^m, N^f) = 0$ for all N^m, that is, the proportion of female gametes fertilized is zero when the ratio of females to males is infinite.

(3) $\lim_{N^f \to 0} \psi(N^m, N^f) = k(N^m)$, that is, for a given N^m the function $\psi(N^m, N^f)$ tends to a limited value determined by the size of N^m, as N^f tends to 0. Taking spatial considerations into account it is reasonable to assume that $\lim_{N^m \to 0} k(N^m) = 0$. That is, the chances of a few mature males and females meeting in a large area are very small.

Bergh (1991) proposed using the modified harmonic mean marriage function

$$\psi(N^m, N^f) = \frac{N_t^m}{\kappa + N_t^m + N_t^f}, \qquad (5.2.2)$$

which does meet the above assumptions. Here, κ is positive and real. This function is an adaptation of the reliable harmonic mean marriage function that is used to model mammal populations (Caswell *et al.*, 1986).

Figure 5.2.1: *The dynamical solution at equilibrium of the two-sex model (5.2.1) using equation (5.2.3) and (5.2.4). (i) Male stock against parameter c', (ii) Female stock against parameter c', where $k_f = 0.4$, survival, $\sigma = 0.0$, and male and female delay factors $u = v = 0.0$.*

Here we use function (5.2.2) to define the recruitment functions H and G. It is likely that in certain populations the number of male to female zygotes are not equal and this is addressed in the model. Let k_m and k_f $(=1 - k_m)$ be the proportion of the zygotes that are males and females respectively. Since there is a delay of u years for males and v years for females before the zygotes become mature, population density at each year is important and should be incorporated. In terms of the model above this implies that

$$H(N^m, N^f) = k_m F(n) \text{ and } G(N^m, N^f) = k_f F(n),$$

where $F(n)$ is the stock recruitment function (Cruywagen, 1996a). If $F(n)$ is the Ricker function as described in Section 5.1.1, then

$$H(N^m, N^f) = k_m n(t - u) \exp\left(c\left(1 - \frac{n(t - u)}{d}\right)\right)$$

and

$$G(N^m, N^f) = k_m n(t - v) \exp\left(c\left(1 - \frac{n(t - v)}{d}\right)\right)$$

or

$$H(N^m, N^f) = k_m \frac{N^m_{t-u} N^f_{t-u}}{\kappa + N^m_{t-u} + N^f_{t-u}} \times \exp\left[c'\left(1 - \frac{N^m_{t-u} N^f_{t-u}}{\kappa + N^m_{t-u} + N^f_{t-u}}\right)\right], \qquad (5.2.3)$$

and

$$G(N^m, N^f) = k_f \frac{N^m_{t-v} N^f_{t-v}}{\kappa + N^m_{t-v} + N^f_{t-v}} \times \exp\left[c'\left(1 - \frac{N^m_{t-v} N^f_{t-v}}{\kappa + N^m_{t-v} + N^f_{t-v}}\right)\right], \qquad (5.2.4)$$

where c' is a constant, for the Ricker function in a slightly different form.

5.2.2 Periodic Solutions and Bifurcations

Here we now address the assumption made by Botsford (1992) namely, that all individuals contribute equally to recruitment. This section goes further than the studies by Botsford and differentiates between the sexes. We use functions (5.2.3) and (5.2.4) in the two-sex delay difference model (5.2.1) and investigate the effect of an added age structure on the model compared to the model in Section 5.1.3 (equation (5.1.7)) by plotting the numerical solution of N^m and N^f over a number of time steps (for example 100 steps) after it has reached equilibrium (we take it that the system has reached equilibrium after 100 steps) as function of c'.
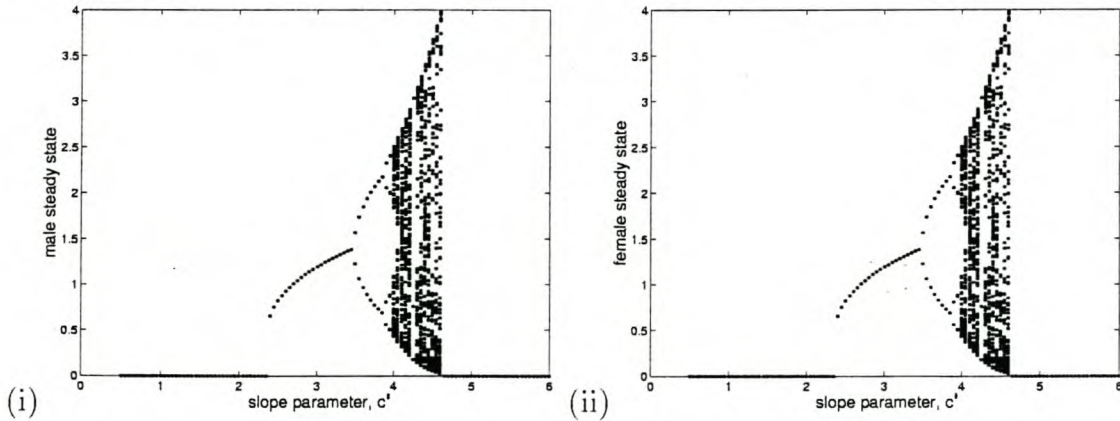
Figure 5.2.2: *The dynamical solution at equilibrium of the two-sex model (5.2.1) using equations (5.2.3) and (5.2.4). (i) Male stock against parameter c', (ii) Female stock against parameter c', where $k_f = 0.5$, survival, $\sigma = 0.0$ and delay factors, $u = v = 0.0$.*

Example 1

Figure 5.2.1 illustrates the dynamical solution of model (5.2.1) for the first example where we have taken $u = v = 0.0$ and $k_f = 0.4$. Similar results are found compared to

those of Section 5.1.3. Note that a series of bifurcations occur. These bifurcations are simultaneous for male and female populations. The regions for periodic solutions are listed in Table 5.2.1 with the interval for a stable steady state being $0.0 < c' < 3.47$. In this example we see that a smaller proportion of zygotes develop into females ($k_f = 0.4$), which causes a female steady state solution which is less than that of the males.

	Example 1	Example 2	Example 3
	$k_f = 0.4$	$k_f = 0.5$	$k_f = 0.5$
	$\sigma_m = \sigma_f = 0.0$	$\sigma_m = \sigma_f = 0.0$	$\sigma_m = \sigma_f = 0.05$
Behaviour	**Parameter, c'**	**Parameter, c'**	**Parameter, c'**
stable steady state	$0.0 < c' < 3.47$	$0.0 < c' < 3.44$	$0.0 < c' < 3.46$
2-point cycle	$3.47 < c' < 3.88$	$3.44 < c' < 3.84$	$3.46 < c' < 3.93$
4-point cycle	$3.88 < c' < 3.98$	$3.84 < c' < 3.94$	$3.93 < c' < 4.07$
chaos	$c' > 4.02$	$c' > 3.97$	$c' > 4.13$

Table 5.2.1: *Approximate bifurcation positions for both male and female populations of model (5.2.1) using equations (5.2.3) and (5.2.4).*

Example 2

The proportion of zygotes that develop into females also has an effect on the stability region, as will be noted by the difference in the stability interval of this example as shown by Figure 5.2.2. Here the only difference in parameter values from example 1 is that $k_f = 0.5$. The dynamical behaviour is also listed in Table 5.2.1. The interval for a stable steady state is now $0.0 < c' < 3.44$.

Example 3

Next we wish to illustrate the effect of the survival factor on the stability intervals. In this example we have introduced an equal survival factor of 0.05 to the male and female stock in model (5.2.1). The rest of the parameter values were taken as in Example 2. The interval on c' for a stable equilibrium population level here is $0.0 < c' < 3.46$, while we find chaos in the region $c' > 4.13$. Thus, this result agrees with the results
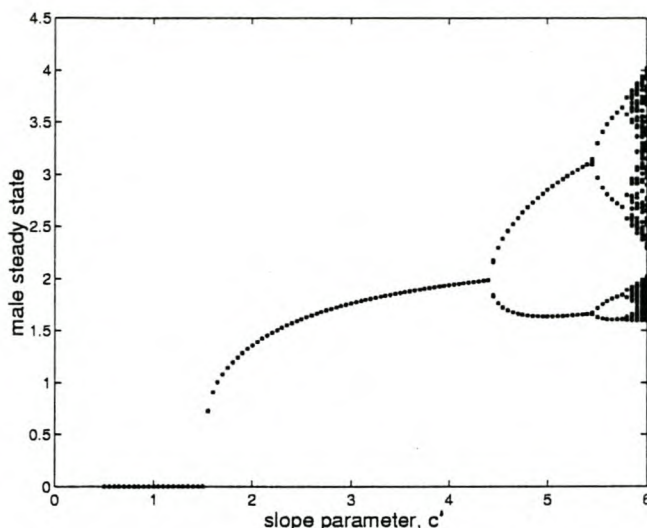
Figure 5.2.3: *The dynamical solution at equilibrium of the two-sex model (5.2.1) using equations (5.2.3) and (5.2.4) Male stock against parameter c' where $k_f = 0.5$, survival, $\sigma = 0.5$, delay factors $u = v = 0.0$.*

of Section 5.1.3, where the introduction of survival increases stability. Compare also the regions for periodic solutions of Examples 2 and 3 in Table 5.2.1. This example is illustrated in Figure 5.2.3. The results for the female stock are identical.

Examples 4 and 5 Here we use the same model and add a delay factor of $u = v = 1$. Figure 5.2.4(i) illustrates the stability behaviour of the system with a survival factor of 0.6. The critical value after which chaos occurs is $c' = 3.45$. To investigate the effect the delay factor has on the biological behaviour of the stock we now increase the delay to $u = v = 3$. Here the critical value is $c' = 2.69$ which indicates a smaller range of c' values where stability in the behaviour exists (see Figure 5.2.4(ii)). Thus, the delay factor destabilizes this equilibrium. This result again agrees with the conclusions of Section 5.1.3.

5.2.3   Harvesting

We introduce here the model of Cruywagen (1996a). Take N_t^m and N_t^f to be the *pre-harvest* densities of the breeding male and female populations at time t. Assume that
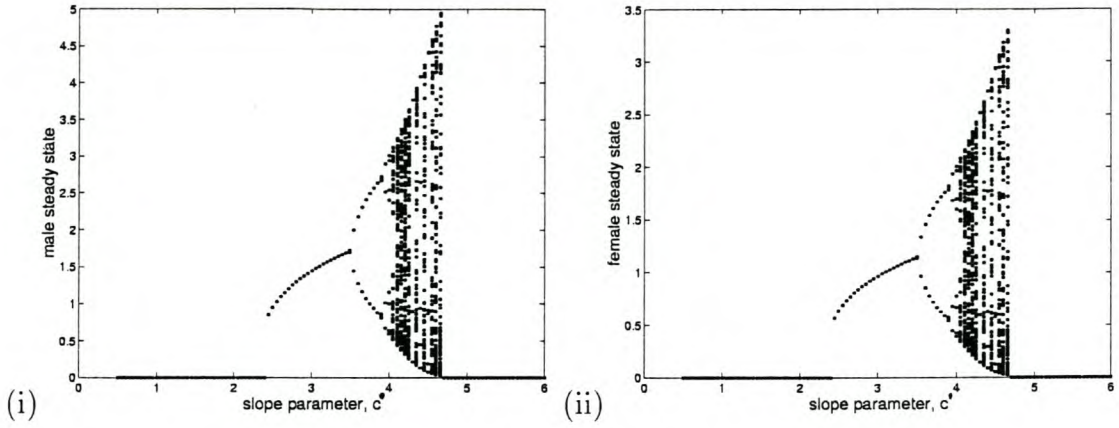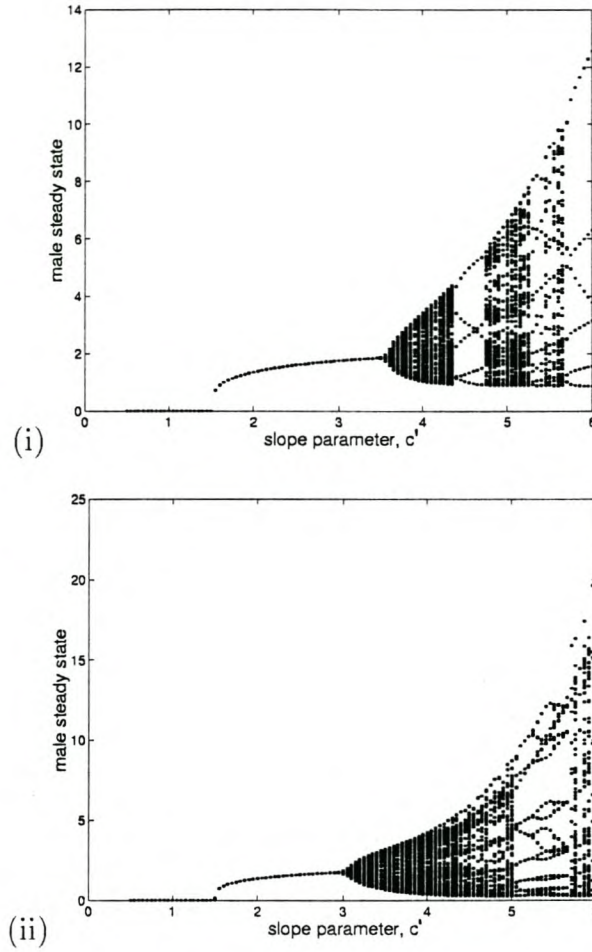
Figure 5.2.4: *The dynamical solution at equilibrium of the two-sex model (5.2.1) using equations (5.2.3) and (5.2.4). Male stock against parameter c' where $k_f = 0.5$, survival, $\sigma = 0.5$, and (i) delay factors, $u = v = 1.0$, (ii) delay factors, $u = v = 3.0$.*

harvesting, reproduction and recruitment takes place during the intervals as described in Section 5.1.4. Let h_t^m and h_t^f be the male and female harvest functions, respectively, then the *post harvest* densities at time t are $S_t^m = N_t^m - h_t^m$ and $S_t^f = N_t^f - h_t^f$. The general two-sex delay difference model (5.2.1) then becomes

$$
\begin{aligned}
N_{t+1}^m &= \sigma_m S_t^m + H(S_{t-u}^m, S_{t-u}^f), \\
N_{t+1}^f &= \sigma_f S_t^f + G(S_{t-v}^m, S_{t-v}^f),
\end{aligned}
\tag{5.2.5}
$$

where $H(S^m, S^f)$ and $G(S^m, S^f)$ denote the male and female recruitment functions as

earlier. In this model it takes males $u+1$ years to reach maturity, while it takes females $v+1$ years. We expect no recruitment when either the male or female population has been depleted, and also that the recruitment functions should stay positive. Therefore we assume the following properties for functions $H(S^m, S^f)$ and $G(S^m, S^f)$:

- $H(S^m, S^f) = G(S^m, S^f) = 0$ if $S^m = 0$ or $S^f = 0$,

- $G(S^m, S^f) > 0$ and $H(S^m, S^f) > 0$ if $S^m > 0$ and $S^f > 0$

(Cruywagen, 1996a).

5.2.4   Stability

Cruywagen (1996a) has shown the existence of a steady state solution and conducted various analyses on how the delay periods, the survival and constant effort harvesting, affect the population stability at the steady state. He made the following simplifying assumptions:

(1) $h^m = q_m E N^m$, $h^f = q_f E N^f$ with q_m and q_f the catchability coefficients of the male and female populations respectively and E is as before. He also assumed that $q_m = q_f = q$,

(2) the male and female survival coefficients are equal, so $\sigma_m = \sigma_f = \sigma$,

(3) the male and female recruitment functions differ by a constant scaling factor k, so $G(S^m, S^f) = kH(S^m, S^f)$ with $k > 0$.

The model then reduces to

$$
\begin{aligned}
S^m_{t+1} &= (1 - qE)[\sigma S^m_t + H(S^m_{t-u}, S^f_{t-u})], \\
S^f_{t+1} &= (1 - qE)[\sigma S^f_t + G(S^m_{t-v}, S^f_{t-v})].
\end{aligned}
\tag{5.2.6}
$$

Here we repeat Cruywagen's (1996a) main results for completeness. In the next section we extend his work by examining whether an optimal harvesting policy exists for this

simplified model. Note that for simplicity we use the general recruitment function rather than a specific one.

Suppose that a steady state exists at (Σ^m, Σ^f). We now linearize about this steady state and set $S_t^m = \Sigma^m + \overline{S}_t^m$ and $S_t^f = \Sigma^f + \overline{S}_t^f$ with $|\overline{S}^m| \ll 1$ and $|\overline{S}^f| \ll 1$. Substituting these into the model (5.2.6) gives for males,

$$\Sigma^m + \overline{S}_{t+1}^m = (1 - qE)[\sigma(\Sigma^m + \overline{S}_t^m) + H(\Sigma^m, \Sigma^f) + \overline{S}_{t-u}^m H_{Sm}^* + \overline{S}_{t-u}^f H_{Sf}^*]$$

where $H_{Sm}^* = \frac{\partial H}{\partial S^m}\big|_{(\Sigma^m, \Sigma^f)}$ and $H_{Sf}^* = \frac{\partial H}{\partial S^f}\big|_{(\Sigma^m, \Sigma^f)}$. A similar equation can be derived for females. Since, at the steady state

$$\Sigma^m = (1 - qE)[\sigma \Sigma^m + H(\Sigma^m, \Sigma^f)],$$

it follows that

$$\overline{S}_{t+1}^m = (1 - qE)[\sigma \overline{S}_t^m + \overline{S}_{t-u}^m H_{Sm}^* + \overline{S}_{t-u}^f H_{Sf}^*].$$

Likewise for females we have

$$\overline{S}_{t+1}^f = (1 - qE)[\sigma \overline{S}_t^f + \overline{S}_{t-v}^m G_{Sm}^* + \overline{S}_{t-v}^f G_{Sf}^*].$$

Assume $\left(\overline{S}_t^m, \overline{S}_t^f\right) = \left(Z_m^k, Z_f^k\right) = (a, b)Z^t$. Then

$$\begin{bmatrix} Z^{t+1} - (1 - qE)\left(\sigma Z^t + Z^{t-u} H_{Sm}^*\right) & (1 - qE)Z^{t-u} H_{Sf}^* \\ (1 - qE)Z^{t-v} G_{Sm}^* & Z^{t+1} - (1 - qE)\left(\sigma Z^t + Z^{t-v} G_{Sf}^*\right) \end{bmatrix} \begin{bmatrix} a \\ b \end{bmatrix} = \underline{0}$$

or

$$A \begin{bmatrix} a \\ b \end{bmatrix} = \underline{0}.$$

Set $\mathrm{Det}\, A = 0$, then

$$Z^t \left(Z + (1 - qE)\sigma\right) \left[Z^{t+1} + (qE - 1)\sigma Z^t + (qE - 1)[Z^{t-v} G_{Sf} + Z^{t-u} H_{Sm}]\right] = 0.$$

$$(5.2.7)$$

The steady state (Σ^m, Σ^f) is locally stable provided that the roots of (5.2.7) are less than unity, thus, $|Z| < 1$.

Cruywagen (1996a) has determined the necessary and sufficient conditions pertaining to the functions G_{Sf}^* and H_{Sm}^* for stability. Suppose the male and female time delays, u and v, are equal. Thus, $u = v = \tau$, then the upper stability bound obtained while $G_{Sf}^* + H_{Sm}^* > 0$ is

$$G_{Sf}^* + H_{Sm}^* < \frac{1}{1 - qE} - \sigma.$$

To determine the lower stability boundary it is necessary to substitute the root of modulus one, $Z = e^{i\lambda}$, into the characteristic polynomial and equate the real and imaginary parts. The real part is

$$\cos \lambda(\tau + 1) - \sigma(1 - qE) \cos \lambda\tau - (1 - qE)\left[G_{Sf}^* + H_{Sm}^*\right] = 0, \tag{5.2.8}$$

while the imaginary part is

$$\sin \lambda(\tau + 1) - \sigma(1 - qE) \sin \lambda\tau = 0. \tag{5.2.9}$$

Substitute the unique positive root, $0 < \lambda < \pi/(\tau + 1)$, of equation (5.2.9) into (5.2.8) to obtain the unique lower stability bound when $G_{Sf}^* + H_{Sm}^* < 0$. If $\tau \to \infty$ then

$$G_{Sf}^* + H_{Sm}^* \to \left(\frac{-1}{1 - qE} + s\right)^-.$$

The general results obtained on stability are:

- an increase in the delay factor destabilizes the population, with σ and E being fixed,

- for all delay factors τ, an increase in E stabilizes the population,

- for $\tau \geq 1$, a decrease in σ stabilizes the population,

- for $\tau = 0$ and $G_{Sf}^* + H_{Sm}^* < 0$, an increase in σ stabilizes the population, and

- an increase in harvesting effort, E, or a decrease in survival, σ, results in a lower steady state population.

Further results for the case $v \neq u$ were obtained by Cruywagen (1996a) but are not addressed here as these were for specific constraints on v and u.

5.2.5 Optimal Harvesting Policy

Here we extend Clark's (1990) work for discrete single-sex delay models to discrete two-sex delay models. We apply this model and determine an optimal harvesting strategy. In Chapter 4 the three management options namely, *open access*, *maximum sustainable yield* and *maximum economic yield* strategies were discussed in terms of the surplus production function. Here we specifically investigate the most suitable maximum economic yield option (see discussion in Chapter 4) by applying the standard Lagrangian optimization method.

Given a feasible harvest policy we model future stock levels using equation (5.2.5). Thus with initial population levels, N_0^m and N_0^f, and past survival levels S_{-w}^m and S_{-w}^f for $w = 1, 2, \ldots, \beta$ known, the population levels could be determined.

The sole owner's bio-economic objective is to maximize the present value function

$$PV = \sum_{k=0}^{\infty} \alpha^k \Pi_{(k)}(N_{(k)}^m, N_{(k)}^f, h_{(k)}^m, h_{(k)}^f),$$

where

$$\alpha = \frac{1}{1+i}$$

with i the discount rate and $\Pi_{(k)}$ the economic rent in period k. Let C_m and C_f be the total cost functions of catching male and female fish respectively. We assume that

$$C_m(N^m) = \frac{c}{q_m N^m} \qquad \text{and} \qquad C_f(N^f) = \frac{c}{q_f N^f},$$

where c is the cost per unit effort and q_m and q_f the catchability coefficients for the male and female populations respectively. If we take p_m and p_f to be the price per unit male and female fish, then the net revenue function is

$$\Pi_{(k)} = \int_{N_{(k)}^m - h_{(k)}^m}^{N_{(k)}^m} [p_m - C_m(x)]dx + \int_{N_{(k)}^f - h_{(k)}^f}^{N_{(k)}^f} [p_f - C_f(x)]dx. \qquad (5.2.10)$$

Use the optimization method with Lagrange multipliers, to determine the steady state population for optimal harvesting. The Lagrangian for the objective functional defined above, subject to the two-sex delay model, is

$$
\begin{aligned}
\mathrm{L} \;=\; & \sum_{k=0}^{\infty}\Big(\alpha^{k}\Pi_{(k)}(N_{(k)}^{m}, N_{(k)}^{f}, h_{(k)}^{m}, h_{(k)}^{f}) \\
& -\lambda_{(1,k)}[N_{(k+1)}^{m} - \sigma_m(N_{(k)}^{m} - h_{(k)}^{m}) - H(N_{(k-u)}^{m} - h_{(k-u)}^{m}, N_{(k-u)}^{f} - h_{(k-u)}^{f})] \\
& -\lambda_{(2,k)}[N_{(k+1)}^{f} - \sigma_f(N_{(k)}^{f} - h_{(k)}^{f}) - G(N_{(k-v)}^{m} - h_{(k-v)}^{m}, N_{(k-v)}^{f} - h_{(k-v)}^{f})]\Big).
\end{aligned}
$$

where $\lambda_{(1,k)}$ and $\lambda_{(2,k)}$ are the Lagrangian multipliers.

The necessary conditions for optimality on all the unknown variables are $\frac{\partial L}{\partial N_{(k)}^{m}} = \frac{\partial L}{\partial N_{(k)}^{f}} = 0$ for $k = 1,\ldots,\infty$ and $\frac{\partial L}{\partial h_{(k)}^{m}} = \frac{\partial L}{\partial h_{(k)}^{f}} = 0$ and $\frac{\partial L}{\partial \lambda_{(1,k)}} = \frac{\partial L}{\partial \lambda_{(2,k)}} = 0$, for $k = 0,\ldots,\infty$. We wish to find an equilibrium solution that satisfies these equations. Such an equilibrium is an optimal harvesting level in the management strategy. Also at the steady states we may drop the subscript, k, on the populations sizes and thus also on Π. Thus at the steady states the population sizes satisfy the equations

$$
\begin{aligned}
N^m &= \sigma_m(N^m - h^m) + H(N^m - h^m, N^f - h^f), & (5.2.11) \\
N^f &= \sigma_f(N^f - h^f) + G(N^m - h^m, N^f - h^f),
\end{aligned}
$$

where

$$
\begin{aligned}
h^m &= N^m - S^m, \\
h^f &= N^f - S^f
\end{aligned}
$$

as was discussed in Section 5.2.3.

Note that $\frac{\partial H}{\partial N^m} = \frac{\partial H}{\partial S^m}$, etc., therefore

$$
\frac{\partial \Pi}{\partial h^m} - \lambda_{(1,0)}\sigma_m - \lambda_{(1,u)}\frac{\partial H}{\partial S^m} - \lambda_{(2,v)}\frac{\partial G}{\partial S^m} = 0, \qquad (5.2.12)
$$

$$
\frac{\partial \Pi}{\partial h^f} - \lambda_{(1,u)}\frac{\partial H}{\partial S^f} - \lambda_{(2,0)}\sigma_f - \lambda_{(2,v)}\frac{\partial G}{\partial S^f} = 0 \qquad (5.2.13)
$$

and

$$
\alpha^k \frac{\partial \Pi}{\partial N^m} - \lambda_{(1,k-1)} + \sigma_m \lambda_{(1,k)} + \lambda_{(1,k+u)}\frac{\partial H}{\partial S^m} + \lambda_{(2k+v)}\frac{\partial G}{\partial S^m} = 0, \quad (5.2.14)
$$

$$\alpha^k \frac{\partial \Pi}{\partial N^f} + \lambda_{(1,k+u)} \frac{\partial H}{\partial S^f} - \lambda_{(2,k-1)} + \lambda_{(2,k)} \sigma_f + \lambda_{(2,k+v)} \frac{\partial G}{\partial S^f} = 0, \quad (5.2.15)$$

$$\alpha^k \frac{\partial \Pi}{\partial h^m} - \lambda_{(1,k)} \sigma_m - \lambda_{(1,k+u)} \frac{\partial H}{\partial S^m} - \lambda_{(2,k+v)} \frac{\partial G}{\partial S^m} = 0, \quad (5.2.16)$$

$$\alpha^k \frac{\partial \Pi}{\partial h^f} - \lambda_{(1,k+u)} \frac{\partial H}{\partial S^f} - \lambda_{(2,k)} \sigma_f - \lambda_{(2,k+v)} \frac{\partial G}{\partial S^f} = 0 \quad (5.2.17)$$

for $k = 1, \ldots, \infty$. Add equation (5.2.14) to (5.2.16) and equation (5.2.15) to (5.2.17), then

$$\lambda_{(1,k-1)} = \alpha^k \left(\frac{\partial \Pi}{\partial N^m} + \frac{\partial \Pi}{\partial h^m} \right) \quad (5.2.18)$$

$$\lambda_{(2,k-1)} = \alpha^k \left(\frac{\partial \Pi}{\partial N^f} + \frac{\partial \Pi}{\partial h^f} \right) \quad (5.2.19)$$

for $k = 1, \ldots, \infty$ and substitute equations (5.2.18) and (5.2.19) into equations (5.2.16) and (5.2.17). Then

$$\alpha^k \frac{\partial \Pi}{\partial h^m} - \sigma_m \alpha^{k+1} \left(\frac{\partial \Pi}{\partial N^m} + \frac{\partial \Pi}{\partial h^m} \right) - \alpha^{(k+u+1)} \left(\frac{\partial \Pi}{\partial N^m} + \frac{\partial \Pi}{\partial h^m} \right) \frac{\partial H}{\partial S^m}$$
$$- \alpha^{k+v+1} \left(\frac{\partial \Pi}{\partial N^f} + \frac{\partial \Pi}{\partial h^f} \right) \frac{\partial G}{\partial S^m} = 0$$

$$\alpha^k \frac{\partial \Pi}{\partial h^f} - \sigma_f \alpha^{k+1} \left(\frac{\partial \Pi}{\partial N^f} + \frac{\partial \Pi}{\partial h^f} \right) - \alpha^{k+u+1} \left(\frac{\partial \Pi}{\partial N^m} + \frac{\partial \Pi}{\partial h^m} \right) \frac{\partial H}{\partial S^f}$$
$$- \alpha^{k+v+1} \left(\frac{\partial \Pi}{\partial N^f} + \frac{\partial \Pi}{\partial h^f} \right) \frac{\partial G}{\partial S^f} = 0$$

or

$$\left[\sigma_m + \alpha^u \frac{\partial H}{\partial S^m} \right] \frac{\frac{\partial \Pi}{\partial N^m} + \frac{\partial \Pi}{\partial h^m}}{\frac{\partial \Pi}{\partial h^m}} + \alpha^v \frac{\partial G}{\partial S^m} \frac{\frac{\partial \Pi}{\partial N^f} + \frac{\partial \Pi}{\partial h^f}}{\frac{\partial \Pi}{\partial h^m}} = \frac{1}{\alpha} \quad (5.2.20)$$

$$\left[\sigma_f + \alpha^v \frac{\partial G}{\partial S^f} \right] \frac{\frac{\partial \Pi}{\partial N^f} + \frac{\partial \Pi}{\partial h^f}}{\frac{\partial \Pi}{\partial h^f}} + \alpha^u \frac{\partial H}{\partial S^f} \frac{\frac{\partial \Pi}{\partial N^m} + \frac{\partial \Pi}{\partial h^m}}{\frac{\partial \Pi}{\partial h^f}} = \frac{1}{\alpha} \quad (5.2.21)$$

Use equations (5.2.20) and (5.2.21) together with the equilibrium equations (5.2.11) to solve for N^m, N^f, h^m and h^f. When we use equation (5.2.10) then

$$\frac{\partial \Pi}{\partial N^m} = \frac{c}{q_m S^m} - \frac{c}{q_m N^m}$$

and

$$\frac{\partial \Pi}{\partial h^m} = p_m - \frac{c}{q_m S^m}.$$

Similar expressions are determined for the females. Equations (5.2.20) and (5.2.21) are now:

$$
\begin{aligned}
\left[\sigma_m + \alpha^u \frac{\partial H}{\partial S^m}\right] \frac{p_m - \frac{c}{q_m N^m}}{p_m - \frac{c}{q_m S^m}} + \alpha^v \frac{\partial G}{\partial S^m} \frac{p_f - \frac{c}{q_f N^f}}{p_m - \frac{c}{q_m S^m}} &= \frac{1}{\alpha}, \\
\left[\sigma_f + \alpha^v \frac{\partial G}{\partial S^f}\right] \frac{p_f - \frac{c}{q_f N^f}}{p_f - \frac{c}{q_f S^f}} + \alpha^u \frac{\partial H}{\partial S^f} \frac{p_m - \frac{c}{q_m N^m}}{p_f - \frac{c}{q_f S^f}} &= \frac{1}{\alpha}.
\end{aligned}
\tag{5.2.22}
$$

Solution (5.2.22) is a generalisation of the optimal yield equation for a single population given in Section 5.1.5.

5.2.6 Sensitivity Analysis

Combining equations (5.2.11) and (5.2.22) we can perform a sensitivity analysis of the optimal harvesting under the maximum economic yield strategy on different parameters, in order to investigate to which parameters the solution is sensitive.

In Section 5.2.2 the effect of the different parameters on the stability of the biological model were given. Here we assume an optimal harvesting policy, as decribed in the previous section and determine the effect of the model parameters from a bio-economic perspective on the total male versus female populations. Short and long term management strategies of fisheries should take these sensitivities into account and include, for example, a decrease in price. In such a case the harvesting strategy should be planned towards a new optimum.

By holding all other factors constant in equations (5.2.22) we can determine algebraically the influence that a single parameter has on the male-female ratio, N^m/N^f, at equilibrium. Take $h^m = q_m E N^m$ and $h^f = q_f E N^f$ such that $S^m = (1 - q_m E)N^m$ and similarly for females. At a steady state the partial derivative of the growth functions, H and G are constant. Although these steady states are not easy to determine explicitly for certain growth functions, we assume that these derivatives are constant, giving the expression for the unknowns, N^m, N^f, h^m, h^f as:
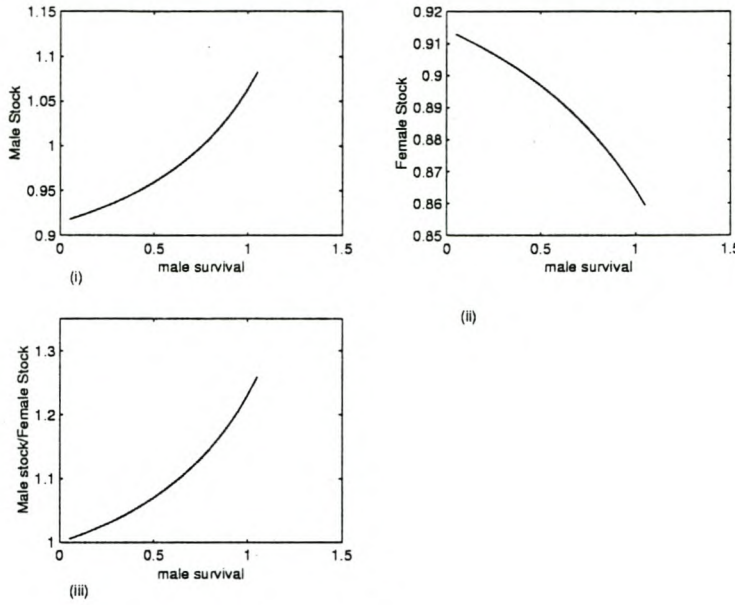
Figure 5.2.5: *Sensitivity of the equilibrium of the general two-sex model (equation 5.2.22) on the survival factor while all other parameters are fixed. (i) male stock against male survival factor, (ii) female stock against male survival factor, (iii) male/female ratio against male survival factor. A Ricker stock-recruitment function,* $F(S) = S \exp\left(c'(1-S)\right)$ *is used.*

$$N^m = \frac{\left[-\Psi\frac{\Theta}{\Phi} + \frac{Bc}{q_f}\right]}{\left[\frac{\Theta}{\Phi}X\right]}$$

$$N^f = \frac{\Theta}{\Phi} N^m$$

$$h^m = q_m E N^m$$

$$h^f = q_f E N^f,$$

where the constants Θ, Φ, Ψ, B and X are given in Appendix 9.4.

Survival Factors

We first look at the survival parameters. Figure 5.2.5 illustrates that the male population size N^m increases in σ_m while σ_f is fixed. At the same time population N_f decreases even though σ_f were left unchanged. This results in an increase in the
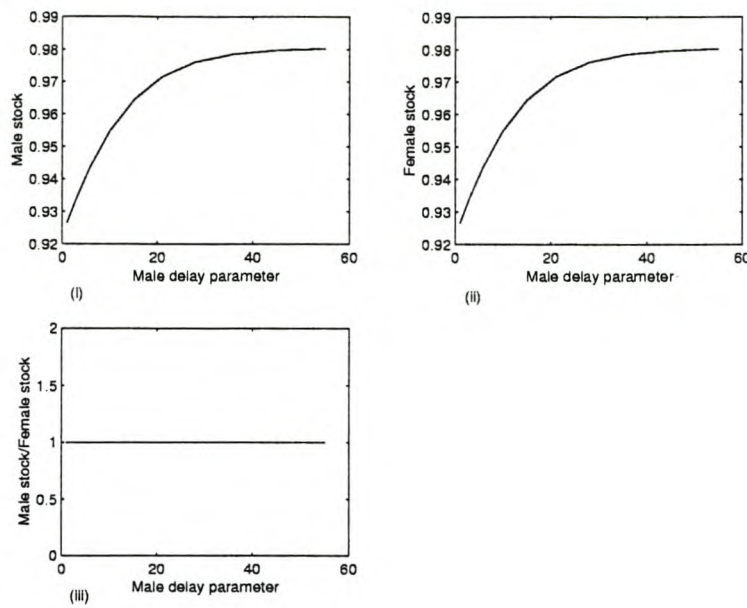
Figure 5.2.6: *Sensitivity of the general two-sex model (equation (5.2.22)) on the male delay factor while all other parameters are fixed. (i) Male stock against male delay factor, (ii) female stock against male delay factor, (iii) male/ female ratio against male delay factor.*

N^m/N^f ratio. Opposite results are found when σ_f is increased and σ_m kept fixed. As expected, the specific survival factor strengthens the corresponding male or female population, but the opposite sex population is dominated, resulting in a lower equilibrium level for this gender. Similarly we can show that when $\sigma_m = \sigma_f = \sigma$ both male and female populations increase at the same rate such that $N^m/N^f = 1$. This result ensures that an equal survival for both sexes would be supportive to the total population. However, the results of Cruywagen (1996a) on the biological model, as discussed in Section 5.2.4, stated that an increase in the survival has a destabilizing effect on the biological system when the delay is greater than 1. That is, a larger population does not necessarily mean that a more stable biological situation exists.

Delay Factors

Next we consider the effect of the delay factors. Figure 5.2.6 contains the graphs of

an increase in both equilibrium levels with the increase in the delay factor of the male population, u. Figures 5.2.6(i) and 5.2.6(ii) are exactly the same, so that $N^m/N^f = 1$ (see Figure 5.2.6(iii)). The same results are found with the delay factor v. So for this model, it does not matter whether a delay factor is implemented in the male or female recruitment functions - both sexes will benefit equally. Again, as was the case with the survival factor, we know that a delay factor has a destabilizing effect on the biological system (Cruywagen, 1996a).
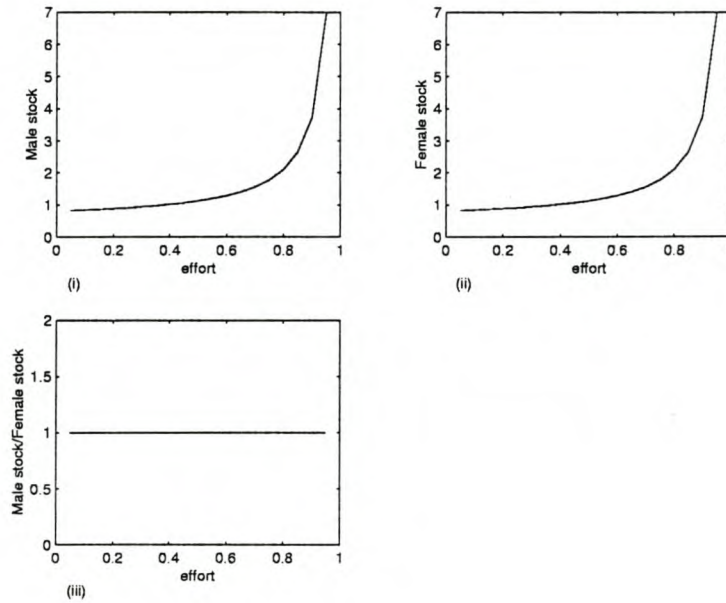
Figure 5.2.7: *Sensitivity of the general two-sex model (equation 5.2.22) on the effort while all other parameters are fixed. (i) Male stock against effort, (ii) female stock against effort, (iii) male/ female stock ratio against effort.*

Effort

The final biological factor to consider is the harvesting effects. When all parameters are fixed and the constant harvesting effort, E, changed, we see from Figure 5.2.7 a steep increase in the male and female populations. That is, the higher effort levels necessitate higher population levels in order to be a sustainable fishery. In Section 5.2.1 it was noted that an increase in E increases the domain of stability of the biological system. This stability may be either a monotone stable state or a periodic oscillation,
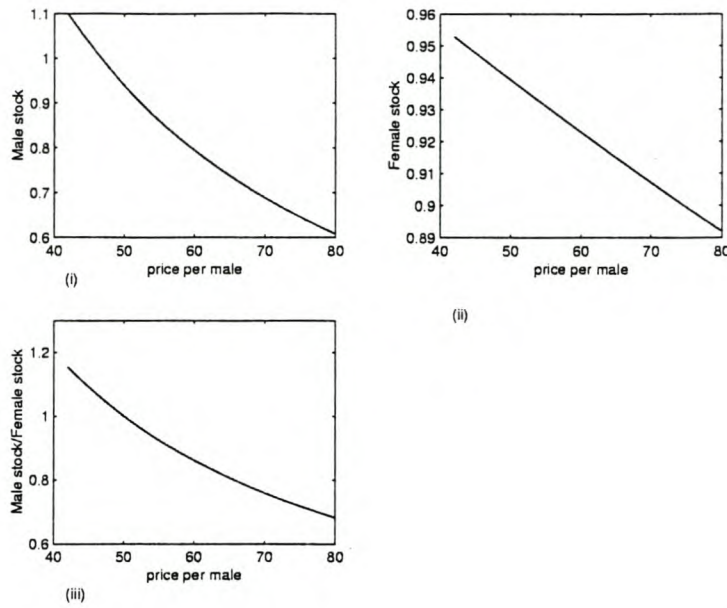
Figure 5.2.8: *Sensitivity of the general two-sex model (equation 5.2.22) on the price per male while all other parameters are fixed, (i) male stock against price per male, (ii) female stock against price per male, (iii) male/female stock ratio against price per male.*

as discussed in Section 5.2.2. Cruywagen (1996a), however, stated that an increase in the harvesting effort are at the cost of a lower steady state population level, which is contrary to the results of Figure 5.2.7. Note, however, that his conclusions were based on the biological model, and the steady state populations levels here are based on a bio-economic approach.

The bio-economic steady state is also dependent on the economic parameters of equations (5.2.22). So we now consider how it is influenced by these parameters.

Price per unit catch

We begin by looking at price. Figure 5.2.8 illustrates the effect of these factors on the populations. In Figure 5.2.8 the female unit price, p_f, is fixed. Here N^m is decreasing in p_m (see Figure 5.2.8(i)), but interestingly the female equilibrium level is also affected negatively (see Figure 5.2.8(ii)). As a result, an increase in the unit price on males has
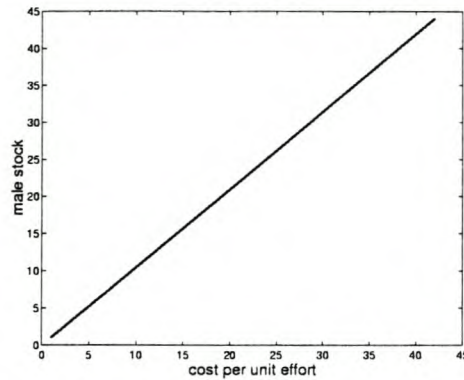
Figure 5.2.9: *Sensitivity of the general two-sex model (equation 5.2.22) on the cost per unit effort while all other parameters are fixed. Male or female stock against cost per unit effort are given.*

a decreasing effect on the male/female ratio at equilibrium, as illustrated in Figure 5.2.8(iii). Also when p_m is fixed we could investigate the effect of p_f. It is possible to illustrate that N^m and N^f decrease with p_f as expected, but here the ratio N^m/N^f increases. Thus it is important to note that a different unit price on male or female animals does effect the steady state of both the male and female populations. The main conclusion is that an increase in any price decreases the population steady state.

Cost per unit effort

Next, we consider only a constant cost per unit effort, c, for both the male and female harvest. With the unit price of male and female set equal, N^m and N^f are linearly dependent on c. Both increase with a constant rate in c (see Figure 5.2.9). This result is in accordance with the results of an increasing constant effort, because these two parameters will increase the operating cost.

Discount Rate

Finally, an increase in the discount rate, i, will encourage an immediate high catch rate as revenues from future catches will decrease and we wish to maximize the total future revenue. Figure 5.2.10 illustrates that the steady state of the total population increases with an increasing discount rate in the range 0.5 to 1. Thus, higher population levels
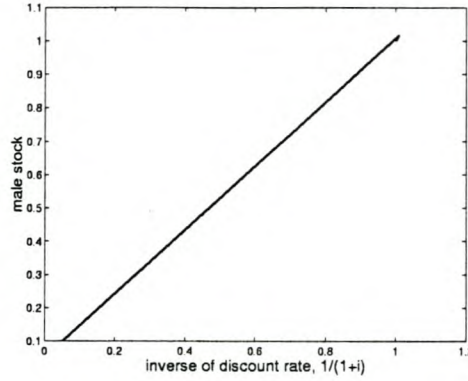
Figure 5.2.10: *Sensitivity of the general two-sex model (equation (5.2.22)) on $\alpha = \frac{1}{1+i}$, i is the discount rate, while all other parameters are fixed.*

will result in higher catches as $h_k^m = q_m E N^m$ and $h_k^f = q_f E N^f$.

5.3 Application to the Cape Rock Lobster

In Chapter 4 the surplus production model was applied to the Cape Rock Lobster resource. In this section the two-sex delay model, as discussed in Section 5.2, is applied to the same species.

5.3.1 Biological Model

Assume the total number of zygotes in year τ to be $Z(S_\tau^m, S_\tau^f)$, where S_τ^m and S_τ^f is the post harvest male and female densities. Assume also that a proportion, θ, of these zygotes will develop into males. It is observed in nature that female juveniles will take longer than males to reach sexual maturity (see Chapter 3). We therefore assume that $v > u$. The general two-sex model (5.2.5) where $H(S_{t-u}^m, S_{t-u}^f) = \theta Z(S_{t-u}^m, S_{t-u}^f)$ and $G(S_{t-v}^m, S_{t-v}^f) = (\sigma_f)^{v-u}(1-\theta)Z(S_{t-v}^m, S_{t-v}^f)$ becomes

$$N_{t+1}^m = \sigma_m S_t^m + \theta Z(S_{t-u}^m, S_{t-u}^f) \tag{5.3.1}$$
$$N_{t+1}^f = \sigma_f S_t^f + (\sigma_f)^{v-u}(1-\theta)Z(S_{t-v}^m, S_{t-v}^f).$$

In Section 5.2.1 the adapted harmonic mean marriage function was discussed along with the Ricker and Beverton-Holt stock-recruitment functions. Here we propose an adapted version of the Ricker-type function to describe recruitment. For the rock lobster, *Jasus lalandii*, we assumed that enough males are available such that

$$Z(S_\tau^m, S_\tau^f) = \kappa + \beta(S_\tau^f - \delta)\exp(-\omega S_\tau^f), \tag{5.3.2}$$

where κ, β, δ and ω are positive constants. In general, with this proposed function, recruitment is higher than that in the original Ricker function in Section 5.1.1 and decreases asymptotically to κ instead of zero. In order to have a zero recruitment with zero stock it is necessary to shift the whole function to the right with the introduction of δ. Also, as with the Ricker function, with an increase in stock size the mortality rate increases for high egg productions.

As the available data are in terms of biomass, rather than in terms of population size, we have to adapt the above model (5.3.2) accordingly. We will use the method followed by Cruywagen (1995b) and do this conversion by using the Ford-Walford model (see Appendix 9.3). That is, assume that the growth in mean body weight at age, a, can be described by the linear relationship

$$w_m(a) = \alpha_m + \rho_m w_m(a - 1),$$

where w is the weight at age a, and α_m and ρ_m are empirical constants (Hilborn *et al.*, 1992). The equations for females are analogous, with f as the subscript instead of m.

Assume $M(t)$ to be the total biomass of males at maturity (age $u + 1$ and older) and similarly $F(t)$ to be the total female biomass age $v + 1$ and older.

Following Cruywagen's (1995b) approach, it is now possible to express biomass, in terms of numbers multiplied by body weight namely,

$$M(t + 1) = \sum_{a=u+1}^{\infty} S_{t+1}^m(a)w_m(a), \tag{5.3.3}$$

$$F(t + 1) = \sum_{a=v+1}^{\infty} S_{t+1}^f(a)w_f(a), \tag{5.3.4}$$

where $S_{t+1}^m(a)$ refers to the number of males aged a, in the mature male population in year $t+1$, while $S_{t+1}^f(a)$ is the equivalent for females. If $h_{t+1}^m(a)$ represents the number of males of age a that have been harvested, and $h_{t+1}^m(u+1)$ represents the number of the previous year's male recruits that have been harvested, then

$$S_{t+1}^m(a) = \sigma_m S_t^m(a-1) - h_{t+1}^m(a) \text{ if } a > u+1, \tag{5.3.5}$$

$$S_{t+1}^m(u+1) = \theta Z\left(S_{t-u}^m, S_{t-u}^f\right) - h_{t+1}^m(u+1) \text{ if } a = u+1.$$

Similar relationships may be obtained for females. After substituting (5.3.5) in (5.3.3) we have

$$M(t+1) = \sigma_m \alpha_m S_t^m + \sigma_m \rho_m M(t) - H^m(t+1) + \theta w_m(u+1)Z(S_{t-u}^m, S_{t-u}^f),$$

where

$$H^m(t+1) = \sum_{a=u+1}^{\infty} h^m(a)\, w_m(a),$$

and similarly for females.

Average weights, $\overline{w}_m(t)$ and $\overline{w}_f(t)$, for mature males and females respectively in year t, are defined as

$$\overline{w}_m(t) = \frac{M(t)}{S_t^m}, \qquad \text{and} \qquad \overline{w}_f(t) = \frac{F(t)}{S_t^f}.$$

This is similar to what was done by Cruywagen (1995b). The equations then reduce to

$$
\begin{aligned}
M(t+1) &= \sigma_m \left(\frac{\alpha_m}{\overline{w}_m(t)} + \rho_m\right) M(t) - H^m(t+1) \tag{5.3.6} \\
&\quad + \theta w_m(u+1)Z\left(\frac{M(t-u)}{\overline{w}_m(t-u)}, \frac{F(t-u)}{\overline{w}_f(t-u)}\right) \\
F(t+1) &= \sigma_f \left(\frac{\alpha_f}{\overline{w}_f(t)} + \rho_f\right) F(t) - H^f(t+1) \tag{5.3.7} \\
&\quad + (1-\theta)(\sigma_f)^{v-u} w_f(v+1)Z\left(\frac{M(t-v)}{\overline{w}_m(t-v)}, \frac{F(t-v)}{\overline{w}_f(t-v)}\right).
\end{aligned}
$$

At the population's pristine level, we assume

$$M(t) = K_M, \qquad F(t) = K_F, \qquad \text{for all } t$$

so

$$k_m = \frac{K_M}{\overline{w}_m}, \qquad \text{and} \qquad k_f = \frac{K_F}{\overline{w}_f}$$

If we ignore the catches because we are at the pristine state we can use the numbers model (5.3.1) and biomass model (5.3.6, 5.3.7) to derive the relation between the average male weight at the pristine state, $\overline{w}_m$, and the natural male survivorship parameter, σ_m, namely

$$\overline{w}_m = \frac{\sigma_m \alpha_m + w_m (u+1)[1 - \sigma_m]}{1 - \sigma_m \rho_m}. \qquad (5.3.8)$$

For the females the equation is

$$\overline{w}_f = \frac{\sigma_f \alpha_f + w_f (v+1)[1 - \sigma_f]}{1 - \sigma_f \rho_f}. \qquad (5.3.9)$$

Use equations (5.3.6) and (5.3.7) at equilibrium and determine the following relationship between the male and female carrying capacities,

$$K_F = \frac{\sigma_f^{v-u} (1-\theta)(1-\sigma_m)\overline{w}_f}{\theta(1-\sigma_f)\overline{w}_m} K_M \qquad (5.3.10)$$

(Cruywagen, 1995b). By using the last three equations it is possible to reduce the numbers of parameters to be estimated as three of them are given here in terms of the others.

5.3.2 Data

As this is a two sex model we seek data sets on both males and females. We now assume that the biological parameters u, v, σ_f, σ_m and θ are known.

The values of the delay times are taken as $u = 6$ and $v = 7$ (according to the base case in the study by Cruywagen, 1995b) and there is no reason not to take $\theta = 0.5$.

Johnston *et al.* (1993) were able to estimate the male survivorship parameter to be in the range 0.82 to 0.95. Here, the values of $\sigma_m = 0.90$ and $\sigma_f = 0.92$, as were used by Cruywagen (1995b), are used. (see also Section 3.3).

The parameter K_F is expressed in terms of the others, by using equation (5.3.10).

Other data sets required are the catch per year, catch per unit effort, Ford-Walford parameter and average weight per year. Parameters needed in the model are the male carrying capacity, K_M and the recruitment modelling parameters κ, δ, ω and β.

Data that are available (see also Chapter 3) for certain years are the total catch per season, the percentage males in the catch and the catch per unit effort series. Also available is tagging data of different fishing areas during different years.

The total catch data is available for the period 1900—1995, together with the proportion of males in the catch (see Appendix 9.3, Table 9.8.1). (Like before, assume the population to have been at its pristine level prior to 1900.) Refer to Cruywagen (1995b) for the detailed discussion on the catch sex ratio.

Also given in Appendix 9.3, Table 9.8.2 is the catch per unit effort data that are available since 1975. Note that the catch per unit effort data for males and females are in the same proportion as in the catch.

We use the Ford-Walford growth parameter (Appendix 9.3, Table 9.8.4) as was calculated using the tagging data in Table 9.8.7 (Cruywagen, 1995b). A detailed discussion on these parameters was given in Chapter 3.

Next it is also necessary to determine the average weights of males and females per year starting at the pristine state. Cruywagen (1995b) also reported that the better way of obtaining size-frequencies is by using the results of diving experiments above the examination of catches as these are selective catching. Such experimental results are reported by Cruywagen (1995b) and repeated here in Appendix 9.3, Table 9.8.5.

We assume that the decline in the average weights is catch related and use a linear interpolation method that reduce the weights $\overline{w}_m(1900)$ and $\overline{w}_f(1900)$ towards the average weights of males, $\overline{w}_m(t)$ and females, $\overline{w}_f(t)$ per year. This decline is proportional to the catch taken in that year, namely,

$$\overline{w}_m(t) = \overline{w}_m(1901) + \frac{[\overline{w}_m(1995) - \overline{w}_m(1901)] \sum_{t'=1901}^{t} H^m(t')}{\sum_{\tau=1901}^{1995} H^m(\tau)},$$

where only the pristine average weights, $\overline{w}_m(1901)$ and $\overline{w}_f(1901)$ and the current average weights, $\overline{w}_m(1995)$ and $\overline{w}_f(1995)$, are known. Equations (5.3.8) and (5.3.9) were

used to calculate the pristine average male weights. In terms of lengths that is 101 mm for the males, and 71 mm for the female. Take the current average mature male weight to be that of a 75 mm animal and that of the females of a 68 mm animal. (These lengths agree well with the experimental data for males but differ to some extent from that of the females.) The calculated average weights for males and females are given in Figure 5.3.1. The length-weight relationship is discussed in detail in Chapter 3.
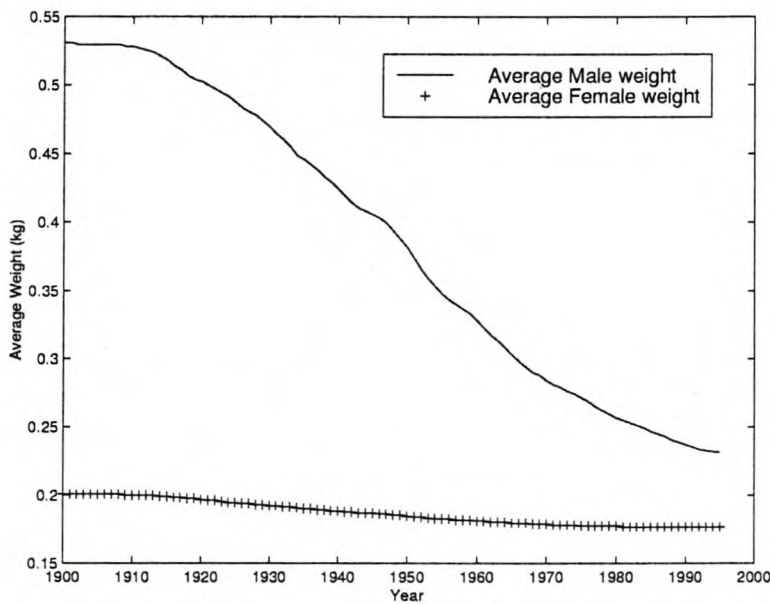
Figure 5.3.1: *Calculated average male and female weight time series for the Cape Rock Lobster resource given in kg.*

The parameter estimation procedure that is described in the following section was used to estimate the other six parameters, K_M K_f,κ, δ, ω and β. Three parameters, κ, δ and ω were fixed at some chosen values and by fitting the model the two remaining parameters could be estimated, namely β, and the male carrying capacity K_M. As before, the Powell optimization method, was used in the parameter estimation prosess (Press *et al.*, 1989).

κ	δ	β	ω	K_m	$-\ln L$
0	0	23.5	1.00×10^{-6}	2.24×10^9	38.13
2.97×10^7	0	3.86×10^4	8.00×10^{-8}	4.18×10^8	42.00
3.00×10^7	6.00×10^7	1.05×10^4	2.00×10^{-6}	5.12×10^8	43.14
3.00×10^7	6.00×10^7	927.60	5.00×10^{-8}	4.64×10^8	42.73
3.00×10^7	3.00×10^7	734.95	5.00×10^{-8}	4.63×10^8	42.67
3.00×10^7	5.00×10^6	624.90	5.00×10^{-8}	4.62×10^8	42.64
3.00×10^7	1.00×10^6	610.30	5.00×10^{-8}	4.61×10^8	42.64

Table 5.3.1: *The results of the model (Section 5.3.4) application on the Cape Rock Lobster with various parameter choices in the model. The parameters κ, δ and ω are chosen while the algorithm searches for K_m and β.*

5.3.3 Estimation of Biological Parameters

In Chapter 4 the maximum likelihood parameter estimation procedure was discussed and used. Here we use the same approach for estimating the male catch-per-unit-effort. Assume that the catch-per-unit-effort is proportional to the average between the pre- and post harvest male population size, namely

$$C\widehat{PU}E_m(t) = \frac{H_m(t)}{E(t)} = \frac{q_m}{2}\left(2M(t) + H_m(t)\right),$$

where q_m is the male catchability coefficient, as before. Similarly the female catch-per-unit-effort is modelled by

$$C\widehat{PU}E_f(t) = \frac{H_f(t)}{E(t)} = \frac{q_f}{2}\left(2F(t) + H_f(t)\right),$$

where q_f is the female catchability coefficient.

By fitting the modelled CPUE series to the observed series the unknown parameters in the delay model (5.3.6, 5.3.7) could be estimated.

As before, we define the likelihood function as

$$L = \left(\frac{1}{\sqrt{2\pi s_m^2}}\right)^p \exp\left(-\sum_t^p [\ln \text{CPUE}_m(t) - \ln \frac{q_m}{2}(2M(t) + H^m(t))]^2/(2s_m^2)\right) \times$$

$$\left(\frac{1}{\sqrt{2\pi s_f^2}}\right)^p \exp\left(-\sum_t^p [\ln \mathrm{CPUE}_f(t) - \ln \frac{q_f}{2}(2F(t) + H^m(t))]^2/(2s_f^2)\right),$$

where p refers to the number of years that data is available. We have discussed in Chapter 3 why the catchability coefficient differs before 1992 and thereafter. Thus take $q_{m,1}$ to be the catchability coefficient for males for the period till 1991 and $q_{m,2}$ to be the coefficient for the period since 1993. Similar notation is used for the females. At the maximum for the log-likelihood function (see Chapter 4) the catchability coefficients satisfy

$$q_{m,1} = \prod_{t=1975}^{1991}\left(\frac{2\mathrm{CPUE}_m}{(2M(t) + H_m(t))}\right)^{\frac{1}{17}},$$

$$q_{m,2} = \prod_{t=1993}^{1995}\left(\frac{2\mathrm{CPUE}_m}{(2M(t) + H_m(t))}\right)^{\frac{1}{3}},$$

$$q_{f,1} = \prod_{t=1975}^{1991}\left(\frac{2\mathrm{CPUE}_f}{(2F(t) + H_f(t))}\right)^{\frac{1}{17}},$$

$$q_{f,2} = \prod_{t=1993}^{1995}\left(\frac{2\mathrm{CPUE}_f}{(2F(t) + H_f(t))}\right)^{\frac{1}{3}}$$

and the standard deviations

$$s_{m,1}^2 = \frac{1}{17}\sum_{t=1975}^{1991}\left[\ln \mathrm{CPUE}_m(t) - \ln \frac{q_{m,1}}{2}(2M(t) + H_m(t))\right]^2,$$

$$s_{,m2}^2 = \frac{1}{3}\sum_{t=1993}^{1995}\left[\ln \mathrm{CPUE}_m(t) - \ln \frac{q_{m,2}}{2}(2M(t) + H_m(t))\right]^2,$$

$$s_{f,1}^2 = \frac{1}{17}\sum_{t=1975}^{1991}\left[\ln \mathrm{CPUE}_f(t) - \ln \frac{q_{f,1}}{2}(2F(t) + H_F(t))\right]^2,$$

$$s_{f,2}^2 = \frac{1}{3}\sum_{t=1993}^{1995}\left[\ln \mathrm{CPUE}_f(t) - \ln \frac{q_{f,2}}{2}(2F(t) + H_F(t))\right]^2.$$

As in Chapter 4, the Powell minimization method was used to perform the CPUE fit to the real data. Various choices for the three parameters κ, δ and ω of the recruitment function were investigated and compared (see Table 5.3.1). As it is not easy to estimate all unknown parameters by the fitting procedure we used trial and error to decide on realistic parameters for the recruitment function, equation (5.3.2). A typical set is $\kappa = 3.0 \times 10^7$, $\delta = 1.0 \times 10^6$ and $\omega = 5.0 \times 10^{-8}$. The best fit for this set estimates

$\beta = 610$ and $K_m = 4.614 \times 10^8$. The curve with these parameter values is given in Figure 5.3.2.

Figure 5.3.3 shows the predicted male and female stock size of the model (5.3.6) and (5.3.7) for each year. Note the general decline since 1900 in stock size for both the males and females.
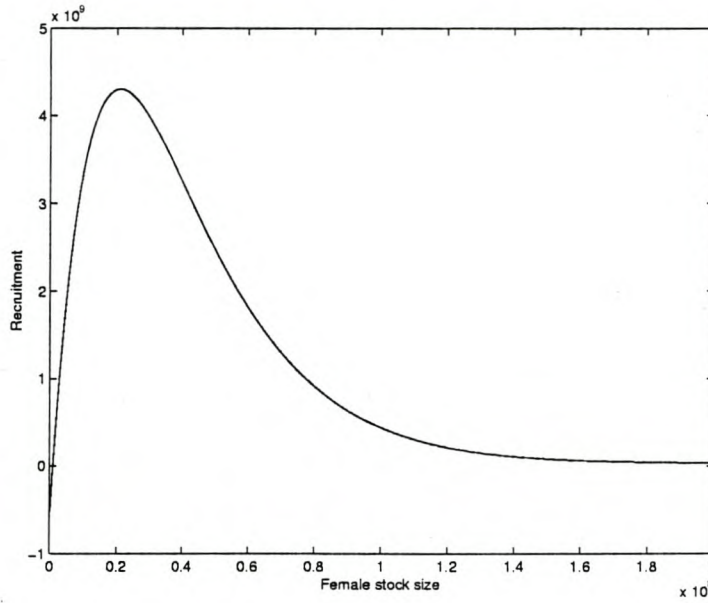
Figure 5.3.2: *The proposed recruitment function for the application to the Cape Rock Lobster resource, namely $Z(S^m, S^f) = \kappa + \beta(S^f - \delta)e^{(-\omega S^f)}$. The parameters are taken as $\kappa 3.0 \times 10^7$, $\beta = 610$, $\delta = 1.0 \times 10^6$, $\omega = 5.0 \times 10^{-8}$.*

Figures 5.3.4 (a) and (b) illustrate the fits of the modelled CPUE to the real male and female CPUE values.

5.3.4 Bio-economic Modelling

It is possible to determine the expressions of the optimal bio-economic population and catch levels in terms of the production function given in Section 5.3.1.

At the bio-economic equilibrium the biological model (5.3.1) and equation (5.2.22)
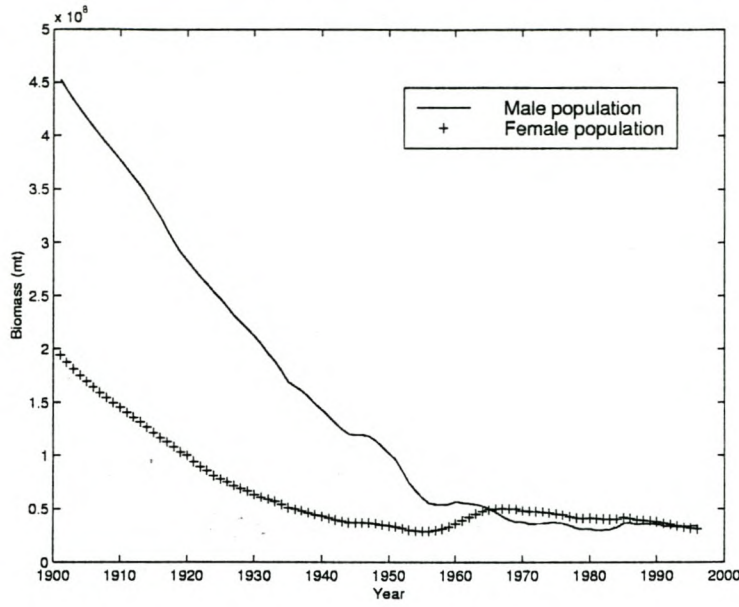
Figure 5.3.3: *Predicted male and female population size in biomass for the Cape Rock Lobster.*

have to be satisfied. Here,

$$H(S^m, S^f) = \theta Z(S^m, S^f)$$

and

$$G(S^m, S^f) = (\sigma_f)^{(v-u)}(1 - \theta)Z(S^m, S^f)$$

and the set of equation becomes

$$N^m = \sigma_m S^m + \theta Z \qquad (5.3.11)$$

$$N^f = \sigma_f S^f + (1 - \theta)\sigma_f^{v-u} Z,$$

$$\sigma_m \left(p_m - \frac{c}{q_m N^m} \right) = \frac{1}{\alpha} \left(p_m - \frac{c}{q_m S^m} \right),$$

$$\left(\sigma_f + \alpha^v(1 - \theta)\sigma_f^{v-u} \frac{\partial Z}{\partial S^f} \right) \left(p_f - \frac{c}{q_f N^f} \right)$$

$$+ \alpha^u \theta \frac{\partial Z}{\partial S^f} \left(p_m - \frac{c}{q_m N^m} \right) = \frac{1}{\alpha} \left(p_f - \frac{c}{q_f S_f} \right),$$

Thus we have four equations in the four unknowns N^m, N^f, S^m, S^f, as all other parameters have been estimated in the previous section.
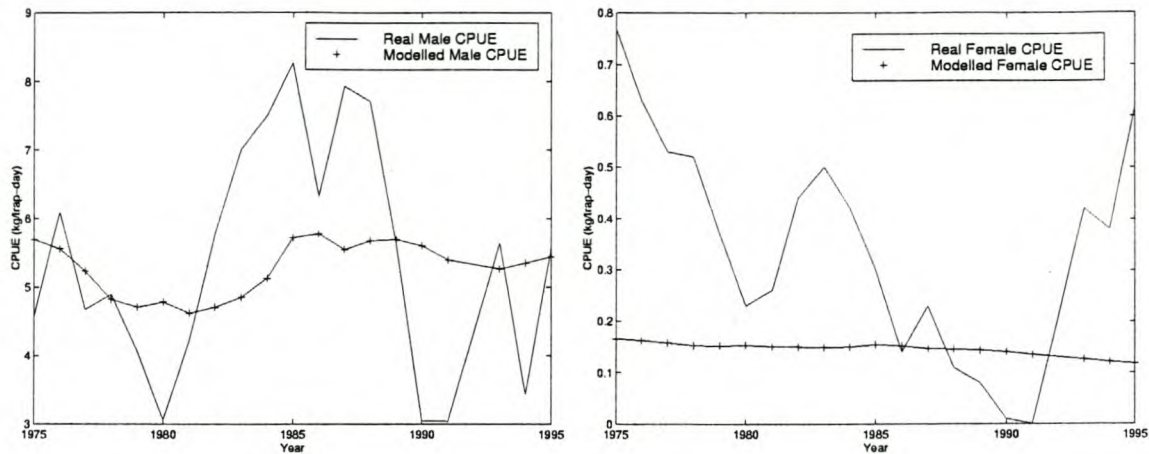
Figure 5.3.4: *(a) Male modelled CPUE fit to real data,(b) Female modelled CPUE fit to real data, for the Cape Rock Lobster.*

We will now find a steady state solution for equations (5.3.11) where we use the estimated biological parameters of the previous paragraph. Take $\Gamma = \exp(-\omega S^f)$ in equation (5.3.2). Then $\Gamma \to 0$ when $S^f \to \infty$. This assuption is not general, but possible for large female stock sizes. Under conditions where the function $\frac{\partial Z}{\partial S^f} \to 0$ the set of equations (5.3.11) simplifies to be solved analytically. The equations reduce to a pair of second order polynomials and the steady state solution thus tends to the roots of these polynomials as $S^f \to \infty$. Take the biological parameter values as in the previous section, then Table 5.3.2 shows these solutions for different economic values. The results of the stock sizes are given in numbers. This table gives the equilibrium stock level to be maintained in order to maximize the total present value for different economical factors.

It shows that the female stock size decreases with the price per female as the resource should be able to account for a higher catch demand. On the other hand the female stock increases with an increase in the cost per unit effort as the catch will probably decrease. As expected, the female stock size decreases as the interest rate increases, because future stock will be worth less under higher rates.

Another interesting result from Table 5.3.2 is that the male catch size is independent

p_m	p_f	c	α	$N^m(10^7)$	$N^f(10^8)$	$S^m(10^7)$	$S^f(10^8)$	$h^m(10^7)$	$h^f(10^8)$	$\Pi(10^9)$
100	100	80	0.98	3.53	1.34	2.26	1.3	1.27	3.38	1.61
100	100	70	0.98	3.37	1.25	2.07	1.21	1.29	4.16	1.71
100	100	50	0.98	3.00	1.05	1.66	1.00	1.33	5.84	1.92
80	80	50	0.98	3.23	1.18	1.93	1.13	1.31	4.76	1.43
50	50	50	0.98	3.84	1.50	2.60	1.48	1.24	1.97	0.72
100	80	50	0.98	3.00	1.18	1.66	1.13	1.33	4.76	1.71
80	100	50	0.98	3.23	1.05	1.93	1.00	1.31	5.84	1.63
100	100	50	0.97	2.92	1.04	1.58	0.98	1.34	5.99	1.94
100	100	50	0.95	2.79	1.01	1.43	0.94	1.36	6.25	1.98

Table 5.3.2: *The bio-economic equilibrium results for different economic values when using the biological values such as given in Table 5.3.1 (last row). N^m is the male pre-harvest stock size in numbers, N^f is the female pre-harvest stock size in numbers, S^m is the male post-harvest stock size in numbers, S^f is the female post-harvest stock size in numbers, h^m is the annual male harvest, h^f is the annual female harvest and Π is the annual net revenue from such an strategy.*

of the price per female fish and vice versa.

5.4   Conclusion

For species like the South African West Coast rock lobster there is a delay before newborns reach sexual maturity. This phenomenon has been addressed by using a delay difference model. The overlap of generations has been incorporated in the model by the use of a survival factor. We started the chapter by first studying single-sex delay difference models. Two stock recruitment relations that satisfy the basic requirements as defined by Ricker (1954) and Hilborn *et al.* (1992) are the Beverton-Holt and Ricker functions. We have shown that the equilibrium population size of the Beverton-Holt function is always stable, but that bifurcation occurs with the Ricker function in the

region outside the stability interval. As an age structure (or increase in survival) is added to the Ricker model the critical value, where bifurcation occurs, increases such that increased survival increases stability. Contrary to that we saw that with the addition of the delay factor, the critical value decreases and delay is thus destabilizing.

For many species the population dynamics of the male and female population are different and it may become necessary to use a two-sex delay difference model in order to distinguish between the sexes. With this two-sex model, as with the single-sex model, bifurcations occur later with added age structure to the Ricker function, which implies an increase of stability with age. In Section 5.3.2 we also conclude that for the two-sex model the delay factor again destabilizes the equilibrium position.

We used the theoretical framework of Cruywagen (1996a) and added bio-economic features to the model. By applying optimal control theory we reached four equations, namely, equations (5.2.11) and (5.2.22), to solve for the four unknowns, N^m, N^f, S^m, S^f, at equilibrium. Some interesting results on the sensitivity of this bio-economical solution on the different biological and economical parameters were shown. Note that a larger population size, e.g. when the survival factor increases, does not necessarily mean a more stable biological situation. It is also interesting to see that although the survival factor, σ_f, may be fixed, N^f decreases with an increase in σ_m, and vice versa. The male delay factor, u, also influences both male and female populations, but in this case equally. Lastly the other biological parameter considered was effort, E, and we note that the stable population size is at an increased level with an increase in effort, contrary to results of other authors. This contradiction is taken to be due to the differences between biological models and our bio-economic model.

The economic factors also affect both sexes simultaneously, for example an increase in price per male animal, p_m, decreases also the female size.

These sensitivity results on the different parameters, emphasize that care should be taken when finding all these parameters as the equilibrium solution may be highly sensitive to these values.

In Section 5.3 the proposed two-sex delay difference model is applied to the Cape Rock

Lobster resource. Data on this fishery are available only in biomass. Consequently a conversion from length to weight was necessary in the model. The pristine average male and female lengths were calculated from equations (5.3.8) and (5.3.9), and the female lengths differ slightly from the range on average length from experimental data. This difference may indicate that the model does not properly describe the population, but note that the experimental data are only for some exploited areas and may therefore only be taken as an indication.

The best fit of the modelled CPUE to the real CPUE was done. A shortcomings of this attempt may be that the total outcome relies only on a CPUE series beyond 1975, when catches were already low. Earlier data are not available. Better model fits are expected in situations where a longer time series is available.

Nevertheless, the model gives a much more detailed description of the resource than the surplus production model in the previous chapter. Although we have made assumptions on the recruitment function and harvesting outcome, the above model and results could be usefull in planning specific future management strategies for male and female populations. Also environmental effects on the current stock will influence the recruitment $T+1$ years in the future as the recruitment depends on the delay factors.

We have emphasized the bio-economic approach as opposed to the pure biological approach for formulating a management strategy. As we have shown, the economic factors do affect the optimal catch size dramatically. Thus, maximizing the total net revenue rather than maximizing the total catch per year does give an improved management strategy.

Future chapters will address the much more complex stage class- and spatial models. Such models need detailed data series to be applicable. However, a more complex model does not necessarily give more accurate predictions. Given the available data the delay difference model, such as we have described here, may be of value.

Chapter 6

Stage-class Models

For species with a life expectancy of several years it is possible to develop a life table consisting of specific parameters like fecundity and mortality. Such a table typically distinguishes between the parameters with respect to the life stages of the population, e.g. age. In this way the total population is classified into subclasses or cohorts. In this chapter information on each subclass will be used to model the population's dynamics in much more detail, in that specific attention will be given to the different stages of development. The general modelling description refers to stage-classes, meaning any suitable subdivision of the population which could be length- or age classes in specific cases.

For many species, including fish, populations consist of different age groups with fecundity and mortality rates varying considerably across the age groups. This provides the motivation for stage class population modelling, as a refinement of models considered in earlier chapters. Moreover, an optimal harvesting strategy might involve different harvesting rates for animals of different stage classes. However, the introduction of different classes to the analysis may complicate the mathematics significantly.

Even though life cycles of different species differ greatly, we assume in this chapter that the dynamics of species may be described by a homogeneous matrix equation

$$\mathbf{n}(t+1) = A\mathbf{n}(t),$$

where A is the projection matrix and the vector $\mathbf{n}(t)$ is the population size distribution at time t. Thus $n_i(t)$ represents the number of individuals of the population in class i at time t. When the biological system can be described by a matrix A that is a constant (it is not dependent on $\mathbf{n}$) the demography depends only on the relative magnitude of the elements of $\mathbf{n}$ rather than on the absolute magnitude of $\mathbf{n}$. This is called a *frequency dependent* system. The system is *density dependent* when absolute population size is important. The projection matrix A then is a function of the vector $\mathbf{n}(t)$. (Caswell *et al.*, 1986).

We first discuss the virtual population analysis that is currently (1999) used internationally to different fish stocks, in Section 6.1. Also a linear model that was introduced as early as 1945 by Leslie (1945) that describes the age distribution of a species at successive time intervals, will be discussed in Section 6.2. Over the years scientists have applied this linear age-class model to many species, see for example the Acto-Norwegian Cod by Reed (1980). Then in Section 6.3 we consider the more general stage-class model described by Getz *et al.* (1989) where the linear Leslie model is modified into a non-linear model, with non-linear density dependent survival during the first year after birth. We also investigate the stability properties of the non-linear model in Section 6.4.

It is often difficult to tell the specific age of a fish that was caught. Therefore size (for example length) classes, rather than age classes, would be more practical. In Section 6.5 we shall discuss a length class model, based on the two-sex-age model of Bergh (1991), and finally apply our proposed model to the Cape Rock Lobster species in Section 6.6.

6.1   Virtual Population Analysis

Virtual population analysis (VPA) is currently (1999) implemented by the International Council for the Exploitation of the Seas (ICES) to different fish stocks, for example the Arctic cod (Sandberg *et al.*, 1998) and the multi-fishery of the English

Channel (Pascoe *et al.*, 1999). These models are age structured and are formulated in terms of numbers, stating that

$$
\begin{bmatrix} \text{numbers alive} \\ \text{at beginning} \\ \text{of next year} \end{bmatrix} = \begin{bmatrix} \text{numbers alive} \\ \text{at beginning} \\ \text{of this year} \end{bmatrix} - \begin{bmatrix} \text{catch} \\ \text{this} \\ \text{year} \end{bmatrix} - \begin{bmatrix} \text{natural} \\ \text{mortality} \\ \text{this year} \end{bmatrix}.
$$

for each cohort of a specific age. Recruitment is only included in the equation of the youngest age group. Take $N_a(t)$ to be the number of fish of age a alive at year t, then

$$
\frac{dN_a}{dt} = -N_a(F + M),
$$

where F is the instantaneous fishing mortality rate and M the natural mortality rate. The number of fish surviving during one year is then

$$
N_a(t + 1) = N_a(t)e^{-(F+M)}
$$

The difference $N_a(t) - N_a(t+1)$ gives the total loss in year t and the catch of a cohort of age a, would thus be

$$
\begin{aligned}
\text{catch}_a(t) &= \frac{F}{F + M}\left(N_a(t) - N_a(t + 1)\right) \\
&= \frac{F \times N_a(t)(1 - e^{-(F+M)})}{F + M}
\end{aligned}
$$

(Hilborn *et al.*, 1992).

6.2 A Modified Leslie Matrix for Linear Stage Structured Models

In this section we will describe the stage-class model as described by Getz *et al.* (1989) that is based on the original Leslie (1954) model. Leslie's model is often implemented when an age distribution is of practical use.

Let the vector

$$\mathbf{x}(t) = \begin{bmatrix} x_1(t) \\ x_2(t) \\ \vdots \\ x_n(t) \end{bmatrix}$$

represent the population, with $x_i(t)$ the number of individuals at stage i and time t. (Without loss of generality we shall take time as years from here onwards.) Let s_i be that proportion of individuals in class i that survive during the time interval $[t, t+1)$. During this time interval a proportion, p_i, of individuals in stage class i, namely $p_i x_i(t)$, where $0 < p_i \le 1$, $i = 1... \ n-1$, have moved to the next stage, while $(1 - p_i)x_i(t)$ remain in class i. So

$$x_{i+1}(t+1) = (1 - p_{i+1})s_{i+1}x_{i+1}(t) + p_i s_i x_i(t), \qquad i = 1, \ldots, n-1.$$

If we define b_i to be the number of zygotes that were born per individual that is currently in stage i, and assume that the newlings immediately enter stage 0 on birth, then

$$x_0(t+1) = \sum_{i=1}^{n} b_i x_i(t+1).$$

The generalized model now becomes

$$\mathbf{x}(t+1) = L\mathbf{x}(t),$$

where

$$L = \begin{bmatrix} (1-p_1)s_1 + b_1 s_0 & s_0 b_2 & \cdots & s_0 b_{n-1} & s_0 b_n \\ p_1 s_1 & (1-p_2)s_2 & 0 & & \\ 0 & p_2 s_2 & \ddots & 0 & \\ \vdots & & 0 & (1-p_{n-1})s_{n-1} & 0 \\ 0 & & 0 & p_{n-1}s_{n-1} & s_n \end{bmatrix}.$$

Matrix L is the Leslie matrix (Leslie, 1945) when $p_i = 1$ for all ages.

Getz *et al.* (1989) described the characteristic polynomial for the eigenvalues of this matrix as

$$\prod_{j=1}^{n} (\lambda - (1 - p_j)s_j) - \sum_{i=1}^{n} s_0 b_i \prod_{j=1}^{i-1} p_j s_j \prod_{j=i+1}^{n} (\lambda - (1 - p_j)s_j) = 0$$

where $\prod_{j=1}^{n}(.) = 1$ and $\prod_{j=n+1}^{n}(.) = 1$,

or

$$\sum_{i=1}^{n} \frac{s_0 b_i}{p_i s_i} \prod_{j=1}^{i} \frac{p_j s_j}{(\lambda - (1 - p_j)s_j)} = 1 \qquad (6.2.1)$$

with $(\lambda - (1 - p_j)s_j) \neq 0$.

For a specific age structured model (that is $x_i(t)$ is the number of individuals of age $i - 1$ at year t) the total population at age $i - 1$ will move to age i in one year, so $p_i = 1$ for all ages. In this case matrix L is the Leslie matrix and,

$$\begin{aligned} x_{i+1}(t+1) &= s_i x_i(t) \\ &= s_i s_{i-1} s_{i-2} \ldots s_0 x_0(t - i), \end{aligned}$$

for $i = 0, \ldots, n - 2$. Now it is convenient to define $l_{i+1} = s_i s_{i-1} \ldots s_0$ with $l_1 = s_0$, so that equation (6.2.1) reduces to

$$\sum_{i=1}^{n} \frac{b_i l_i}{\lambda^i} = 1, \qquad (6.2.2)$$

provided that $\lambda \neq 0$. In Section 6.4 equation (6.2.2) is used to establish stability bounds on the eigenvalues for the steady states of the age structured models considered.

When n is the maximum age expected in the population and $s_n = 0$, then

$$\begin{aligned} x_0(t+1) &= \sum_{i=1}^{n} b_i x_i(t+1) \\ &= b_1 s_0 x_0(t) + b_2 s_1 x_1(t) + b_3 s_2 x_2(t) + \ldots + b_n s_{n-1} x_{n-1}(t) \\ &= b_1 s_0 x_0(t) + b_2 l_2 x_0(t-1) + b_3 l_3 x_0(t-2) + \ldots + b_n l_n x_0(t-n+1) \\ &= \sum_{i=1}^{n} b_i l_i x_0(t - i + 1). \end{aligned}$$

Getz *et al.* (1989) refer to the term $B_0 = \sum_{i=1}^{n} b_i l_i$ as the *net reproduction value* which represents the expected births from one female in her lifespan.

6.3   A Non-linear Age Class Model

Getz *et al.* (1989) have studied a specific (and simpler) age-structured model than was described in Section 6.2. They introduced a non-linear density dependent survival function during the first year after birth as individuals are then most at risk. The linear age-structured model of Section 6.2 (where $p_i = 1$ for all ages) is generalized here to a non-linear model. We know that $x_0(t)$ is the number of newborns at stage t. Now let $\phi(x_0(t))$ be a density-dependent survival function in x_0 during the first year, so that $0 < \phi(x_0(t)) < 1$ and $\phi(0) = 1$, where the survival rate decreases with an increase in density of newborns, that is

$$\frac{d\phi(x_0)}{dx_0} < 0 \qquad \text{for } x_0 > 0.$$

They further assume that the first year's density-dependent survival factor is s_0 and that all subsequent years' survival factors are density-independent. That is

$$x_1(t+1) = s_0 \phi(x_0(t)) x_0(t), \qquad (6.3.1)$$

where

$$x_0(t) = \sum_{i=1}^{n} b_i x_i(t)$$

and

$$x_{i+1}(t+1) = s_i x_i(t), \qquad i = 1, 2, \ldots, n-1.$$

Thus the full non-linear model is now

$$\mathbf{x}(t+1) = A\mathbf{x}(t),$$

where

$$A = \begin{bmatrix} b_1 s_0 \phi(x_0(t)) & b_2 s_0 \phi(x_0(t)) & \cdots & b_{n-1} s_0 \phi(x_0(t)) & b_n s_0 \phi(x_0(t)) \\ s_1 & 0 & & & \\ \vdots & s_2 & \ddots & & \\ & & & 0 & \\ 0 & \cdots & & s_{n-1} & 0 \end{bmatrix}.$$

According to the definition of l_i in the previous section, equation (6.3.1) may be simplified by substituting

$$x_i(t) = \frac{l_i}{l_1} x_1(t - i + 1),$$

so that it becomes

$$x_1(t + 1) = \sum_{i=1}^{n} b_i l_i x_1(t - i + 1) \phi \left(\sum_{i=1}^{n} b_i \frac{l_i}{l_1} x_1(t - i + 1) \right). \qquad (6.3.2)$$

From equation (6.3.2) above it follows that at the steady state, $\mathbf{x}^*$, the zygote equation is

$$\phi(x_0^*) = \frac{1}{\sum_{i=1}^{n} b_i l_i} = \frac{1}{B_0},$$

where B_0 is the net reproduction value as defined in Section 6.2.

The stability properties of this system will be discussed further in the Section 6.4.

6.4   Stability of Steady States in a Non-Linear Age Structured Model

In this section the stability properties of a general non-linear age structured population model as described by Getz *et al.* (1989), are investigated. The discussion uses the theory of linear models, as is discussed in Appendix 9.5, to determine a sufficient condition for stability.

Let

$$\mathbf{x}(t + 1) = \begin{bmatrix} f_1(\mathbf{x}(t)) \\ f_2(\mathbf{x}(t)) \\ \vdots \\ f_n(\mathbf{x}(t)) \end{bmatrix} \qquad (6.4.1)$$

with $\mathbf{x}$ the population *age* distribution as described earlier and f_i a non-linear function of $\mathbf{x}$ for $i = 1, 2, ..., n$. To study the local stability properties of the steady states, as was done in Chapters 4 and 5, we linearize the system about its steady states.

Suppose a steady state solution exists. Let $\hat{\mathbf{x}}$ be such an equilibrium solution for equation (6.4.1). Thus

$$\hat{\mathbf{x}} = \mathbf{f}\left(\hat{\mathbf{x}}\right), \qquad \text{for all } t.$$

To linearize, assume that

$$\mathbf{x}(t) = \hat{\mathbf{x}} + \Delta\mathbf{x}(t) \qquad t = 0, 1, 2, \ldots, \qquad \text{where } |\Delta\mathbf{x}(t)| \ll 1$$

and use the Taylor expansion about $\hat{\mathbf{x}}$. Then

$$\hat{\mathbf{x}} + \Delta\mathbf{x}(t+1) = \mathbf{f}(\hat{\mathbf{x}}\,(t)) + \mathbf{f}'\left(\mathbf{x}(t)\right)\big|_{\mathbf{x}=\hat{\mathbf{x}}} \Delta\mathbf{x}(t) + O\left[\Delta\mathbf{x}(t)^T \cdot \Delta\mathbf{x}(t)\right]$$

where $\mathbf{f}'\left(\mathbf{x}(t)\right)\big|_{\mathbf{x}=\hat{\mathbf{x}}}$ is the Jacobian matrix of f with respect to $\mathbf{x}$ evaluated at $\hat{\mathbf{x}}\,(t)$. The linearized equation therefore is

$$\Delta\mathbf{x}(t+1) = \mathbf{f}'\left(\mathbf{x}(t)\right)\big|_{\mathbf{x}=\hat{\mathbf{x}}} \Delta\mathbf{x}(t)$$

and according to the theory of linear models (see the discussion of Appendix 9.5) the stability depends on the eigenvalues, λ_i, of the Jacobian matrix. Thus, when seeking the non-linear solution in the neighbourhood of $\hat{\mathbf{x}}$ the solution will be stable if $|\lambda_i| < 1$. We should emphasize that the equilibrium solution of the non-linear problem is only locally stable and that linear stability would not guarantee global stability. Naturally it is also true that the equilibrium solution is unstable when $|\lambda_i| > 1$. Thus the condition for the eigenvalues of the Jacobian matrix to be strictly in the unit circle is a necessary and sufficient condition for *local* stability.

We now discuss the stability properties of the system that is described in Section 6.3.

Refer to equations (6.3.1) and (6.3.2) then we know that according to the notation used, $f_1(\mathbf{x}) = s_0 x_0 \phi(x_0)$. For notational simplicity set $k = \frac{d}{dx_0}\left[x_0\phi\left(x_0\right)\right]\big|_{x_0^*}$, then $\frac{d}{dx_i}\left[s_0 x_0 \phi(x_0)\right] = k s_0 b_i$ and the Jacobian matrix is

$$\frac{d\mathbf{f}}{d\mathbf{x}} = \begin{bmatrix} k s_0 b_1 & \ldots & k s_0 b_{n-1} & k s_0 b_n \\ s_1 & 0 & & \\ \vdots & s_2 & \ddots & \\ 0 & & s_{n-1} & 0 \end{bmatrix}. \tag{6.4.2}$$

If k is positive, expression (6.4.2) becomes a Leslie matrix and it is possible to apply the Perron-Frobenius theorem that is discussed in Appendix 9.5.

The characteristic polynomial equation (6.2.2) for the eigenvalues, λ_i, of this Jacobian matrix is

$$k \sum_{i=1}^{n} \frac{b_i l_i}{\lambda_i} = 1,$$

if $\lambda_i \neq 0$ for all i. Thus, the sufficient condition for stability is

$$-1 < k B_0 < 1 \tag{6.4.3}$$

(Bergh *et al.*, 1988).

6.5 A Non-linear Sex Stage Structured Model

Bergh (1991) discussed an *age*-class model where the sexes are separated, that is based on the non-linear optimal age-specific harvesting model of Reed (1980), with density dependence in juvenile mortality. In this section we generalise the model of Bergh and propose a maximum sustainable yield of a sex-*stage* structured model. We shall discuss this more general model here and refer to that of Bergh when there are similarities.

In accordance with the model of Bergh we define the population vectors at the beginning of year t as

$$\mathbf{N}^m(t) = (N_1^m(t), N_2^m(t), N_3^m(t), \ldots, N_n^m(t))^T,$$
$$\mathbf{N}^f(t) = \left(N_1^f(t), N_2^f(t), N_3^f(t), \ldots, N_n^f(t)\right)^T,$$

where $N_i^m(t)$ and $N_i^f(t)$ are the number of individuals (male indicated by m and females by f) that are in stage class i at the beginning of year t. We also assume here that the population breeds at the beginning of the year.

As was done by Bergh, we also define the female fecundity parameter, b_i^f, to be the number of zygotes produced by a single female of class i, per annum, when the number of males of any stage is unlimited. Likewise, define the male fecundity parameter, b_i^m,

as the number of zygotes produced from the participation of a single male of class i per annum, with an unlimited number of females in all stages. The number of zygotes produced when the males are unlimited is defined as

$$F_f(t) = \sum_{i=1}^{n} b_i^f N_i^f(t) \tag{6.5.1}$$

and the number of zygotes produced when the females are unlimited as

$$F_m(t) = \sum_{i=1}^{n} b_i^m N_i^m(t). \tag{6.5.2}$$

As in Chapter 5, let the density dependent function $\psi(\mathbf{N}^m, \mathbf{N}^f)$ be the number of zygotes produced each year taken as a proportion of the number produced when the number of males is unlimited. Then the total number of zygotes produced will be

$$n_0(t) = F_f(t)\psi(\mathbf{N}^m, \mathbf{N}^f).$$

As was motivated before in Section 5.2.1 we assume

$$\psi(\mathbf{N}^m, \mathbf{N}^f) = \frac{F_m(t)}{\kappa + F_f(t) + F_f(t)}.$$

for κ a positive real number. The zygote production is thus density dependent.

It is further assumed that for the eggs-to-recruitment period that there is no competition for space and food so that natural mortality is density independent initially. So, the recruitment function is defined as

$$N_0(t) = \sigma n_0(t),$$

where σ is the density independent juvenile survival factor and

$$N_0(t) = \frac{\sigma F_f(t) F_m(t)}{\kappa + F_f(t) + F_m(t)}. \tag{6.5.3}$$

We assume, for the sake of simplicity, that male and female survivorship after recruitment are density independent. Let the density independent survivorship factors for males and females at stage i be s_i^m, s_i^f respectively, where $0 < s_i^m < 1$ and $0 < s_i^f < 1$,

$i = 0, 1, \ldots, n - 1$. Let r_i^m be the proportion of males of stage i that moved to the next stage in one year, so that $(1 - r_i^m)$ is the proportion that remains in class i, with $(0 < r_i < 1, \; i = 1, \ldots, n - 1)$. Likewise, let the proportion of females of stage i that moved to the next stage in a year be r_i^f, and $(1 - r_i^f)$ the proportion that remains in class i. The number of males and females at stage $i + 1$ will then respectively be

$$N_i^m(t + 1) = s_i^m(1 - r_i^m)N_i^m(t) + s_{i-1}^m r_{i-1}^m N_{i-1}^m(t) \qquad (6.5.4)$$

$$N_i^f(t + 1) = s_i^f(1 - r_i^f)N_i^f(t) + s_{i-1}^f r_{i-1}^f N_{i-1}^f(t). \qquad (6.5.5)$$

Bergh (1991) assumes that half of the juveniles develop into males and the other half into females, that is

$$N_0^f(t) = N_0^m(t) = \frac{N_0(t)}{2},$$

which is possible, but does not necessarily hold in nature. For the sake of simplicity we make the same assumption.

As we have done in Section 6.2 we also define here $l_i^m = s_0^m s_1^m \ldots s_{i-1}^m$ and $l_i^f = s_0^f s_1^f \ldots s_{i-1}^f$, $i = 1, 2, \ldots, n$ where $l_0^m = 1$ and $l_0^f = 1$. At equilibrium, equations (6.5.4) and (6.5.5) will then become

$$N_i^{m*} = \frac{l_i^m \prod_{k=0}^{i-1} r_k^m}{\prod_{k=1}^{i} \left[1 - s_k^m(1 - r_k^m)\right]} \frac{N_0^*}{2} = S_i^m \frac{N_0^*}{2},$$

$$N_i^{f*} = \frac{l_i^f \prod_{k=0}^{i-1} r_k^f}{\prod_{k=1}^{i} \left[1 - s_k^f(1 - r_k^f)\right]} \frac{N_0^*}{2} = S_i^f \frac{N_0^*}{2},$$

for $i = 1, 2, \ldots, n$, where $S_i^m = \frac{l_i^m \prod_{k=0}^{i-1} r_k^m}{\prod_{k=1}^{i}\left[1 - s_k^m(1 - r_k^m)\right]}$ and $S_i^f = \frac{l_i^f \prod_{k=0}^{i-1} r_k^f}{\prod_{k=1}^{i}\left[1 - s_k^f(1 - r_k^f)\right]}$. Equations (6.5.1) and (6.5.2) at equilibrium simplify to

$$F_f^* = \sum_{i=1}^{n} b_i^f S_i^f \frac{N_0^*}{2},$$

$$F_f^* = \sum_{i=1}^{n} b_i^m S_i^m \frac{N_0^*}{2}.$$

6.5.1 Harvesting Strategy

In this section we wish to include the harvesting effort in the model to be able to determine an optimal management strategy. Here we assume that it is possible to

harvest the sexes separately, as is most likely the case for most inshore fisheries.

In accordance with Bergh (1991), we specify that fish are susceptible to harvesting from stage $i = 0$ to $i = n - 1$. Breeding occurs at stages $i = 1$ to $i = n$ and it is also assumed that pulse fishing takes place in the middle of the year. Let u_i^m and u_i^f be the proportion of males and females of stage i that are harvested each year, where $0 < u_i^m < 1$ and $0 < u_i^f < 1$ for $i = 0, 1, \ldots, n - 1$.

Define the parameters h_i^m and h_i^f to be

$$
\begin{aligned}
h_i^m &= (1 - u_0^m)(1 - u_1^m)(1 - u_2^m)\ldots(1 - u_{i-1}^m) \\
h_i^f &= (1 - u_0^f)(1 - u_1^f)(1 - u_2^f)\ldots(1 - u_{i-1}^f).
\end{aligned}
$$

It can now be shown that in this case an equilibrium state will be reached at

$$
\begin{aligned}
N_i^{m*} &= \frac{l_i^m h_i^m \prod_{k=0}^{i-1} r_k^m}{\prod_{k=1}^{i} [1 - s_k^m(1 - u_k^m)(1 - r_k^m)]} \frac{N_0^*}{2} \\
N_i^{f*} &= \frac{l_i^f h_i^f \prod_{k=0}^{i-1} r_k^f}{\prod_{k=1}^{i} \left[1 - s_k^f(1 - u_k^f)(1 - r_k^f)\right]} \frac{N_0^*}{2}.
\end{aligned}
$$

Use the substitutions

$$
R_i^m = \frac{l_i^m \prod_{k=0}^{i-1} r_k^m}{\prod_{k=1}^{i} [1 - s_k^m(1 - u_k^m)(1 - r_k^m)]} \tag{6.5.6}
$$

and

$$
R_i^f = \frac{l_i^f \prod_{k=0}^{i-1} r_k^f}{\prod_{k=1}^{i} \left[1 - s_k^f(1 - u_k^f)(1 - r_k^f)\right]} \tag{6.5.7}
$$

to simplify the expressions to

$$
N_i^{m*} = R_i^m h_i^m \frac{N_0^*}{2}
$$

and

$$
N_i^f = R_i^f h_i^f \frac{N_0^*}{2}.
$$

Define H_0^m and H_0^f to be the *net reproductive potentials*

$$
H_0^f = \sum_{i=1}^{n} b_i^f R_i^f h_i^f \tag{6.5.8}
$$

and

$$H_0^m = \sum_{i=1}^{n} b_i^m R_i^m h_i^m. \tag{6.5.9}$$

Refer to Getz *et al.* (1989) and Bergh (1991) for similar definitions. The substitution of equations (6.5.1) and (6.5.2) in (6.5.3) results in

$$N_0^* = \frac{\sigma H_0^f H_0^m \frac{N_0^{*2}}{4}}{\kappa + H_0^f \frac{N_0^*}{2} + H_0^m \frac{N_0^*}{2}}.$$

This equation has two solutions, namely

$$N_0^1 = 0 \quad \text{and} \quad N_0^2(h) = \frac{\kappa}{\frac{\sigma}{4} H_0^f H_0^m - \frac{1}{2}\left(H_0^m + H_0^f\right)}. \tag{6.5.10}$$

6.5.2 Stability

The stability of these steady state solutions (as discussed in Sections 9.5 and 6.4) depend on the properties of the Jacobian matrix. Let

$$\mathbf{N}(t) = \left[N_1^m(t), N_2^m(t), ..., N_n^m(t), N_1^f(t), N_2^f(t), ..., N_n^f(t)\right]^T.$$

Then, in the notation of Section 6.4, we may write

$$\mathbf{N}(t+1) = \left[f_1\left(\mathbf{N}(t)\right), f_2\left(\mathbf{N}(t)\right), ..., f_{2n}\left(\mathbf{N}(t)\right)\right]^T.$$

More specifically, for the model discussed above the population dynamics is given by

$$
\begin{bmatrix}
N_1^m(t+1) \\
\vdots \\
N_n^m(t+1) \\
\cdots \\
N_1^f(t+1) \\
\vdots \\
N_n^f(t+1)
\end{bmatrix}
= \mathbf{A}
\begin{bmatrix}
N_1^m(t) \\
\vdots \\
N_n^m(t) \\
\cdots \\
N_1^f(t) \\
\vdots \\
N_n^f(t)
\end{bmatrix}
+
\begin{bmatrix}
s_0^m(1 - u_0^m)r_0^m \frac{N_0}{2} \\
0 \\
\vdots \\
0 \\
\cdots \\
s_0^f(1 - u_0^f)r_0^f \frac{N_0}{2} \\
0 \\
\vdots \\
0
\end{bmatrix}.
$$

See Appendix 9.6 for the detailed description of matrix A.

Define $\frac{\partial N_0}{\partial F_m}|_{N_0^*} = D^m$ and $\frac{\partial N_0}{\partial F_f}|_{N_0^*} = D^f$, then the following derivatives that appear in the Jacobian matrix may be expressed as

$$\frac{dN_0(t)}{dN_i^m(t)} = \frac{\partial N_0(t)}{\partial F_m(t)}\frac{\partial F_m(t)}{\partial N_i^m(t)} = \frac{\partial N_0(t)}{\partial F_m(t)}b_i^m = D^m b_i^m$$

and

$$\frac{dN_0(t)}{dN_i^f(t)} = \frac{\partial N_0(t)}{\partial F_f(t)}\frac{\partial F_f(t)}{\partial N_i^f(t)} = \frac{\partial N_0(t)}{\partial F_f(t)}b_i^f = D^f b_i^f.$$

The full Jacobian matrix is described in Appendix 9.6.

Although it is much more complex to determine the eigenvalues of this Jacobian matrix than that of the age-structured model we could establish some upper bounds on the dominant eigenvalue. First we know that the Jacobian matrix is positive and thus, according to the Perron-Frobenius theorem, the spectral radius, λ_Δ, is positive. Secondly we know from the theory of matrix norms (Stewart, 1973) that the spectral radius, λ_C, of any matrix C is bounded by

$$\lambda_C \leq \|C\|,$$

where $\|\cdot\|$ is any consistent matrix norm. Use the norm $\|\cdot\|_\infty = \max_i \left(\sum_{j=1}^n c_{ij}\right)$, where c_{ij} is the ij-th matrix element, then

$$0 < \lambda_\Delta \leq \left\|\frac{\partial \mathbf{f}}{\partial \mathbf{N}}\right\|_\infty.$$

Depending on the harvesting strategy and the survival- and growth rates of the species the maximum row-sum of the Jacobian matrix where $N_0^* = N_0^1$, or $N_0^* = N_0^2$ could both be less than unity. In such circumstances the origin is a stable steady state and a harvesting strategy predicts either extinction or a positive equilibrium state depending on the initial conditions. Care should be taken that the population does not reach conditions where the origin is the attractor, as recovery would then be impossible.

6.5.3 Ultimate Sustainable Yield

We define ultimate sustainable yield (USY) as the maximum sustainable yield over all possible kinds of selective fishing where one is allowed to catch any portion of any stage-class. Then, at mid-year the number of male and female individuals caught in class i in year t, represented by $Y_i^m(t)$ and $Y_i^f(t)$ respectively, are

$$Y_i^m(t) = N_i^m(t)\sqrt{s_i^m(1 - r_i^m)}\, u_i^m$$

and

$$Y_i^f(t) = N_i^f(t)\sqrt{s_i^f(1 - r_i^f)}\, u_i^f.$$

Let w_i^m and w_i^f respectively be the body weight of a single male and female animal of class i. Similarly let p_i^m and p_i^f respectively be the net price per body weight for class i. The total economic yield is therefore

$$Y(t) = \sum_{i=0}^{n-1} \left(N_i^m(t)\sqrt{s_i^m(1 - r_i^m)}\, u_i^m w_i^m p_i^m + N_i^f(t)\sqrt{s_i^f(1 - r_i^f)}\, u_i^f w_i^f p_i^f \right)$$

and at equilibrium

$$Y^* = \sum_{i=0}^{n-1} \frac{N_0^*(h)}{2} \left(R_i^m h_i^m \sqrt{s_i^m(1 - r_i^m)}\, u_i^m w_i^m p_i^m + R_i^f h_i^f \sqrt{s_i^f(1 - r_i^f)}\, u_i^f w_i^f p_i^f \right). \tag{6.5.11}$$

From the definition of h_i we know that $h_i - h_{i+1} = u_i h_i$. Substitute this identity into equation (6.5.11), then

$$Y^* = \sum_{i=0}^{n-1} \frac{N_0^*(h)}{2} \left(R_i^m \sqrt{s_i^m(1 - r_i^m)}(h_i^m - h_{i+1}^m) w_i^m p_i^m + R_i^f \sqrt{s_i^f(1 - r_i^f)}(h_i^f - h_{i+1}^f) w_i^f p_i^f \right) \tag{6.5.12}$$

(Bergh, 1991). We now apply the solution approach that was first introduced by Reed (1980). If the net reproduction potentials, R_i^m and R_i^f are known, the ultimate sustainable yield (that is the proportions of each male and female stages that should be harvested) could be found as a solution of a non-linear programming problem. Equations (6.5.8), (6.5.9) and (6.5.10) and the definition of h_i^m and h_i^f together with equation (6.5.11) define our model, namely

maximize

$$\sum_{i=0}^{n-1} \frac{N_0^*(h)}{2} \left(R_i^m \sqrt{s_i^m(1-r_i^m)}(h_i^m - h_{i+1}^m)w_i^m p_i^m + R_i^f \sqrt{s_i^f(1-r_i^f)}(h_i^f - h_{i+1}^f)w_i^f p_i^f \right)$$

subject to

$$N_0^*(h) \;=\; \frac{\kappa}{\frac{\sigma}{4}H_0^f H_0^m - \frac{1}{2}\left(H_0^m + H_0^f\right)} \tag{6.5.13}$$

$$H_0^m \;=\; \sum_{i=1}^{n} b_i^m R_i^m h_i^m \tag{6.5.14}$$

$$H_0^f \;=\; \sum_{i=1}^{n} b_i^f R_i^f h_i^f \tag{6.5.15}$$

$$N_0^1 \;\leq\; N_0^2$$

$$1 \;=\; h_0^m \geq h_1^m \geq h_2^m \geq \cdots \geq h_n^m \geq 0$$

$$1 \;=\; h_0^f \geq h_1^f \geq h_2^f \geq \cdots \geq h_n^f \geq 0.$$

The following substitution that was suggested by Reed (1980) simplifies the non-linear model to a linear model. Introduce the parameters $z_i^m = h_{i-1}^m - h_i^m$ and $z_i^f = h_{i-1}^f - h_i^f$ for $i = 1, 2, \ldots, n$ and $c_j^m = \sum_{i=j}^{n} b_i^m R_i^m$ and $c_j^f = \sum_{i=j}^{n} b_i^f R_i^f$ for $j = 1, 2, \ldots, n$, then

$$h_i^m \;=\; 1 - \sum_{j=1}^{i} z_j^m$$

$$\text{and} \qquad h_i^f \;=\; 1 - \sum_{j=1}^{i} z_j^f \qquad \text{for } i = 1, 2, \ldots, n$$

and constraints (6.5.14) and (6.5.15) reduce to

$$c_1^m z_1^m + c_2^m z_2^m + \ldots + c_n^m z_n^m \;=\; c_1^m - H_0^m$$

$$c_1^f z_1^f + c_2^f z_2^f + \ldots + c_n^f z_n^f \;=\; c_1^f - H_0^f.$$

The parameters R_i^m in the model are defined in terms of the survival factors, s_i^m, the growth proportions, r_i^m, and harvesting proportions, u_i^m, while the definition of R_i^f is similar (see equations (6.5.6) and (6.5.7)). Note also that once R_i^m and R_i^f are known, the factors H_0^m and H_0^f are also known. Here we assume that the parameters, s_i^m, s_i^f, r_i^m, r_i^f, b_i^m and b_i^f have been estimated. Then the only other unknown parameter sets in R_i^m and R_i^f are the sets u_i^m, u_i^f. However, our problem, unlike that of Reed (1980)

and Bergh (1991), is implicit as R_i^m and R_i^f depend on the harvesting proportions u_i^m and u_i^f respectively, which is not the case in the aforementioned models. We wish to solve this problem by using a recursive procedure where initial values for u_i^m and u_i^f are being estimated.

Our solution is to use the suggestion of Reed (1980) at each iteration and to solve the optimisation problem iteratively as follows.

Take fixed values for the sets u_i^m and u_i^f for all i (that is determine R_i^m and R_i^f) and solve for z_i^m and z_i^f in the linear programming (LP) problem

maximize

$$\sum_{i=0}^{n-1} \frac{N_0^*(h)}{2} \left(R_i^m \sqrt{s_i^m(1-r_i^m)}\, z_{i+1}^m w_i^m p_i^m + R_i^f \sqrt{s_i^f(1-r_i^f)}\, z_{i+1}^f w_i^f p_i^f \right)$$

subject to

$$c_1^m z_1^m + c_2^m z_2^m + \ldots + c_n^m z_n^m \;=\; c_1^m - H_0^m$$

$$c_1^f z_1^f + c_2^f z_2^f + \ldots + c_n^f z_n^f \;=\; c_1^f - H_0^f$$

$$z_1^m + z_2^m + \ldots + z_n^m \;\leq\; 1$$

$$z_1^f + z_2^f + \ldots + z_n^f \;\leq\; 1$$

$$z_i^m \;\geq\; 0, \quad z_i^f \geq 0 \qquad i = 1, 2, \ldots, n$$

by using the simplex algorithm. Now determine new improved values for the sets u_i^m and u_i^f for all i from the solution for the sets z_i^m and z_i^f for all i. Repeat the above procedure until convergence occurs. Rektorys (1969) shows that if the procedure converges the limit is a local optimal solution.

It should be emphasized here that this recursive process will not necessarily converge for every initial set u_i^m and u_i^f used. It could happen that the solution oscillates for bad initial choices.

Note also that the constraints in the model for males and females are independent, which means that the linear programming problem could be separated into two problems, one each for the two sexes.

The theory of the simplex tableau (Winston, 1994) indicates that when the simplex method is used at most four of the sets of variables z_i^m, z_i^f (two of the set of male- and two of the set of females variables) will be nonzero or basis variables as there are four constraints. For the same reason this is also the case for the age-class model. The solution thus implies selective harvesting of both males and females, namely

(a) harvest two stage classes partially, or

(b) harvest one stage class partially, and another completely, or

(c) harvest one stage class partially, or

(d) harvest one class completely, with no other harvesting (Bergh, 1991).

It is interesting to note that bimodal harvesting, that is harvesting of two age classes, was also suggested by earlier age class models (see Rorres *et al.*, 1975) without the use of the simplex method.

6.6   Application to the Cape Rock Lobster

In this section we determine a steady state harvesting strategy for the Cape Rock Lobster species based on the model described in the previous section (see equations (6.5.13), (6.5.14) and (6.5.15)). A biological length based model has been applied to the resource by the Sea Fisheries Research Institute of South Africa between 1992 and 1997 in their efforts to determine a reliable TAC (Johnston *et al.*, 1993). Their model differs from what we aim to do here. Firstly the whole life cycle of the lobster was modelled. Secondly a size class difference of 1mm was used. Also proportions of fish caught in each class were modelled using certain fishing selectivity functions for the different fishing methods (Johnston *et al.*, 1993). The natural survival parameters were set to

$$s_i^m = s_i^f = 0.9 \quad \text{for all } i \geq 70$$
$$s_i^m = s_i^f = (i-1)\frac{(0.9 - 0.01)}{69} + 0.01 \qquad \text{for all } i < 70.$$

Recruitment was assumed to occur in the classes $0-15$ mm at a constant rate, R, and 0 otherwise, and a beta-probability distribution was used to model the movement from one size class to the next.

A maximum likelihood estimation (see Chapter 4) was done by fitting the modelled CPUE to the logged CPUE data set, where parameters that were estimated by the fit are the constant recruitment, R, and the fishing selectivity parameters (Johnston *et al.*, 1995).

A possible shortcoming of Johnston's application is that they attempt to extract too many parameters from a limited time series. (The CPUE time series is only available since 1975 as discussed in Chapter 3.) As more data become available as time passes their approach could become more relevant. For this reason the biological parameters in the model are addressed in a simpler fashion in our bio-economic attempt.

The algorithm based on the bio-economic sex-stage class model, as developed in the previous sections, is applied to the Cape Rock Lobster industry. The species reaches maturity at an average of $60-65$ mm carapace length (Johnston *et al.*, 1993). Here we set classes of 5mm length difference such that $i = 0$ is the class 60 mm to < 65 mm, and $i = 1$, 65 mm to < 70 mm, etc. with $i = 10$ the class ≥ 110 mm (see Table 6.6.1).

6.6.1   Parameter values

Biological parameter sets that are input to the algorithm of Section 6.5, (refer to equations (6.5.6), (6.5.7),(6.5.13), (6.5.14) and (6.5.15)) are the juvenile survival factor, σ, survival factors, s_i^m, s_i^f the growth proportions, r_i^m, r_i^f, fecundity factors, b_i^m, b_i^f, the constant κ and the length-weight conversion factors, w_i^m and w_i^f.

The economic factors that are used in the algorithm, in order to find the maximum yield, are the net prices per animal of size i, that is p_i^m and p_i^f.

Studies on the survival factors were done by Johnston *et al.* (1993) and Cruywagen (1999). Johnston *et al.* (1993) used the sum of squares best fit criterion and informa-

i	Carapace length (mm)	Male Growth Proportion	Female Growth Proportion	Fecundity Parameter
0	60 to < 65	0.85	0.1	64 909
1	65 to < 70	0.8	0.1	82 083
2	70 to < 75	0.8	0.1	99 257
3	75 to < 80	0.7	0	116 430
4	80 to < 85	0.6	0	133 604
5	85 to < 90	0.6	0	150 777
6	90 to < 95	0.5	0	167 952
7	95 to < 100	0.4	0	185 126
8	100 to < 105	0.3	0	202 299
9	105 to < 110	0.2	0	219 473
10	110+	0.016 7	0	236 647

Table 6.6.1: *Parameters that were used in the sex-stage class algorithm for the Cape Rock Lobster resource.*

tion on somatic growth rates. The results have shown variable estimates of natural survivorship in the range $0.88 < s_i < 0.95$ for both sexes. Cruywagen (1999) used the Ford-Walford model (see Appendix 9.3) with adjustment terms for years and areas, and agrees that for both sexes the range $0.88 < s_i < 0.95$ is plausible. Here we compare the outcome of different applications, using three constant values of (i) $s_i^m = s_i^f = 0.9$, (ii) $s_i^m = s_i^f = 0.88$ and (iii) $s_i^m = s_i^f = 0.95$, each taken for the whole adult population.

The juvenile survival is probably much smaller and taken at 0.45 for each juvenile year till it reaches maturity six years later. This figure is not based on scientific evidence, but due to lack of data we took an average number between 0 and 0.9. Thus after six years the survival factor, σ, accumulates to 0.01.

The value of κ is taken as 1×10^{10} which is a realistic order size.

In order to determine the proportion of class i that grows to class $i+1$ we use the general

Ford-Walford growth relationship for the Cape Rock Lobster, used by Cruywagen (1999), where l_t is the length at the beginning of year t and L_t the length at the end of year t. The relations used are averaged over all years and all areas, namely,

$$L_t = 10.064\,5 + 0.922\,4 l_t \quad \text{for males and}$$

$$L_t = 1.421\,1 + 0.982\,1 l_t \quad \text{for females.}$$

Assume that the lengths of the population in class i are evenly spaced, then with the use of the above equations we can determine approximately that proportion of the class that will transfer to the next size class in one year. The results are given in Table 6.6.1. (Refer also to Melville-Smith (1993) for information on the growth of the species). Note that the above growth equation for females indicate hardly any growth after a 75 mm carapace length is reached. Cruywagen (1999) has shown with a multifactor model that growth factors for both males and females are currently much lower than in the past.

The third set, namely the fecundity parameters, are the most difficult to determine. Survey data are available and list the female size and the number of eggs per female per sample taken (see Chapter 3). We have fitted linear relations through these data sets and the average fit of this relationship is

$$\text{number of eggs} = 3\,435 \times \text{length(mm)} - 141\,177 \tag{6.6.1}$$

Some of these linear fits are given in Appendix (9.8.1) with the numerical values for the intercept and slope coefficients given in Table 9.8.7.

The lowest carapace lengths are taken in each class and the number of eggs, according to equation (6.6.1), is set equal to the fecundity parameter, b_i^f. There are no scientific data available on the male fecundity, thus we assume the male fecundity, b_i^m, is equal to that of the females because mating occurs only once a year (see Chapter 3). These numbers are also listed in Table 6.6.1.

The net price is measured in Rand per kilogram and it is thus necessary to convert the

catch measured in length into weights. The length-weight conversion that was used is

$$w_i^m(\text{kg}) \quad = \quad 0.822\,445 \times l_i^{2.89} \text{ (mm)}$$

$$w_i^f(\text{kg}) \quad = \quad 0.624\,689 \times l_i^{2.97} \text{ (mm)}$$

(Heydorn, 1969).

Prices for classes 0 to 3 (column 1 of Table 6.6.2) differ from that of classes 4 to 10 (column 2 of Table 6.6.2) as it sometimes happens that smaller animals are sold at a higher price.

6.6.2   Results and Discussion

p_0 to p_3	p_4 to p_{10}	$\mathbf{u^m} = \mathbf{0}$	$u_6^m = 0.2$	$u_7^m = 0.2$	$u_8^m = 0.2$
120	90	$u_9^m = 1$	$u_6^m = 0.222$ $u_9^m = 1$	$u_6^m = 0.144$ $u_9^m = 1$	$u_6^m = 0.067$ $u_9^m = 1$
90	120	$u_9^m = 1$	$u_6^m = 0.222$ $u_9^m = 1$	$u_6^m = 0.144$ $u_9^m = 1$	$u_6^m = 0.067$ $u_9^m = 1$
140	90	$u_9^m = 1$	$u_6^m = 0.222$ $u_9^m = 1$	$u_8^m = 0.144$ $u_9^m = 1$	$u_6^m = 0.067$ $u_9^m = 1$
100	100	$u_9^m = 1$	$u_6^m = 0.222$ $u_9^m = 1$	$u_8^m = 0.144$ $u_9^m = 1$	$u_6^m = 0.067$ $u_9^m = 1$

Table 6.6.2: *Output of the sex-stage class algorithm for the male catch proportions where the catch proportions in the first row were taken as input and survival, s = 0.9. The first column indicates the constant net price per kg fish at stages 0 to 3 and the second for stages 4 to 10. (Elements of male specific catch, $\mathbf{u^m}$, not in the table are zero.)*

The male and female catches can be solved separately, as explained earlier, due to the independent constraints. Some results of the algorithm are given in Tables 6.6.2, 6.6.3 and 6.6.4 where the catch proportions in the first line are taken as initial values and the

values in the table as the proportions to which the algorithm has converged. Tables 6.6.2 and 6.6.3 show the output of the sex-stage class algorithm for the male catch proportions. In the first table the adult survival factor is assumed to be $s_i^m = 0.9$ (see Section 3.3) with each solution obtained using different initial values. For example, if we set each element of the vector $\mathbf{u^m}$ as zero except $u_6^m = 0.2$, then the algorithm converges to the only non-zero values $u_6^m = 0.222$ and $u_9^m = 1$. This result indicates that maximum economic yield will be obtained when the catch in the male group is restricted to lengths greater than 90 mm. Similar results are reached using various sets of initial values.

It is interesting to find that in all cases the net price values do not influence the proposed proportions. Note that although the prices of the smaller stage classes were greater in some cases the model does not indicate a catch in the smaller classes.

Table 6.6.3 shows the results of the algorithm for male catch proportions where the adult survival factor is taken $s_i^m = 0.88$. Here the convergence is reached at slightly different proportions but at the same age groups as is the case with $s_i^m = 0.9$ (Table 6.6.2).

Results of the third case where $s_i^m = 0.95$, are not listed here, but are similar to the previous two cases. For example, the results $u_6^m = 0.229$ and $u_9^m = 1$ are reached from the initial condition $u_6^m = 0.2$. We could thus conclude that the final proportions are influenced by the survival factor, s_i^m, however it does not drastically change harvesting strategies. Table 6.6.4 shows the results for the female catch proportions. For the three cases $s_i^f = 0.9$, $s_i^f = 0.88$ and $s_i^f = 0.95$ the results were exactly the same, with the proportion proposed by the model in all cases $u_3^f = 1$. The 75 mm to 80 mm length class is indicated for catch targeting as female growth after 75 mm carapace lengths is almost zero as is shown in Tabel 6.6.1. It should again be emphasized that the outcome is not influenced at all by the price factors.

p_0 to p_3	p_4 to p_{10}	$\mathbf{u^m} = \mathbf{0}$	$u_6^m = 0.2$	$u_7^m = 0.2$	$u_8^m = 0.2$
120	90	$u_9^m = 1$	$u_6^m = 0.219$	$u_6^m = 0.133$	$u_6^m = 0.059$
			$u_9^m = 1$	$u_9^m = 1$	$u_9^m = 1$
90	120	$u_9^m = 1$	$u_6^m = 0.219$	$u_6^m = 0.133$	$u_6^m = 0.059$
			$u_9^m = 1$	$u_9^m = 1$	$u_9^m = 1$
140	90	$u_9^m = 1$	$u_6^m = 0.219$	$u_6^m = 0.133$	$u_6^m = 0.059$
			$u_9^m = 1$	$u_9^m = 1$	$u_9^m = 1$
100	100	$u_9^m = 1$	$u_6^m = 0.219$	$u_6^m = 0.133$	$u_6^m = 0.059$
			$u_9^m = 1$	$u_9^m = 1$	$u_9^m = 1$

Table 6.6.3: *Output of the sex-stage class algorithm for the male catch proportions where the catch proportions in the first row were taken as input and survival, $s = 0.88$. The first column indicates the constant net price per kg fish at stages 0 to 3 and the second for stages 4 to 10. (Elements of male specific catch, $\mathbf{u^m}$, not in the table are zero.)*

6.7 Conclusion

In this chapter we have considered the stage class models and specifically addressed the stability properties of the linear and non-linear models. Using the Perron-Frobenius theorem a sufficient condition for stability was determined. In all cases the stability of the steady state depends on the properties of the eigenvalues of the Jacobian matrix of the original projection matrix in the model.

Bergh's (1991) specific age-class model for two sexes was generalised and we proposed a bio-economic sex-stage class model. Due to the iterative properties of this model the solution thereof becomes much more involved. The non-linear programming problem was solved using a numerical algorithm that incorporates the simplex algorithm. This algorithm is based on the work by Reed (1980). We applied the generalized model to the Cape Rock Lobster resource to find a sustainable harvesting strategy for specific size classes.

p_0 to p_3	p_4 to p_{10}	$\mathbf{u^f} = \mathbf{0}$	$u_6^f = 0.2$	$u_7^f = 0.2$	$u_8^f = 0.2$
120	90	$u_3^f = 1$	$u_3^f = 1$	$u_3^f = 1$	$u_3^f = 1$
90	120	$u_3^f = 1$	$u_3^f = 1$	$u_3^f = 1$	$u_3^f = 1$
140	90	$u_3^f = 1$	$u_3^f = 1$	$u_3^f = 1$	$u_3^f = 1$
100	100	$u_3^f = 1$	$u_3^f = 1$	$u_3^f = 1$	$u_3^f = 1$

Table 6.6.4: *Output of the sex-stage class algorithm for the female catch proportions where the catch proportions in the first were taken as input. The first column indicates the constant net price per kg fish at stages 0 to 3 and the second for stages 4 to 10. (Elements of female specific catch, $\mathbf{u_f}$ not in the table are zero.)*

Although the results seem rewarding, the algorithm does not always converge to one solution, but rather oscillates between two or three values depending on the initial estimate.

It might not always be practical to harvest males and females of a species separately but when it is possible these results could help in finding the optimal classes to target for harvesting. Note that the results that were discussed above is valid only once the stable steady state is reached. If the species is not in this state it should be managed towards such a state.

The inclusion of the maximum economic yield in the model addresses the bio-economic arguments that were discussed in Chapter 2. These results could be trusted to better ensure a sustainable fishery, in contrast with a modelling approach where only biological factors are included. In our model the net price was taken as a constant, but in some cases the market price could be determined by availability and a variable to this effect should be included in the model.

It is also important to have better knowledge of the biological parameters in the model, but the results show that it is possible to apply the algorithm successfully. This model may be helpful to set size limits when managers are to determine a harvesting strategy that is also economically viable.

Chapter 7

Reaction Diffusion Models

In previous chapters we assumed that the population distribution is in a homogeneous environment where spatial factors are constant. In other words the population dynamics are not influenced by spatial variation. In this chapter we extend the surplus production model of Chapter 4 to include spatial movement of the population.

Animals usually move around in a random way. In some species there might occur some interaction between individuals such that they flock together in groups, for example, fish schools. Another phenomenon is the movement from weak to better conditions in a non-homogeneous environment (Okuba, 1980). An example of such spatial differences is where warmer sea currents enter the fish habitat due to the movement of the water. Individuals that find themselves in an environment where conditions differ might move to areas where, for example, density and concentration are more favourable. Suppose that for reasons such as harvesting, the population density is unevenly distributed over some area. We assume that when there is no interference with the population, through competition for space and food, the population will eventually become evenly spread with the passing of time. If we consider one animal as a particle in a system of particles, such a movement may be described by a diffusion process (Murray, 1989). Shigesada *et al.* (1986) use the travelling wave solution of a reaction-diffusion system and analysed the propagation of the frontal wave in a heterogeneous unbounded habitat.

The next section will discuss diffusion in general and define the reaction-diffusion

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models as it is applied in biology and ecology. One such equation is the classical Fisher equation that is discussed in Section 7.1. In the following sections we investigate a travelling wave solution to such a reaction-diffusion population model. In Section 7.2 we propose an adjusted Fisher equation for a fishery and study the conditions to have a travelling wave solution with a spatially homogeneous harvesting strategy. We find a perturbation solution for the travelling wave and illustrate the travelling wave effect numerically. In Section 7.3 we investigate the new proposed model with a non-homogeneous harvesting strategy. A spatially periodic harvesting strategy is used when stability of the zero level steady state is investigated. We also illustrate the travelling wave effect here, using the same approach as Section 7.2. Finally, we investigate the bio-economic model in Section 7.4 for the periodic harvesting strategy. This analysis is used to determine an optimal feasible effort level for harvesting at maximum total present value.

7.1   The Fisher Equation

To be complete we shall firstly discuss diffusivity, defined to be the phenomenon by which a system of particles spreads according to the irregular motion of each particle.

Fickian diffusion in one dimension is when the flux, J, of particles, in our case fish, is proportional to the gradient of the concentration of the population (Murray, 1989). Thus

$$J \propto -\frac{\partial N}{\partial x} \Rightarrow J = -D\frac{\partial N}{\partial x}$$

where N is the population density, D the diffusivity function and x the one dimentional spatial variable.

We now show how the conservation argument in a general natural environment may be used to define a reaction-diffusion model. The rate of change of the number of animals in space, V, is equal to the number that crossed the surface of that space, S,

plus the growth in that space. Thus

$$\frac{\partial}{\partial t} \int_V N(\mathbf{x}, t) dv = -\int_s \mathbf{J} \cdot \mathbf{ds} + \int_V f(N, \mathbf{x}, t) dv, \qquad (7.1.1)$$

where $\mathbf{J}$ is the flux and f the growth of the population (Murray, 1989). When we apply the divergence theorem, namely

$$\int_V \nabla \cdot \mathbf{J} dv = \int_S \mathbf{J} \cdot \mathbf{ds},$$

to equation (7.1.1) we get

$$\int_V \left[\frac{\partial N}{\partial t} + \nabla \cdot \mathbf{J} - f(N, \mathbf{x}, t) \right] dv = 0. \qquad (7.1.2)$$

When we use the classical diffusion relation where

$$\mathbf{J} = -D(\mathbf{x}, N) \nabla N,$$

equation (7.1.2) results in

$$\frac{\partial N}{\partial t} = f + \nabla \cdot (D \nabla N). \qquad (7.1.3)$$

Such a system is referred to as a *reaction-diffusion* system (Murray, 1989). When the function D is constant, equation (7.1.3) simplifies to

$$N_t = f(N, \mathbf{x}, t) + D \nabla^2 N.$$

Usually the initial conditions, being the initial population, for such a system is known, say

$$N(\mathbf{x}, 0) = g(\mathbf{x}), \quad \text{where} \quad \phi_0 < \mathbf{x} < \phi_1.$$

Here $g(\mathbf{x})$ is a function of $\mathbf{x}$, and so the solution for this initial value problem is sought.

A classical reaction-diffusion partial differential equation in one dimension is the Fisher equation, namely

$$\frac{\partial n(x, t)}{\partial t} = \underbrace{rn(x, t) \left(1 - n(x, t)\right)}_{f(n, x, t)} + D \frac{\partial^2 n}{\partial x^2}(x, t),$$

where $n(x,t)$ is the density of an entity at position, x, and at time, t (Fisher, 1937). The first term on the right is the logistic growth function with r the natural growth factor of the entity while diffusion occurs in space at a constant rate, D.

As populations do not grow to infinite sizes, but given constant environmental factors they reach steady state solutions. The inclusion of spatial effects gives one the ability to model spatially non-homogeneous external effects on the population. In this chapter we shall in particular consider a travelling wave-type solution to the above initial value problem.

If a partial differential equation in the function $u(x,t)$ may be simplified to an ordinary differential equation in $U(z)$, by using the transformation $z = x + ct$ (or $z = x - ct$) it may have a travelling wave solution. That is, it is assumed that the solution $u(x,t) = U(z)$. When the specific initial and boundary values are also satisfied a travelling wave solution exists with wave speed c (Murray, 1989). Figure 7.1.1 illustrates a wave that has travelled a distance ct during a time span of t units.
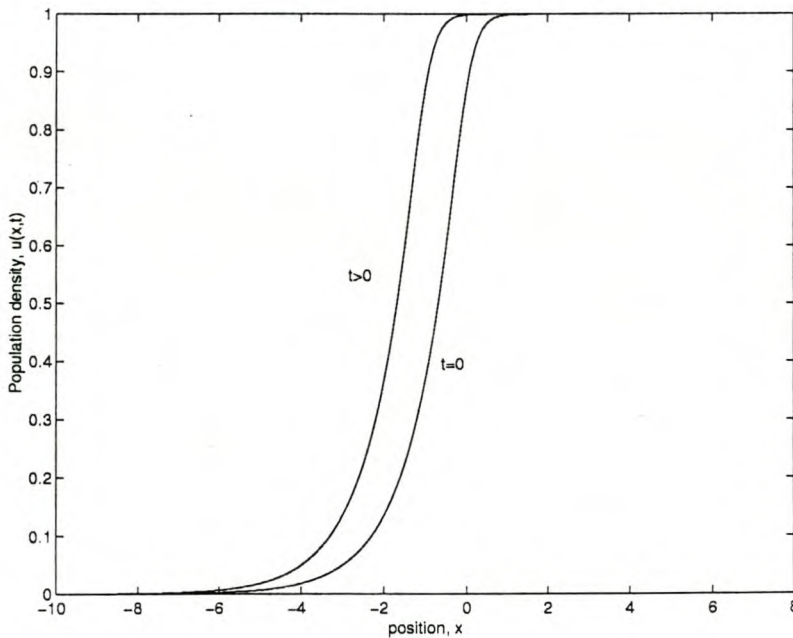
Figure 7.1.1: *Example of the movement of a travelling wave with wave speed c, and $z = x + ct$.*

7.2 Biological Modelling with an Adjusted Fisher's Equation

Here, we modify the Fisher equation and propose a reaction-diffusion equation for modelling fish populations that includes harvesting. We find a travelling wave solution to a population distribution in space, in one dimension, at a certain time.

Take $N(x,t)$ to be the stock density at area x at time t, and define a harvest function, similar to that in Chapter 4, as

$$H(N,x,t) = q(x)E(N,x,t)N(x,t)$$

where q is the catchability function and E is the effort function. Instead of using the logistic function as population growth function we use the more general Pella-Tomlinson function as discussed in Chapter 4. The model that includes harvesting is then

$$\frac{\partial N(x,t)}{\partial t} = \overbrace{rN(x,t)\left[1 - \left(\frac{N(x,t)}{K}\right)^{\alpha}\right]}^{\text{growth}} + \overbrace{D\frac{\partial^2 N(x,t)}{\partial x^2}}^{\text{diffusion}} - \overbrace{q(x)E(x)N(x,t)}^{\text{harvest}}, \quad (7.2.1)$$

where r is the intrinsic growth rate, K is the carrying capacity, D the diffusivity constant and $\alpha > 0$ a shape parameter. We call equation (7.2.1) the *adjusted Fisher's equation.*

The dimension of r and that of the fishing mortality, qE, is [time^{-1}], with that of D, [length^2/time]. To non-dimensionalise the differential equation, we set

$$T = rt$$
$$X = \sqrt{\frac{r}{D}}x$$
$$R = \frac{(r - qE)}{r}.$$

Equation (7.2.1) in terms of the non-dimensional variables, X and T, where

$$N(x,t) = P(X,T)$$

and

$$\frac{\partial N}{\partial t} = r\frac{\partial P}{\partial T}, \qquad \frac{\partial^2 N}{\partial x^2} = \frac{r}{D}\frac{\partial^2 P}{\partial x^2}$$

is

$$P_T = RP - \frac{1}{K^\alpha}P^{\alpha+1} + P_{XX}. \tag{7.2.2}$$

Let $U = \frac{1}{K}P$, then

$$U_T = RU - U^{\alpha+1} + U_{XX}. \tag{7.2.3}$$

7.2.1   Spatially Homogeneous Harvesting

Murray (1989) has shown, for the Fisher equation (7.1), that a spatially homogeneous situation is

$$n_t = rn(1-n)$$

and the steady states are $n = 0$ and $n = 1$ which are respectively unstable and stable. Here we carry out a similar analysis on equation (7.2.3). In the spatially homogeneous situation equation (7.2.3) is

$$U_T = U(R - U^\alpha) = f(U).$$

In this case, the linearized solution is unstable, at the steady state $U = 0$, because $f'(0) = R > 0$, and at $U = R^{\frac{1}{\alpha}}$, it is stable as $f'(R^{\frac{1}{\alpha}}) = -\alpha R < 0$.

Travelling Wave Solution

We now obtain the travelling wave solution for (7.2.3) in the interval $0 \le U \le R^{\frac{1}{\alpha}}$.

The transformation $z = X + cT$, $c > 0$ will result in a wave that travels to $x \to -\infty$ with wave speed c. Then

$$U_X = U_z, \qquad U_T = cU_z$$

and the partial differential equation reduces to an ordinary differential equation

$$cU_z = U(R - U^\alpha) + U_{zz}. \tag{7.2.4}$$

We simplify this equation to a set of first order differential equations, namely

$$U_z = V = f(U, V)$$

$$V_z = cV - U(R - U^\alpha) = g(U, V)$$

and linearize about the non-trivial steady states. Thus the stability of a steady state depends on the Jacobian matrix

$$A = \begin{bmatrix} \frac{\partial f}{\partial U} & \frac{\partial g}{\partial U} \\ \frac{\partial f}{\partial V} & \frac{\partial g}{\partial V} \end{bmatrix}_{(U^*, V^*)}$$

$$= \begin{bmatrix} 0 & 1 \\ -R + (\alpha + 1)U^\alpha & c \end{bmatrix}_{(U^*, V^*)}.$$

If $(U^*, V^*) = (0, 0)$, then the eigenvalues of A are

$$\lambda = \frac{c \pm \sqrt{c^2 - 4R}}{2}.$$

If $Re(\lambda) > 0$ this will be a unstable node in the phase plane, which is the case for $c > c_{\min} = 2\sqrt{R}$. If $c < c_{min}$ it indicates an unstable spiral. For the spiral solution $U < 0$ for some values of z, which is not realistic and therefore the relation $c > c_{\min} = 2\sqrt{R}$, should be true.

When $(U^*, V^*) = (R^{\frac{1}{\alpha}}, 0)$ the eigenvalues are

$$\lambda = \frac{c \pm \sqrt{c^2 + 4\alpha R}}{2}$$

so that the two roots $\lambda_1 \geq 0$ and $\lambda_2 \leq 0$, thus indicating a saddle point. Figure 7.2.1 illustrates the dynamics of such a solution, where one trajectory connects $(0, 0)$ to $(R^{\frac{1}{\alpha}}, 0)$ as z increases. Given the conditions that $U \to R^{\frac{1}{\alpha}}$ as $z \to \infty$ and $U \to 0$ as $z \to -\infty$, only one such solution, $U(z)$, exists represented in Figure 7.2.1(b). This
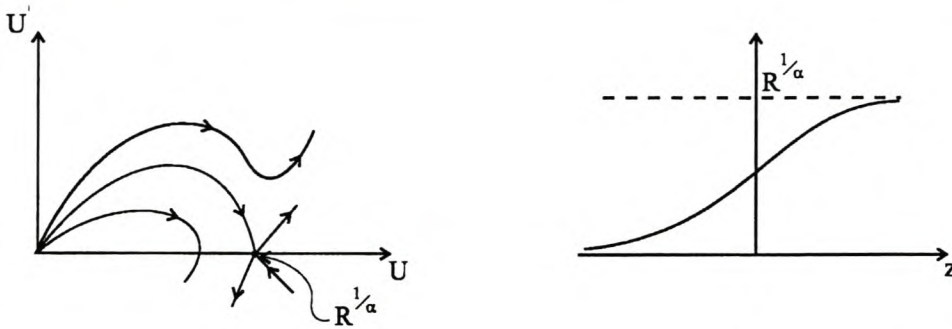
Figure 7.2.1: *(a) Phase plane of equation (7.2.4). (b) Solution of separatrix in phase plane in (a).*

unique solution, which is fixed in z, corresponds to the separatrix in the phase plane in Figure 7.2.1(a). See Grimshaw (1990) for the explanation and definition of the stable manifold.

Equation (7.2.2) is invariant when $x \to -x$ which means that we could also use the transformation $z' = -x + ct$ with exactly the same results. Note also that the solution for $U(-z') = U(x - ct)$ is the mirror image of that of $U(z) = U(x + ct)$. The solution will thus be symmetric about $x = 0$ with an initial condition such as in Figure 7.2.2. The wave front moves to the right and the left as indicated, with wave speed $c > 0$.
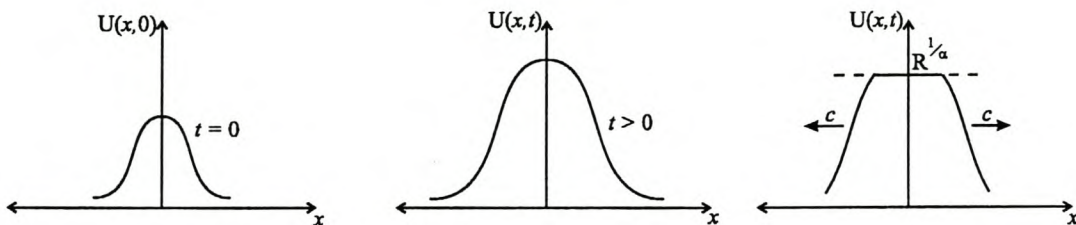
Figure 7.2.2: *Example of travelling wave front as time increases.*

7.2.2   Perturbation Solution

Here we attempt to obtain a perturbation solution for the travelling wave. We use the same methodology as Murray (1989). We know that the parameter $\frac{1}{c^2}$ is small and therefore set $\rho = \frac{1}{c^2}$ such that $\rho \ll 1$, to find the perturbation solution. Use the transformation $s = \frac{z}{c}$, where $U(z) = g(s)$, so that

$$U_z = \frac{1}{c}g_s$$

$$U_{zz} = \frac{1}{c^2}g_{ss} = \rho g_{ss}.$$

Equation (7.2.4) then becomes

$$\rho g_{ss} + g(R - g^\alpha) - g_s = 0 \tag{7.2.5}$$

$$g(-\infty) = 0, \qquad g(\infty) = R^{\frac{1}{\alpha}}.$$

Now we look for a perturbation solution for equation (7.2.5) in ρ. Thus expand $g(s)$ in the form

$$g(s) = g_0(s) + \rho g_1(s) + \rho^2 g_2(s) + \dots$$

so that

$$\frac{\partial g}{\partial s} = \frac{\partial g_0}{\partial s} + \rho \frac{\partial g_1}{\partial s} + \rho^2 \frac{\partial g_2}{\partial s} + \dots$$

Substitute these expansions into (7.2.5), then

$$\rho \left\{ (g_0)_{ss} + \rho(g_1)_{ss} + \rho^2(g_2)_{ss} + \dots \right\} - \left\{ (g_0)_s + \rho(g_1)_s + \rho^2(g_2)_s + \dots \right\}$$
$$= -\left\{ g_0 + \rho g_1 + \rho^2 g_2 + \dots \right\} \left[R - \left\{ g_0 + \rho g_1 + \rho^2 g_2 + \dots \right\}^\alpha \right].$$

Equating terms of the same order of magnitude gives:

$$O(1) \quad : \quad -(g_0)_s + (g_0)R - (g_0)^{\alpha+1} = 0 \tag{7.2.6}$$

$$O(\rho) \quad : \quad (g_0)_{ss} - (g_1)_s + (g_1)R - (\alpha+1)g_0^\alpha g_1 = 0 \tag{7.2.7}$$

$$O(\rho^2) \quad : \quad (g_3)_{ss} - (g_2)_s + (g_2)R - \left(\alpha + \frac{\alpha(\alpha-1)}{2}\right)(g_0)^{\alpha-1}(g_1)^2$$

$$-(\alpha+1)g_0^\alpha g_2 = 0. \tag{7.2.8}$$

The solution of (7.2.6) is the solution of the integral equation

$$\int \frac{dg_0}{g_0 \left(R - (g_0)^\alpha\right)} = \int ds + C$$

with C an arbitrary constant. Integration gives

$$(g_0)^\alpha \left(C_0 e^{-\alpha Rs} + 1\right) = R$$

or

$$g_0 = \left[\frac{R}{C_0 e^{-\alpha Rs} + 1}\right]^{\frac{1}{\alpha}},$$

with C_0 a constant.

Without any loss of generality take $U(0) = \left[\frac{R}{2}\right]^{\frac{1}{\alpha}}$, thus we require $g(0, \rho) = \left[\frac{R}{2}\right]^{\frac{1}{\alpha}}$. The boundary conditions at $\pm\infty$ are

$$g_0(0) = \left[\frac{R}{2}\right]^{\frac{1}{\alpha}}, \qquad g_0(-\infty) = 0, \qquad g_0(\infty) = R^{\frac{1}{\alpha}}, \quad \text{and}$$

$$g_i(0) = 0, \qquad g_i(-\infty) = 0, \qquad g_i(\infty) = 0, \qquad\qquad (7.2.9)$$

then $C_0 = 1$.

With coefficient g_0 known, it is possible to solve equation (7.2.7), that is

$$(g_1)_s - g_1 \left(R - (\alpha + 1)g_0^\alpha\right) = (g_0)_{ss}.$$

From equation (7.2.6) we know that

$$\left[\frac{(g_0)_{ss}}{(g_0)_s}\right] = R - (\alpha + 1)g_0^\alpha. \qquad\qquad (7.2.10)$$

Substitute (7.2.10) in equation (7.2.7), then

$$(g_1)_s - \left[\frac{(g_0)_{ss}}{(g_0)_s}\right] g_1 = (g_0)_{ss}.$$

Using an integration factor of $\frac{1}{(g_0)_s}$, we obtain

$$\frac{1}{(g_0)_s} g_1 = \int \left[\frac{(g_0)_{ss}}{(g_0)_s}\right] ds + K,$$

where K is an arbitrary constant. When we apply the boundary conditions (7.2.9), the solution for g_1 is

$$g_1(s) = \left[\frac{R}{(1 + e^{-\alpha Rs})} \right]^{\frac{1}{\alpha}+1} e^{-\alpha Rs} \left[\ln \frac{2^{\alpha+1} e^{Rs}}{(1 + e^{Rs})^{\alpha+1}} \right].$$

Figure 7.2.3 illustrates the relative small contribution g_1 has to the solution compared to g_0, when using parameter values of $R = 0.5$, $c = 2$ and $\alpha = 1$. Thus we could expect to get highly accurate solutions using only one or two terms in the asymptotic expansion. Thus

$$U(z) = \left[\frac{R}{C_0 e^{-\frac{\alpha Rz}{c}} + 1} \right]^{\frac{1}{\alpha}} + \frac{1}{c^2} \left[\frac{R}{(1 + e^{-\frac{\alpha Rz}{c}})} \right]^{\frac{1}{\alpha}+1} e^{-\frac{\alpha Rz}{c}} \left[\ln \frac{2^{\alpha+1} e^{\frac{Rz}{c}}}{(1 + e^{\frac{Rz}{c}})^{\alpha+1}} \right] + O(c^{-4}).$$
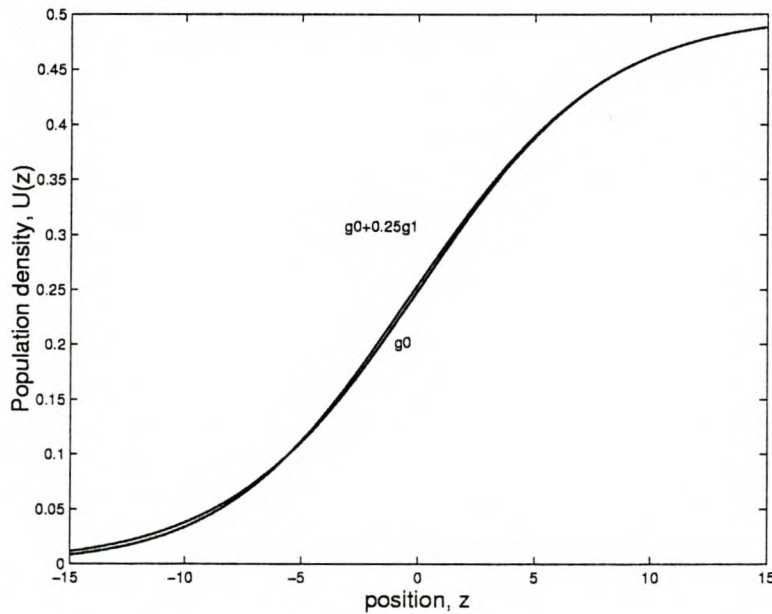
Figure 7.2.3: *Perturbation solutions g_0 and $g_0 + \rho g_1$ taking parameter values $R = 0.5$, $c = 2$ and $\alpha = 1$.*

7.2.3 Numerical Solution

In this section we find a numerical solution to equation (7.2.3). In the application of a finite difference method to equation (7.2.3) we divide the interval $[0, X]$ into $N + 1$

subintervals, such that $x_\iota = \iota h$, where $h = \frac{X}{N+1}$. Let t_j be a specific time where the solution is to be found and $k = \Delta t = t_{j+1} - t_j$ such that the finite difference solution $v_{\iota j} \approx U(x_\iota, t_j)$. The Euler finite difference method (Smith, 1978) gives

$$\frac{v_{\iota,j+1} - v_{\iota,j}}{k} = v_{\iota,j}(R - v_{\iota,j}^\alpha) + \frac{v_{\iota+1,j} - 2v_{\iota,j} + v_{\iota-1,j}}{h^2}$$

or

$$v_{\iota,j+1} = v_{\iota,j}(Rk+1) - kv_{\iota,j}^{\alpha+1} + \sigma(v_{\iota+1,j} - 2v_{\iota,j} + v_{\iota-1,j}),$$

with

$$v_{1,j} = v_{0,j} \quad \text{and} \quad v_{N+1,j} = v_{N,j}$$

where $\sigma = \frac{k}{h^2} < \frac{1}{2}$.

Table 7.2.1 illustrates the numerical solutions after i iterations with $U = 1$ initially, where $\sigma = 0.3$, $R = 0.5$ and $\alpha = 1$ for example (a) and $\alpha = 5$ for example (b). Note that the solution for example (a) converges to the steady state solution $U = 0.5$, while the solution of Figure 5.5 (b) converges to the steady state solution $U = (0.5)^{\frac{1}{5}}$. These results agree with the analytical expectation.

i-th iteration	parameter, $\alpha = 1$	parameter, $\alpha = 5$
10	0.9867	0.9873
100	0.8785	0.9189
500	0.6547	0.8726
2000	0.5127	0.8706
2500	0.5059	0.8706
4000	0.5006	0.8706
5000	0.5001	0.8706

Table 7.2.1: *Numerical solution of homogeneous system of equation (7.2.3) after i iterations when $\sigma = 0.3$, $R = 0.5$.*

In Figure 7.2.4 we illustrate the travelling wave effect where we have introduced initially only a few fish at the origin. Notice the growth in both directions to eventually reach the steady state $U = (0.5)^{\frac{1}{5}}$.
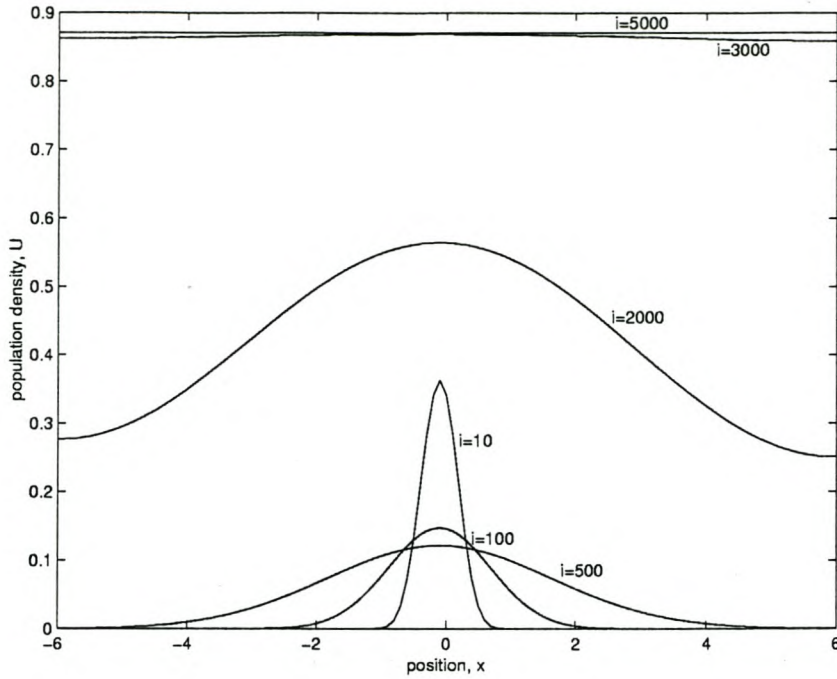
Figure 7.2.4: *Numerical solution of homogeneous system of equation (7.2.3) with only a few fish introduced at the origin for $\sigma = 0.3$, $R = 0.5$ and $\alpha = 5$. (Here i indicates the number of iterations.)*

7.3 Non-homogeneous Harvesting

When effort is a periodic function in space with constant steps such that

$$qE = \begin{cases} \varepsilon, & ml < x < ml + l_1 \\ 0, & ml + l_1 < x < ml + l_1 + l_2 \end{cases}, \qquad m = 0, \pm 1, \pm 2, \ldots$$

where $\varepsilon > 0$ and $l > 0$, there will be discontinuities on the boundaries where $x = ml + l_1$. Figure 7.3.1 illustrates the effort levels in periodic lanes with lengths l_1 and l_2 respectively.

We assume that the solution $N(x,t)$ is continuous at the boundaries and therefore the conditions

$$\lim_{x \to x_m^+} N(x,t) = \lim_{x \to x_m^-} N(x,t), \qquad \text{for all } m$$
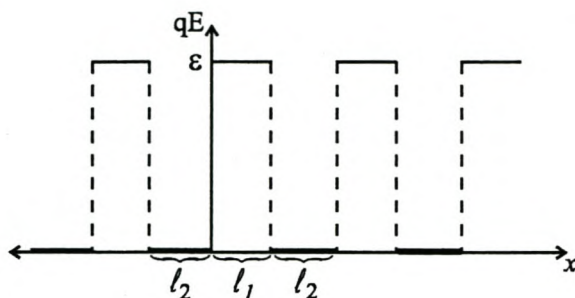
Figure 7.3.1: *Constant effort levels at periodic steps.*

and

$$\lim_{x \to x_m^+} \frac{\partial N(x,t)}{\partial x} = \lim_{x \to x_m^-} \frac{\partial N(x,t)}{\partial x}, \qquad \text{for all } m$$

are introduced. Similar approaches were taken by Shigesada *et al.* (1986) and Cruywagen (1996b).

The non-dimensional equation similar to equation (7.2.3) for non-homogeneous harvesting is

$$U_T = R(X)U - U^{\alpha+1} + U_{XX}, \qquad (7.3.1)$$

where

$$R = \begin{cases} \frac{(r-\varepsilon)}{r} & ml < X < ml + l_1 \\ 1 & ml + l_1 < X < ml + l_1 + l_2 \end{cases}. \qquad (7.3.2)$$

The conditions at the discontinuities are

$$\lim_{X \to X_m^+} U(X,T) = \lim_{X \to X_m^-} U(X,T), \qquad \text{for each } m$$

and

$$\lim_{X \to X_m^+} \frac{\partial U(X,T)}{\partial X} = \lim_{X \to X_m^-} \frac{\partial U(X,T)}{\partial X}, \qquad \text{for each } m.$$

7.3.1   Stability of Steady State

The following section investigates the stability of the steady state solutions of equation (7.3.1). One steady state solution for equation (7.3.1) is the trivial solution. Only if

this steady state is unstable will the population be able to grow from a very low density level. Thus, we try to find conditions for which $U = 0$ is unstable.

When equation (7.3.1) is linearized with respect to $U = 0$, then

$$U_T - U_{XX} - UR(X) = 0, \text{ with } R(X + l) = R(X).$$ (7.3.3)

We now apply the method of separation of variables, by substituting $U(X, T) = P(T)Q(X)$, which results in

$$\frac{P'}{P}(T) = \frac{Q'' + QR}{Q}(X) = \text{constant} = -\lambda.$$

For the solution $P(T) = P_0 e^{-\lambda T}$ to be bounded $Re(\lambda)$ must be greater than zero. In other words where $Re(\lambda) < 0$ the steady state $U = 0$ is unstable and the population density will increase.

If the expression $U(X, T) = e^{-\lambda T}Q(X)$ is substituted in (7.3.3), Hill's equation (Magnus *et al.*, 1966) results, namely

$$Q'' + (R(X) + \lambda)Q = 0.$$ (7.3.4)

We also learn from the oscillation theorem of the theory on the Hill equation (Magnus, *et al.*, 1966) that there exists a monotonically increasing infinite series of real numbers

$$\lambda_0 < \lambda_1 \leq \lambda_2 < \lambda_3 \leq \lambda_4 \ldots$$

such that the Hill equation has a solution of period l.

If we take $Y(X) = Q'(X)$ this second order differential equation (7.3.4) may be reduced to a first order system where

$$\begin{bmatrix} Q'(X) \\ Y'(X) \end{bmatrix} = \begin{bmatrix} 0 & 1 \\ -(R(X) + \lambda) & 0 \end{bmatrix} \begin{bmatrix} Q(X) \\ Y(X) \end{bmatrix}$$

or

$$\mathbf{Z}'(X) = \mathbf{A}(X)\mathbf{Z}(X),$$ (7.3.5)

with $\mathbf{Z}(\mathbf{X}) = \begin{bmatrix} Q(X) \\ Y(X) \end{bmatrix}$ and $\mathbf{A}(X) = \begin{bmatrix} 0 & 1 \\ -(R(X) + \lambda) & 0 \end{bmatrix}$.

Here we consider the periodic coefficient for $R(X)$ as defined in equation (7.3.2). Let $\frac{(r-\varepsilon)}{r} = r_1$ for notational convenience.

As $R(X)$ is a periodic function of X, we can use Floquet's theory to solve equation (7.3.5) (Coddington *et al.*, 1997). Appendix 9.7 discusses the Floquet theory applied to ordinary differential equations, such as Hill's equation, with periodic coefficients. Applying this to equation (7.3.4) we begin by seeking two independent solutions, $Q_1(X)$ and $Q_2(X)$, to this second order equation in order to define the basis for the solution.

Our approach will be to solve equation (7.3.5) for the first interval, $0 \leq X \leq l$ and assume the solution to be periodic with period, l. We use the initial conditions $Q_1(0) = 1$, $Q_1'(0) = 0$, $Q_2(0) = 0$ and $Q_2'(0) = 1$. Now, one solution for equation (7.3.4) that satisfies these conditions is

$$Q_1(X) = \begin{cases} C_1 \cos\left(\sqrt{r_1 + \lambda}\, X\right), & 0 < X < l_1 \\ C_2 \cos\left(\sqrt{1 + \lambda}(X + \alpha_1)\right), & l_1 < X < l \end{cases}$$

with C_1, C_2 and α_1 arbitrary constants. Then, from the initial condition, we have $C_1 = 1$.

To satisfy the continuity conditions we require that

$$\lim_{X \to l_1^-} Q_1(X) = \lim_{X \to l_1^+} Q_1(X) \tag{7.3.6}$$

which becomes

$$\cos\left(\sqrt{r_1 + \lambda}\, l_1\right) = C_2 \cos\left(\sqrt{1 + \lambda}\,(l_1 + \alpha_1)\right), \tag{7.3.7}$$

and also

$$\lim_{X \to l_1^-} Q_1'(X) = \lim_{X \to l_1^+} Q_1'(X) \tag{7.3.8}$$

or

$$-\sqrt{r_1 + \lambda}\, \sin\left(\sqrt{r_1 + \lambda}\, l_1\right) = C_2 \sqrt{1 + \lambda}\, \sin\left(\sqrt{1 + \lambda}\,(l_1 + \alpha_1)\right). \tag{7.3.9}$$

Equation (7.3.7) divided by equation (7.3.9) gives

$$\sqrt{r_1 + \lambda} \tan\left(\sqrt{r_1 + \lambda}\, l_1\right) = \sqrt{1 + \lambda} \tan\left(\sqrt{1 + \lambda}\,(l_1 + \alpha_1)\right). \qquad (7.3.10)$$

A second independent solution to equation (7.3.4) is

$$Q_2(X) = \begin{cases} C_3 \sin\left(\sqrt{r_1 + \lambda}\, X\right), & 0 < X < l_1 \\ C_4 \sin\left(\sqrt{1 + \lambda}\,(X + \alpha_2)\right), & l_1 < X < l \end{cases}$$

with C_3, C_4 and α_2 arbitrary constants. When we apply the initial conditions then

$$Q_2(0) = 0, \qquad Q_1'(0) = 1 = C_3\sqrt{r_1 + \lambda}.$$

Again the continuity conditions at $x = l_1$ is applied such that

$$\sqrt{r_1 + \lambda} \cot\left(\sqrt{r_1 + \lambda}\, l_1\right) = \sqrt{1 + \lambda} \cot\left(\sqrt{1 + \lambda}\,(l_1 + \alpha_2)\right). \qquad (7.3.11)$$

In the case of the general solution equations (7.3.10) and (7.3.11) must be satisfied simultaneously, because $Q(X) = AQ_1(X) + BQ_2(X)$ for A and B arbitrary constant. Thus

$$(l_1 + \alpha_2) = \frac{1}{\sqrt{1 + \lambda}} \arctan \frac{(1 + \lambda)}{(r_1 + \lambda)} \tan \sqrt{1 + \lambda}(l_1 + \alpha_1). \qquad (7.3.12)$$

Now we use Floquet theory, as discussed in Appendix 9.7, to solve for $\mathbf{Z}(X)$ in equation (7.3.5). When we use the functions $Q_1(X)$ and $Q_2(X)$ as defined earlier, the matrix

$$\mathbf{C} = \begin{bmatrix} Q_1(l) & Q_2(l) \\ Q_1'(l) & Q_2'(l) \end{bmatrix},$$

of which we need to find the eigenvalues, is

$$\begin{bmatrix} C_2 \cos \sqrt{1 + \lambda}\,(l + \alpha_1) & C_4 \sin \sqrt{1 + \lambda}\,(l + \alpha_2) \\ -C_2\sqrt{1 + \lambda} \sin \sqrt{1 + \lambda}\,(l + \alpha_1) & C_4\sqrt{1 + \lambda} \cos \sqrt{1 + \lambda}\,(l + \alpha_2) \end{bmatrix}.$$

These eigenvalues, β_1 and β_2, are the solutions of the quadratic equation

$$\beta^2 + b\beta + \varsigma = 0,$$

where

$$b = -\left\{ C_4 \sqrt{1 + \lambda} \cos \sqrt{1 + \lambda}\,(l + \alpha_2) + C_2 \cos \sqrt{1 + \lambda}\,(l + \alpha_1) \right\} \qquad (7.3.13)$$

and

$$\varsigma = C_2 C_4 \sqrt{1 + \lambda} \cos \sqrt{1 + \lambda}\,(\alpha_1 - \alpha_2). \qquad (7.3.14)$$

We know that the properties of the solution in terms of periodicity and boundedness depend on the values of these eigenvalues. To complete the solution for the whole spatial region we have assumed earlier that the solution is periodic. The only way that this could be true is for the eigenvalues to be equal, that is

$$\beta_1 = \beta_2 = 1$$

(see Appendix 9.7). That means $b = -2$ and $\varsigma = 1$. These conditions could be used to determine values for l_1 and l_2 for specific values for α_1 and α_2.

We now want to set a condition on l_1 and l_2 for instability at the steady state. The condition for $U(X)$ to be unstable at $U = 0$ was $Re(\lambda) < 0$. For that we use equation (7.3.12).

Thus for feasible values for α_1 and α_2, the instability condition is

$$l_1 + \alpha_2 < 2 \arctan\left[\frac{1}{r_1} \tan(l_1 + \alpha_1) \right].$$

7.3.2 Numerical Solution

We illustrate here a numerical solution to equation (7.3.1) using the same numerical method of Section 7.2.3. Again we introduce a few individuals at the origin.

In Figure 7.3.2 (a) and (b) the numerical solution after the i'th iteration is given when a periodic harvesting strategy is imposed. Here we use

$$R = \begin{cases} 0.6, & ml < X < ml + l_1 \\ 1.0, & ml + l_1 < X < (m+1)l \end{cases}, \quad m = 0, \pm 1, \pm 2$$

with $l_1 = 1$ and $l_2 = 2.5$.
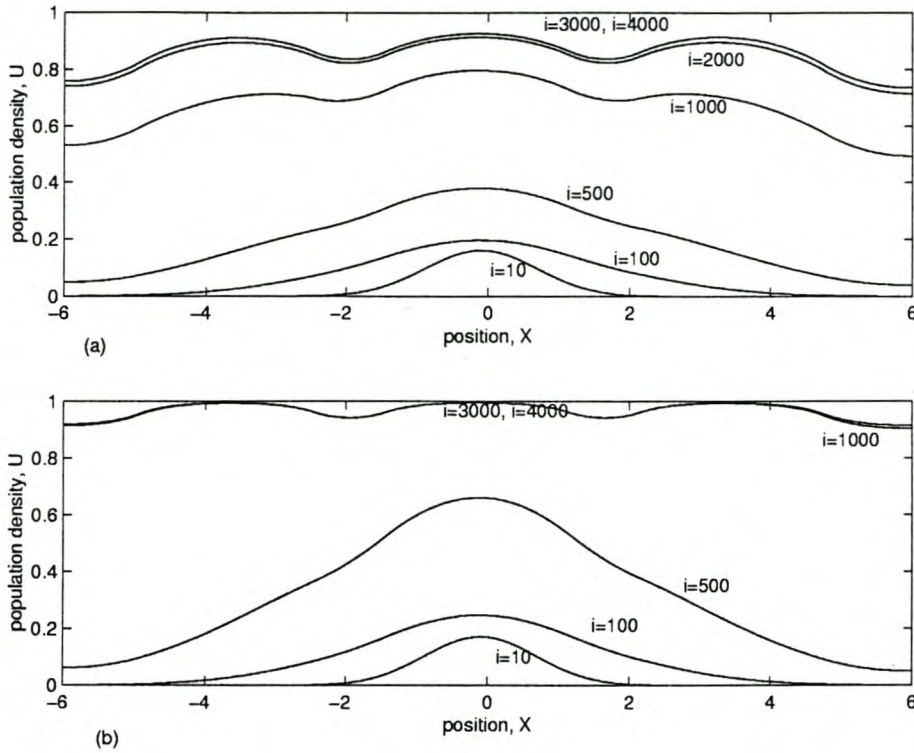
Figure 7.3.2: *Numerical solution of equation (7.3.1) with a periodic harvesting strategy. Parameter values are $l_1 = 1$ and $l_2 = 2.5$ and (a) $\alpha = 1$ and (b) $\alpha = 5$. (Here i indicates the number of iterations.)*

In Figure 7.3.2 (a) the value for α is 1, such that the numerical solution converges to a periodic solution where $0.6 \leq U \leq 1$. In Figure 7.3.2 (b), where $\alpha = 5$, the solution converges to a periodic solution such that $(0.6)^{\frac{1}{5}} \leq U \leq 1$. It illustrates the general periodic steady state solution which is bounded such that $\left(\frac{r-\varepsilon}{r}\right)^{\frac{1}{\alpha}} \leq U \leq 1$.

7.4 Bio-economic Modelling

In this section we include the economic factors in the model and study towards a bio-economic optimal solution. Clark (1990) mentioned this approach when he modelled inshore-offshore movement of fish but did not perform the complex analysis thereof. Very little other work on this could be found in the literature.

Take $U(X,T)$ to be the population density at area X at time T, and define a harvest function as

$$H(U,X,T) = q(X)E(U,X,T)U(X,T),$$

where q is the catchability function and E is the effort function. The total harvest at time T is then represented by

$$\int_{X_a}^{X_b} q(X)E(U,X,T)U(X,T)dX,$$

where $X_a \leq X \leq X_b$. Similar to what we have done in the previous chapters we again aim to maximize the *total net present value*, namely

$$PV = \int_0^\infty e^{-\delta T} \int_{X_a}^{X_b} \left\{ p - \frac{\kappa}{qU} \right\} qEU \, dX \, dT, \qquad (7.4.1)$$

where p is the constant price per unit of fish harvest, κ the constant cost per unit effort and δ the discount rate. (Refer to Chapter 4). This objective function is subject to the biological dynamics of the population, represented as before by

$$U_T(X,T) = U(X,T)\left[R(X) - U(X,T)^\alpha\right] + U_{XX}(X,T), \qquad (7.4.2)$$

where $R(X)$ is periodic, namely

$$R = \begin{cases} \frac{(r-\varepsilon)}{r}, & ml < X < ml + l_1 \\ 1, & ml + l_1 < X < ml + l_1 + l_2 \end{cases}.$$

We simplify the problem and solve the problem at a specific position, $X = X^*$ in a harvested lane. Thus we seek the optimal solution $U^*(T)$ at X^* such that

$$PV^* = \int_0^\infty e^{-\delta T} \left\{ p - \frac{\kappa}{qU^*} \right\} qEU^* \, dT, \qquad (7.4.3)$$

is maximised subject to

$$\frac{U^*(T)}{dT} = U^*(T)\left[\frac{(r-\varepsilon)}{r} - [U^*(T)]^\alpha \right], \qquad (7.4.4)$$

The optimal constant density U^* should be greater than $\left(\frac{r-\varepsilon}{r}\right)^{\frac{1}{\alpha}}$ and less than 1 which are the steady state solutions of the biological model for the harvested and

non-harvested lanes. An upper bound for the present value would be when U equals the steady state and no harvesting occurs in a homogeneous region, and a lower bound for the present value when U equals the steady state solution and a homogeneous harvesting strategy is applied. In Appendix 9.2 the theory of optimization with variational methods is explained, to solve for ε. For our problem the *Hamiltonian* is

$$H = e^{-\delta T} \left[p - \frac{\kappa}{qU^*} \right] \varepsilon U^* + \lambda U^* \left(\frac{r - \varepsilon}{r} - (U^*)^\alpha \right),$$

and the canonical equation is

$$\frac{d\lambda}{dT} = - \left[e^{-\delta T} p\varepsilon + \lambda \left(\left(\frac{r - \varepsilon}{r} \right) - (\alpha + 1)(U^*)^\alpha \right) \right]. \tag{7.4.5}$$

The necessary condition for a maximum is

$$\frac{\partial H}{\partial \varepsilon} = e^{-\delta T} \left[p - \frac{\kappa}{qU^*} \right] U^* - \frac{1}{r}\lambda U^* = 0,$$

or

$$\lambda = e^{-\delta T} \left[pr - \frac{\kappa r}{qU^*} \right]. \tag{7.4.6}$$

Therefore

$$\frac{d\lambda}{dT} = \delta r e^{-\delta T} \left[\frac{\kappa}{qU^*} - p \right] + e^{-\delta T} \left[-\frac{\kappa r}{q(U^*)^2} \frac{dU^*}{dT} \right],$$

but from equation (7.4.5) we know that

$$\frac{d\lambda}{dT} = - \left[e^{-\delta T} p\varepsilon + \lambda \left(\left(\frac{r - \varepsilon}{r} \right) - (\alpha + 1)(U^*)^\alpha \right) \right].$$

Substitute equations (7.4.4) and (7.4.6) into the equation above then the relation for an optimal steady state population density at an allowable effort level is

$$-\frac{p(\alpha + 1)}{\kappa}(U^*)^{\alpha+1} + \frac{(\alpha + 2)}{q}(U^*)^\alpha + \left(\frac{p}{\kappa}(1 - \delta) \right) U^* + \frac{1}{q} \left(\frac{2\varepsilon}{r} - 2 + \delta \right) = 0. \tag{7.4.7}$$

7.4.1 Numerical Results

In this section we determine some numerical results from equation (7.4.7). We took $q = 1$ and $r = 0.1$. Three different values for α were used, namely $\alpha = 1$ in Table 7.4.1,

$\frac{p}{\kappa}$	δ	ε	U^*	$\left(\frac{r-\varepsilon}{r}\right)$	$\frac{p}{\kappa}$	δ	ε	U^*	$\left(\frac{r-\varepsilon}{r}\right)$
1.4	1	0.03	0.9154	0.6	1.3	1	0.025	0.9518	0.7
1.3	1	0.025	0.9518	0.7	1.3	0.8	0.025	9788	0.7
1.25	1	0.02	0.9234	0.8	1.3	0.7	0.025	0.9944	0.8
1.2	1	0.015	0.9396	0.8	1.3	0.6	0.02	0.9482	0.8
1.1	1	0.009	0.9854	0.91	1.3	0.5	0.02	0.9658	0.8
1	1	0	1	1	1.3	0.4	0.02	0.9855	0.8

Table 7.4.1: *Bio-economic steady state solutions of equation (7.4.7) where $\alpha = 1$. (i) Different feasible solutions for ε and U^*, where $\delta = 1$ and the ratio $\frac{p}{\kappa}$ varies. (ii) Different feasible solutions for ε and U^*, where $\frac{p}{\kappa} = 1.3$ and δ varies.*

$\alpha = 2$ in Table 7.4.2 and $\alpha = 5$ in Table 7.4.3. In these tables we listed some solutions to equation (7.4.7) for values of ε where the response is such that $\left(\frac{r-\varepsilon}{r}\right)^{\frac{1}{\alpha}} \leq U^* \leq 1$. Other feasible solutions also exist.

7.5   Conclusion

Considering spatial movement of animals in a non-homogeneous environment we used reaction-diffusion models. The Pella-Tomlinson surplus production model that was described in Chapter 4 is here expanded to include diffusivity. We investigated under which circumstances a travelling wave solution exists. We also proposed a sustainable harvesting strategy of constant exploitation in every alternative lane and determined a bio-economic steady state solution.

We have seen that the value $c = 2 \geq 2\sqrt{R}$ is a necessary condition for the travelling wave solution to exist. Thus, if the conditions of Section 7.1 are also satisfied, it will be possible to estimate the steady state optimal population density in the harvested lanes for every feasible effort level. By feasible effort level we refer to those levels that have a response such that $\left(\frac{r-\varepsilon}{r}\right)^{\frac{1}{\alpha}} \leq U^* \leq 1$. We have assumed that $U(X) = U^*$ in

$\frac{p}{\kappa}$	δ	ε	U^*	$\left(\frac{r-\varepsilon}{r}\right)^{\frac{1}{2}}$	$\frac{p}{\kappa}$	δ	ε	U^*	$\left(\frac{r-\varepsilon}{r}\right)^{\frac{1}{2}}$
1.4	1	0.04	0.8926	0.77	1.3	1	0.03	0.8886	0.84
1.3	1	0.03	0.8986	0.84	1.3	0.8	0.03	0.9146	0.84
1.25	1	0.03	0.9480	0.84	1.3	0.7	0.03	0.9235	0.84
1.2	1	0.02	0.9097	0.89	1.3	0.6	0.03	0.9328	0.84
1.1	1	0.01	0.9346	0.92	1.3	0.5	0.03	0.9428	0.84
1	1	0	1	1	1.3	0.4	0.03	0.9533	0.84

Table 7.4.2: *Bio-economic steady state solutions of equation (7.4.7) where $\alpha = 2$. (i) Different feasible solutions for ε and U^*, where $\delta = 1$ and the ratio $\frac{p}{\kappa}$ varies. (ii) Different feasible solutions for ε and U^*, where $\frac{p}{\kappa} = 1.3$ and δ varies.*

$\frac{p}{\kappa}$	δ	ε	U^*	$\left(\frac{r-\varepsilon}{r}\right)^{\frac{1}{5}}$	$\frac{p}{\kappa}$	δ	ε	U^*	$\left(\frac{r-\varepsilon}{r}\right)^{\frac{1}{5}}$
1.4	1	0.06	0.8788	0.83	1.3	1	0.06	0.9336	0.83
1.3	1	0.06	0.9336	0.83	1.3	0.8	0.06	0.9401	0.83
1.25	1	0.05	0.9333	0.87	1.3	0.7	0.06	0.9434	0.83
1.2	1	0.04	0.9329	0.90	1.3	0.6	0.06	0.9467	0.83
1.1	1	0.025	0.9743	0.93	1.3	0.5	0.06	0.9500	0.83
1	1	0	1	1	1.3	0.4	0.06	0.9534	0.83

Table 7.4.3: *Bio-economic steady state solutions of equation (7.4.7) where $\alpha = 5$. (i) Different feasible solutions for ε and U^*, where $\delta = 1$ and the ratio $\frac{p}{\kappa}$ varies. (ii) Different feasible solutions for ε and U^*, where $\frac{p}{\kappa} = 1.3$ and δ varies.*

the harvested lanes and found that for $\alpha = 1$ and $\alpha = 2$ the feasible effort levels are more easily found in the lower range than when $\alpha = 5$.

In all three cases we have found that the ratio, unit price/cost per unit effort, $\frac{p}{\kappa}$ does affect the solution such that, for more favourable economic factors, the feasible effort level is higher than in the less favourable cases. In these circumstances the total harvest per spatial area, εU^*, is higher. Note that because the feasible range for U^* decreases as ε decreases the steady state solution is higher in such cases.

The other economic parameter, namely the discount rate, δ, does not have much influence on the effort level, but a decrease in the discount rate implies an increase in the steady state solution. That is, future stock will be worth more and is considered an asset. Here higher population densities also imply a higher harvesting rate.

Naturally we note that the biological growth parameter, α, does have an impact on the steady state solution. The feasible effort levels tend to be higher for the growth function more shifted to the right (that is, higher values for α).

In this chapter we proposed a well controlled harvesting strategy were no harvesting in alternative lanes should be enforced, to ensure a sustainable population distribution. Such a fishery could only be modelled once the diffusion factor for that population is known. When enough knowledge is gained on the growth parameters of the population and the travelling periodic wave solutions is found it should be practically possible to subdivide any inshore area into lanes of appropriate width and harvest these lanes at optimal levels. When these optimal levels, as determined from equation (7.4.7), are not exceeded and harvesting is controlled such that fishing takes place only in harvested lanes, an economically optimal fishery could be established.

Chapter 8

Conclusion

Some of our daily needs are met by the exploitation of natural resources, e.g. marine resources. A renewable resource could be exhausted when the rate of depletion is higher than the production rate of the resource. Thus the efficient utilization of these resources is necessary to provide for the needs of communities. Most fisheries worldwide are harvested to capacity as these sectors employ many fishers. Hence fisheries should be managed efficiently to be sustainable and policy makers should address conservation issues and economic aspects simultaneously. Currently (2001) no economic factors have yet been incorporated in setting the total allowable catch per season for fisheries in South Africa. Thus only biological factors play a role in the decision making process. In this thesis we used mathematical models to determine the sustainable quota size where the total present value of all future income from the fishery is maximized, subject to the dynamics of the fish population. We addressed this problem using surplus production models, delay difference models, stage class models and reaction diffusion models. These bio-economic models were applied specifically to the South African Cape Rock Lobster resource.

The most basic of these models are the surplus production models. We used the Pella-Tomlinson model to compare fisheries under no control to that of a sole owner control strategy. Naturally no control in the open access fishery is to the disadvantage of either the fishers or the species once the fishery approaches equilibrium. The maximum

sustainable yield (MSY) management option based on biological considerations is also compared to the maximum economic yield (MEY) option. However at a lower sustainable harvesting level the economic income from the fishery is maximized following the latter option because all cost factors are now incorporated. Thus both the species and the fishers benefit from such an option once the sustainable harvesting level is reached. The application of the MEY management strategy to the Cape Rock Lobster species suggests a low quota level for a few years as the current population size is lower than the sustainable level given by the model. Thus, although limited, some useful information could be gathered from these models.

Most inshore species are slow growing species. This phenomenon should also be addressed in the modelling process. We used delay difference models to address the fact that recruitment takes place years after birth. The time to reach maturity often differs for males and females and we therefore used a sex-structured delay difference model to incorporate such differences. We found that the equilibrium population levels bifurcate outside the stability interval for increasing values of the Ricker slope parameter. Choas occurs for even higher values for this parameter. This phenomenon could well be mis-interpreted and be taken as stochastic fluctuations in the population size. To address the bio-economic problem, optimal control theory was applied to determine the equilibrium male and female population sizes. Many of the biological parameters were estimated by means of a model fit to the real catch per unit effort time series. Although results similar to those of the surplus production model were found, the total outcome relies on a relatively short time series. In future (with a longer time series available) these models might give more insight into the Cape Rock Lobster fishery as it is much more descriptive of the resource. Again we saw that the economic factors do influence the results on catch sizes dramatically and management strategies should be planned accordingly.

Size limits are often used in management strategies. Here we have proposed a stage-class model in an attempt to set such harvesting limits. The model includes survival factors, fecundity factors and growth proportions to determine the optimal harvesting

strategies. This bio-economic model is a generalization of the model recently (1997) used by the South African Marine and Coastal management in the stock assessment process. A solution to our iterative non-linear programming problem was proposed and applied to the Cape Rock Lobster fishery. The algorithm converged to size limits much larger than the current size limit allowed. The maximum economic yield is attained when the total catch proportion is taken from the bigger animals in the population, even when the smaller animals are more expensive. Using a constant economic factor in this model is therefore a shortcoming, as the net revenue per fish does not influence the catch proportions in the different stages.

Spatial movement of animals becomes important within a non-homogeneous environment. We have proposed a fishing strategy where harvesting is done in alternative lanes. Thus diffusion across these lines of fishing will probably occur. We used the theory of reaction-diffusion models and travelling waves to investigate the optimal sustainable harvesting level in these harvested lanes where the width of the lanes depends on the wave speed. The population density within the harvested lanes were taken as approximately constant. A bio-economic solution was then found, subject to the population dynamics of the species. We used the Pella-Tomlinson growth model for the natural growth of the population. Again we found that for higher revenue factors the feasible effort level is higher, which means that the total catch per spatial area is higher. Also as found by the models described earlier, was a decrease in the discount rate, implying an increase in the steady state solution. Thus future stock is considered an asset under such conditions. The management strategy proposed here is especially suitable for harvesting inshore species and is easily controllable.

Policy makers have the complex task to set quota levels every season. The models discussed in this thesis may assist them in this process to set fair and practical harvesting levels such that the current and future generations could benefit from these national assets.

Chapter 9

Appendices

9.1 Basic Economic Principles

Economics concerns the study of how man provides firstly for his necessities from the natural environment and secondly for his less important needs. Natural resources form one of four vital components required for production in a community (Schumann *et al.*, 1964). Labour, capital, natural resources and entrepreneurial skills and activity are all dependent on one another for success in allocating the means of production. Without labour there can be no production and exploitation of a resource even with the proper capital and skills available. For example, fish must be caught, and in some cases canned, to produce a usable product. Countries may gain from the investment in *capital goods* of past generations where these capital goods, such as machinery, tools, buildings and boats, can be used either to produce new capital goods, or *consumer goods*. Rich countries have invested in industries providing consumer goods like articles, services, food and transport. The human input and effort are rewarded according to the "scarcity value" of the input. The technical ability and skills, or *human capital*, of a nation is an asset that should be carefully and properly used to improve the productivity and wealth of a country (Schumann *et al.*, 1964).

Natural resources are, contrary to capital goods, freely accessible and not man-made. Human effort is necessary for the utilization of a resource but the supply does not

increase with an increase in demand (Schumann *et al.*, 1964). A higher demand or need for a limited resource will result in an increase in value of the product. That is, the value of the product may indicate the scarcity of the product. However, an increase in effort and capital expended on the resource is not proportional to an increase in production (Schumann *et al.*, 1964). For example, a boat that doubles its time at sea can not expect an increase of double the size in returns. Otherwise it would have been possible to fulfil all the food necessities of the community with an increase in the intensity of labour. Thus, an increase in effort (taking all other conditions to be constant) will not result in a perpetual increase in production. Economically this is referred to as the principle of *decreasing returns* (Schumann *et al.*, 1964).

The consumers' *demand* for a certain product is predicted by

- the price of the product,

- the prices of competitive products,

- the consumers' income and expectations of future income and

- the consumers' taste.

Given that all other factors remain constant, the higher the price of a fish product, the lower the demand for it by the consumer and *vice versa*. This is illustrated by the Marshall or demand curve, (see Figure 9.1.1) (Schumann *et al.*, 1964).
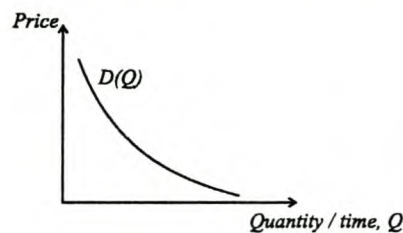
Figure 9.1.1: *Marshall's demand curve,* $D(Q)$

In the demand curve price is expressed as a function of quantity available per unit time (quantity /time).

When there is a scarcity of products the consumer is forced to make choices. *Opportunity cost* is a measure of what sacrifices are made when selecting one alternative above others. This measure is more than money value. If there were no scarcity, opportunity costs would be zero (Scott *et al.*, 1982). For example, suppose we have a canning plant. When we decide to can pilchard we will receive an income of Rx per unit time. But in the same plant we will receive Ry per unit time when we can mussels. The opportunity cost of deciding on mussel canning is Rx for not canning pilchard. Both alternatives are not possible due to a scarcity of space and time. Scott *et al.* (1982) define opportunity cost as the value of the highest valued, sacrificed alternative coincident with a choice of decision.

The *supply* curve is obtained when the opportunity cost of the firm is plotted against the units of production gained. It is an increasing function of quantity per unit time. (see Figure 9.1.2).
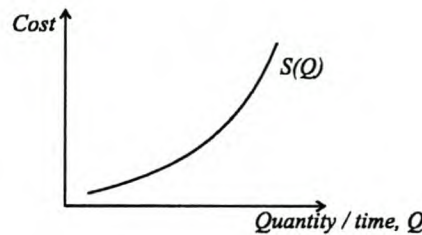
Figure 9.1.2: *Supply curve, $S(Q)$*

When *perfect competition* exists there are many buyers and sellers trading a given product, and no one player is large enough to move the market price. In a competitive situation there is only one price at which supply equals demand - this is called the *equilibrium price*. The demand price of buyers coincides with the supply price of sellers (see Figure 9.1.3). When a market has reached equilibrium, E, it usually only moves away from E when there is an interference into the market by government or a change in parameters such as new technology or income of buyers (Scott *et al.*, 1982).

From Figure 9.1.3 we see that there are many buyers who are willing to pay a higher price, say P_D, for a product than the lower market price, P_E. The *consumers' surplus* is
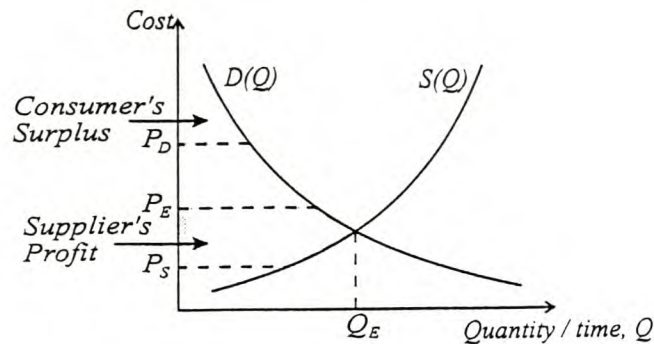
Figure 9.1.3: *The equilibrium point, Q_E where the quantity supplied equals the quantity demanded.*

what a consumer will "save" by buying the product for a price P_E rather than P_D (see Figure 9.1.3). Suppose a consumer is willing to pay R40 for a fish product while the market price is R30. He would then gain R10 to spend otherwise. Another consumer was willing to pay R35. The consumer surplus for this consumer will be only R5.

The *supplier's profit* on the other hand is the gain due to selling the product for a price P_E rather than the lower price, say P_S, at which the supplier is willing to sell the product (see Figure 9.1.3). A seller who is willing to sell a product for R10 while the market price is R15 has a supplier's profit of R5. He then gains R5 more than he has bargained for (Scott *et al.*, 1982).

On the other extreme of perfect competition a *monopoly* exists if there is one supplier to many buyers. The supplier has the freedom to set the market price. When he claims a bigger profit than the social optimum price, P_E, it leads to a overall loss of social benefits. The monopolist may produce less and charge more, which results in a decrease in the consumers' surplus and an associated *social loss* to the community (see Figure 9.1.4) (Clark, 1990).

In constrast to a monopoly, we may have a situation where there is only one buyer, or a group of colluding buyers. This is called a *monopsony* where the buyer determines what is paid for goods (Samuelson *et al.*, 1989). An example of such a market is the 1999 squid permit market in South Africa, where the small established industry could
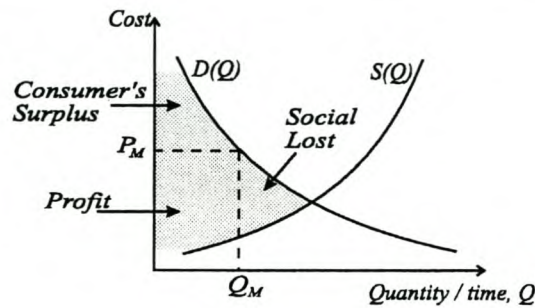
Figure 9.1.4: *The effect of a monopoly ruling the market price .*

set the price they are willing to pay on the "paper" market for permits owned by new entrants (Mather *et al.*, 1999).

The producer faces various costs which are the sacrifices he has to make when he has made a certain production choice. *Fixed costs* are commonly referred to as overheads (for example, mortgage payments) and have to be paid irrespective of whether anything is produced.

Variable costs are those costs associated with the output or production. It includes the operating costs, for example the fuel, oil and repairs of the vessels in a fishing operation.

Production decisions are made based on the concept of *marginal cost*. The economic term "marginal" is equivalent to the mathematical definition of "derivative". Marginal cost describes how the changes of one unit in total variable costs effect changes in revenues (Samuelson *et al.*, 1989).

The basic aim of any supplier is to maximize the profits or net revenue. The accounting revenue is defined as

$$\Pi = \text{total revenue} - \text{total cost}$$
$$= pQ - C(Q),$$

where p is the price per quantity, Q and C the total cost. This total cost may include risk and opportunity costs (Scott *et al.*, 1982). To make a profit, the price per unit must exceed the minimum average cost per unit. In our work we shall consider price

as constant, as was indicated by the South African lobster industry (personal communication), but in some markets these fish prices are determined by the scarcity factor of the species (Sandberg *et al.*, 1998).

Through capital investment one is in effect saving for the future. The *interest rate, i*, defines the return on capital when invested. After time, t, if an investment, P, has been made the value of the capital will have increased to a future value at time t, by

$$\text{Future value} = Pe^{\delta t},$$

where

$$\delta = \ln(1 + i).$$

is the discount rate. Similarly, the *present value* of a future income, P, due t years from now, is

$$\text{Present value} = Pe^{-\delta t}$$

(Clark, 1990). Let $P(t, x, E)$ represent the net revenue to be gained t years from now. If $\delta\ (> 0)$ is the discount rate of future cash flows starting in year $t = T$, the expression

$$PV(T) = \int_T^\infty e^{-\delta t} P(t, x, E) dt \qquad (9.1.1)$$

calculates the present value of a continuous time-stream of future revenues.

9.2   An Optimal Control Solution

The following optimization method for continuous systems, with a variational approach, is from the book of Denn (1969):

Suppose it is possible to describe the state of a system by N variables, namely $x_1, x_2, ..., x_N$, with control variables $u_1, u_2, ..., u_R$, by

$$\dot{x}_1 = f_1(x_1, x_2, ..., x_N, u_1, u_2, ..., u_R)$$
$$\dot{x}_2 = f_2(x_1, x_2, ..., x_N, u_1, u_2, ..., u_R)$$
$$\vdots$$
$$\dot{x}_N = f_N(x_1, x_2, ..., x_N, u_1, u_2, ..., u_R)$$

for $0 < t < T$.

Suppose also that the control functions, $u_1, u_2, ..., u_R$, are all specified for $0 < t < T$.

We wish to find the functions $u_i(t), i = 1, 2...R$ that maximize the function

$$J(u_1, ..., u_R) = \int_0^T F(x_1, x_2, ...x_N, u_1, u_2...u_R)dt.$$

It is possible to find the optimal solution $\overline{x}_1(t), \overline{x}_2(t)...\overline{x}_N(t)$, which is the response to the optimal control variables, $\overline{u_1}, \overline{u}_2, ...\overline{u}_R$, once initial values are specified.

We can use variational methods to find a necessary condition for optimality. Small variations about the optimal control variables such that

$$u_i(t) = \overline{u}_i(t) + \delta u_i(t), \quad i = 1 \dots R \quad \text{and} \quad |\delta u_i(t)| \le \epsilon$$

where ϵ is a small positive constant. Use also similar variations about the response variables,

$$x_j(t) = \overline{x}_j(t) + \delta x_j(t) \quad j = 1 \dots N.$$

Now the objective function becomes

$$J[u_1, ..., u_R] = J[\overline{u}_1, ..., \overline{u}_R] + \delta J.$$

Also

$$\frac{d}{dt}\left(\overline{x}_j + \delta x_j\right) - \frac{d}{dt}\left(\overline{x}_j\right) = \delta \dot{x}_j$$

$$= f_j\left(\overline{x}_1 + \delta x_1, \overline{x}_2 + \delta x_2, ..., \overline{x}_N + \delta x_N, \overline{u}_1 + \delta u_1, ..., \overline{u}_R + \delta u_R\right)$$

$$- f_j\left(\overline{x}_1, \overline{x}_2, ..., \overline{x}_N, \overline{u}_1, ..., \overline{u}_R\right).$$

and

$$\delta J = J[\overline{u}_1(t) + \delta u_1(t), ..., \overline{u}_R(t) + \delta u_R(t)] - J[\overline{u}_1, ..., \overline{u}_R]$$

$$= \int_0^T F(\overline{x}_1 + \delta x_1, ..., \overline{x}_N + \delta x_N, \overline{u}_1 + \delta u_1, ..., \overline{u}_R + \delta u_R) dt$$

$$- \int_0^T F(\overline{x}_1, \overline{x}_2, ..., \overline{x}_N, \overline{u}_1, ..., \overline{u}_R) dt.$$

Use the Taylor expansions with respect to the optimum, then

$$\delta J = \int_0^T \left[\frac{\partial F}{\partial x_1}\delta x_1 + \cdots + \frac{\partial F}{\partial x_N}\delta x_N, \frac{\partial F}{\partial u_1}\delta u_1, \cdots \frac{\partial F}{\partial u_R}\delta u_R\right] dt + O(\epsilon) \qquad (9.2.1)$$

and also

$$\delta \dot{x}_j = \frac{\partial f_j}{\partial x_1}\delta x_1 + \cdots + \frac{\partial f_j}{\partial x_N}\delta x_N, \frac{\partial f_j}{\partial u_1}\delta u_1, \cdots \frac{\partial f_j}{\partial u_R}\delta u_R = O(\epsilon), \quad j = 1 \ldots N. \quad (9.2.2)$$

Now multiply each of the N equations (9.2.2) with a multiplier $\lambda_j(t)$, integrate from 0 to T and add these new expressions to equation (9.2.1). Then

$$\delta J = \int_0^T \left\{\left[\frac{\partial F}{\partial x_1} + \lambda_1\frac{\partial f_1}{\partial x_1} + \cdots + \lambda_N\frac{\partial f_N}{\partial x_1}\right]\delta x_1 - \lambda_1\delta \dot{x}_1\right.$$

$$\vdots$$

$$+ \left[\frac{\partial F}{\partial x_N} + \lambda_1\frac{\partial f_1}{\partial x_N} + \cdots + \lambda_N\frac{\partial f_N}{\partial x_N}\right]\delta x_N - \lambda_N\delta \dot{x}_N$$

$$+ \left[\frac{\partial F}{\partial u_1} + \lambda_1\frac{\partial f_1}{\partial u_1} + \cdots + \lambda_N\frac{\partial f_N}{\partial u_1}\right]\delta u_1$$

$$\vdots$$

$$\left. + \left[\frac{\partial F}{\partial u_R} + \lambda_1\frac{\partial f_1}{\partial u_R} + \cdots + \lambda_N\frac{\partial f_N}{\partial u_R}\right]\delta u_R\right\} dt + O(\epsilon). \qquad (9.2.3)$$

Integration by parts gives

$$\int_0^T \lambda_j\delta \dot{x}_j\, dt = (\lambda_j\delta x_j)\, \big|_0^T - \int_0^T \dot{\lambda}_j\, \delta x_j dt, \qquad j = 1 \ldots N.$$

Substitute these into equation (9.2.3) such that

$$
\begin{aligned}
\delta J = \int_0^T \Bigg\{ & \left[\frac{\partial F}{\partial x_1} + \lambda_1 \frac{\partial f_1}{\partial x_1} + \cdots + \lambda_N \frac{\partial f_N}{\partial x_1} + \dot{\lambda}_1 \right] \delta x_1 + \cdots \\
& + \left[\frac{\partial F}{\partial x_N} + \lambda_1 \frac{\partial f_1}{\partial x_N} + \cdots + \lambda_N \frac{\partial f_N}{\partial x_N} + \dot{\lambda}_N \right] \delta x_N \\
& + \left[\frac{\partial F}{\partial u_1} + \lambda_1 \frac{\partial f_1}{\partial u_1} + \cdots + \lambda_N \frac{\partial f_N}{\partial u_1} \right] \delta u_1 + \cdots \\
& + \left[\frac{\partial F}{\partial u_R} + \lambda_1 \frac{\partial f_1}{\partial u_R} + \cdots + \lambda_N \frac{\partial f_N}{\partial u_R} \right] \delta u_R \Bigg\} dt \\
& - (\lambda_1 \delta x_1)|_0^T - \ldots - (\lambda_N \delta x_N)|_0^T + O(\epsilon).
\end{aligned}
$$

Now require that

$$
\dot{\lambda}_j = -\frac{\partial F}{\partial x_j} - \lambda_1 \frac{\partial f_1}{\partial x_j} - \ldots - \lambda_N \frac{\partial f_N}{\partial x_j}, \qquad j = 1 \ldots N.
$$

The variables $\delta x_j(T)$ are free variables therefore we set $\lambda_j(T) = 0$ and for similar reasons $\lambda_j(0) = 0$, such that

$$
\begin{aligned}
\delta J = \int_0^T \Bigg\{ & \left[\frac{\partial F}{\partial u_1} + \lambda_1 \frac{\partial f_1}{\partial u_1} + \cdots + \lambda_N \frac{\partial f_N}{\partial u_1} \right] \delta u_1 + \cdots \\
& + \left[\frac{\partial F}{\partial u_R} + \lambda_1 \frac{\partial f_1}{\partial u_R} + \cdots + \lambda_N \frac{\partial f_N}{\partial u_R} \right] \delta u_R \Bigg\} dt + O(\epsilon).
\end{aligned}
$$

For $J[\overline{u}_1, ..., \overline{u}_R]$ to be a maximum the variance δJ must be less or equal than zero.

Suppose the control variables u_i are bounded such that

$$
u_i^L \leq u_i \leq u_i^U.
$$

Define the *Hamiltonian*

$$
H = F + \lambda_1 f_1 + \cdots + \lambda_N f_N,
$$

then

$$
\begin{aligned}
\delta J &= \int_0^T \left[\frac{\partial H}{\partial u_1} \delta u_1 + \cdots \frac{\partial H}{\partial u_R} \delta u_R \right] dt + O(\epsilon) \\
&\leq 0,
\end{aligned}
$$

and the *canonical* equations are

$$\dot{\lambda}_j = -\frac{\partial H}{\partial x_j}, \qquad j = 1 \ldots N.$$

When

$$\delta u_i = \epsilon' \frac{\partial H}{\partial u_i}$$

and where $\lim_{\epsilon' \to 0} \frac{O(\epsilon)}{\epsilon'} = 0$, then

$$\delta J = \epsilon' \int_0^T \left[\left(\frac{\partial H}{\partial u_1}\right)^2 + \cdots + \left(\frac{\partial H}{\partial u_R}\right)^2 \right] dt + O(\epsilon)$$
$$\leq 0.$$

This inequality only holds if the integrand is zero. That is

$$\frac{\partial H}{\partial u_i} = 0, \qquad i = 1 \ldots R,$$

which is the *necessary conditions* for a maximum.

9.3   Ford-Walford Model

In this section we will derive the Ford-Walford growth model in terms of weights.

It is known that in general the length-weight relation is $w_t = a(l_t)^b$, where w_t is the weight of an individual at time t, l_t is the length of this individual at the time t and a and b are constants. The von Bertalanffy model in terms of weight is then

$$w_t = w_\infty \left[1 - e^{-k(t-t_0)}\right]^b,$$

where k is the Brody growth coefficient and t_0 a shift parameter along the age axis (Hilborn *et al.*, 1992). Thus

$$w_t = w_\infty \left[1 - be^{-k(t-t_0)}\right] + O\left(e^{-2k(t-t_0)}\right)$$

using the Taylor series expansion.

If we take $\triangle w_t$ the change in weight during period $\triangle t$, then

$$w_t + \triangle w_t = w_\infty \left[1 - be^{-k(t+\triangle t-t_0)}\right] + O\left(e^{-2k(t-t_0)}\right)$$

and

$$\triangle w_t = w_\infty be^{-k(t-t_0)} \left[1 - e^{-k\delta t}\right] + O\left(e^{-2k(t-t_0)}\right). \qquad (9.3.1)$$

It is now easy to show that

$$w_\infty - w_t = w_\infty be^{-k(t-t_0)} + O\left(e^{-2k(t-t_0)}\right). \qquad (9.3.2)$$

Substitute equation (9.3.2) in equation (9.3.1), then the Ford-Walford model in terms of weight is

$$w_t + \triangle w_t = \alpha + \rho w_t + O\left(e^{-2k(t-t_0)}\right) \qquad (9.3.3)$$

where $\alpha = w_\infty \left[1 - e^{-k\triangle t}\right]$ and $\rho = e^{(-k\triangle t)}$ (Hilborn *et al.*, 1992).

The delay difference model that we apply in Chapter 5 makes the assumption that body weight can be described by a linear relation. That is, the error term in equation (9.3.3) is not significant.

9.4 Analytical Steady State Solution of Section 5.2.6

Here we wish to analyse the equation for an optimal steady state solution, equation (5.2.22), namely

$$
\left[\sigma_m + \alpha^u H_{Sm}\right]\frac{p_m - \frac{c}{q_m N^m}}{p_m - \frac{c}{q_m S^m}} + \alpha^v G_{Sm}\frac{p_f - \frac{c}{q_f N^f}}{p_m - \frac{c}{q_m S^m}} = \frac{1}{\alpha},
$$

$$
\left[\sigma_f + \alpha^v G_{Sf}\right]\frac{p_f - \frac{c}{q_f N^f}}{p_f - \frac{c}{q_f S^f}} + \alpha^u H_{Sf}\frac{p_m - \frac{c}{q_m N^m}}{p_f - \frac{c}{q_f S^f}} = \frac{1}{\alpha}.
$$

Take $h^m = q_m E N^m$ and $h^f = q_f E N^f$, giving $S^m = (1 - q_m E)N^m$ and $S^f = (1 - q_f E)N^f$. We assume that at the steady state the derivatives H_{Sm}, H_{Sf}, G_{Sm} and H_{Sf} are constant. Now let

$$
\begin{aligned}
A &= \sigma_m + \alpha^u H_{Sm} \\
B &= \alpha^v G_{Sm} \\
F &= \sigma_f + \alpha^v G_{Sf} \\
D &= \alpha^u H_{Sf},
\end{aligned}
$$

then from equation (5.2.22)

$$
\left(Ap_m + Bp_f - \frac{p_m}{\alpha}\right)N^m N^f + \left(-\frac{Ac}{q_m} + \frac{c}{\alpha q_m (1 - q_m E)}\right)N^f - \frac{Bc}{q_f}N^m = 0
$$

and

$$
\left(Fp_f + Dp_f m - \frac{p_f}{\alpha}\right)N^m N^f - \frac{Dc}{q_m}N^f + \left(-\frac{Fc}{q_f} + \frac{c}{\alpha q_f (1 - q_f E)}\right)N^m = 0.
$$

Say

$$
X = Ap_m + Bp_f - \frac{p_m}{\alpha}
$$

$$
Y = Fp_f + Dp_m - \frac{p_f}{\alpha},
$$

then

$$
N^m = \frac{\left[-\Psi\frac{\Theta}{\Phi} + \frac{Bc}{q_f}\right]}{\left[\frac{\Theta}{\Phi} \times X\right]}
$$

$$N^f = \frac{\Theta}{\Phi} N^m$$

$$h^m = q_m E N^m$$

$$h^f = q_f E N^f,$$

where

$$\Phi = \left(-\frac{Ac}{q_m} + \frac{c}{\alpha q_m \left(1 - q_m E\right)} \right) Y + \frac{Dc}{q_m} X$$

$$\Theta = \frac{Bc}{q_f} Y + \left(-\frac{Fc}{q_f} + \frac{c}{\alpha q_f \left(1 - q_f E\right)} \right) X$$

$$\Psi = -\frac{Ac}{q_m} + \frac{c}{\alpha q_m \left(1 - q_m E\right)}.$$

9.5 Biological Stability of Linear Stage-Structured Models

In order to help us understand the dynamics of the non-linear models we first investigate the stability of the linear model of the form,

$$\mathbf{x}(t+1) = A\mathbf{x}(t) \tag{9.5.1}$$

where A is a $n \times n$ real matrix.

An eigenvalue, λ_i, of the matrix A and its associated eigenvector $\mathbf{y}$ satisfy the equation

$$A\mathbf{y} = \lambda_i \mathbf{y}.$$

Suppose the non-singular matrix T consists of the eigenvectors of A with the ith column of T corresponding to λ_i. Now A may be diagonalized in the form $A = T\Lambda T^{-1}$, with Λ a diagonal matrix (containing the eigenvalues of A). It then follows that

$$\mathbf{x}(t+1) = A^t\mathbf{x}(0) = T\Lambda^t T^{-1}\mathbf{x}(0).$$

The solution $\mathbf{x}(t+1)$ will tend to $\mathbf{0}$ when t tends to ∞ if $|\lambda_i| < 1$ for all $i = 1, 2, ..., n$. No matter what the initial conditions are, the trivial equilibrium state, $\mathbf{x} = \mathbf{0}$, will be reached. When $|\lambda_i| > 1$, then the solution increases without bound and becomes unstable. That is, for the system to be stable a necessary condition is that $|\lambda_i| \leq 1$. Note that eigenvectors that correspond to the eigenvalue $\lambda_i = 1$ are steady state solutions (Getz *et al.*, 1989).

A dominant eigenvalue (if it exists) of a matrix A is defined as an eigenvalue, $\lambda_\triangle$, with the property that $|\lambda_i| < \lambda_\triangle$ for all eigenvalues λ_i of A, $i \neq \triangle$. Luenberger (1979) proves that, if the initial vector $\mathbf{x}(0)$ is not an eigenvector of A, then the solution will align in the direction of the dominant eigenvector, $\mathbf{x}_\triangle$. The following theorem is often used to prove stability.

Part of Perron Frobenius Theorem

If matrix $A \geq 0$ and all elements of A^t are strictly positive for some positive integer t, then there exists an eigenvalue $\lambda_\triangle > 0$ of A (called the Perron root) that is dominant. The corresponding eigenvector is also positive. (see proof in Luenberger 1979).

As was also proven by Luenberger (1979) this theorem guarantees stability, since for such a dynamic system, with A^t strictly positive, all the eigenvalues are strictly within the unit circle.

9.6 Appendix to Section 6.5.2

Matrix A of Section 6.5.2 is

$$
\mathbf{A} = \begin{bmatrix}
s_1^m(1-u_1^m)(1-r_1^m) & 0 & \cdots & & 0 \\
s_1^m(1-u_1^m)r_1^m & s_2^m(1-u_2^m)(1-r_2^m) & & & \vdots \\
0 & s_2^m(1-u_2^m)r_2^m & & & \\
\vdots & 0 & \ddots & & 0 \\
0 & \cdots & 0 & s_{n-1}^m(1-u_{n-1}^m)r_{n-1}^m & s_n^m(1-u_n^m)(1-r_n^m) \\
s_1^f(1-u_1^f)(1-r_1^f) & 0 & \cdots & \cdots & 0 \\
s_1^f(1-u_1^f)r_1^f & s_2^f(1-u_2^f)(1-r_2^f) & & & \vdots \\
0 & s_2^f(1-u_2^f)r_2^f & & & \\
\vdots & 0 & \ddots & & 0 \\
0 & \cdots & 0 & s_{n-1}^f(1-u_{n-1}^f)r_{n-1}^f & s_n^f(1-u_n^f)(1-r_n^f)
\end{bmatrix}
$$

The Jacobi matrix of Section 6.5.2 is

$$\frac{\partial \mathbf{f}}{\partial \mathbf{N}} =
\begin{bmatrix}
s_1^m(1-u_1^m)(1-r_1^m)+\frac{1}{2}D^m s_0^m(1-u_0^m)r_0^m b_1^m & \frac{1}{2}D^m s_0^m(1-u_0^m)r_0^m b_2^m & & & \frac{1}{2}D^m s_0^m(1-u_0^m)r_0^m b_n^m \\
s_1^m(1-u_1^m)r_1^m & s_2^m(1-u_2^m)(1-r_2^m) & & & \\
0 & s_2^m(1-u_2^m)r_2^m & \ddots & & \\
& & 0 & s_{n-1}^m(1-u_{n-1}^m)r_{n-1}^m & s_n^m(1-u_n^m)(1-r_n^m) \\
\cdots & \cdots & \cdots & \cdots & \cdots \\
\frac{1}{2}D^m s_0^f(1-u_0^f)r_0^f b_1^m & \frac{1}{2}D^m s_0^f(1-u_0^f)r_0^f b_2^m & & & \frac{1}{2}D^m s_0^f(1-u_0^f)r_0^f b_n^m \\
& & 0 & & \\
& & & & \\
\cdots & \cdots & \cdots & \cdots & \cdots \\
\frac{1}{2}D^f s_0^m(1-u_0^m)r_0^m b_1^f & \frac{1}{2}D^f s_0^m(1-u_0^m)r_0^m b_2^f & \cdots & & \frac{1}{2}D^f s_0^m(1-u_0^m)r_0^m b_n^f \\
& & 0 & & \\
& & & & \\
\cdots & \cdots & \cdots & & \cdots \\
s_1^f(1-u_1^f)(1-r_1^f)+\frac{1}{2}D^f s_0^f(1-u_0^f)r_0 b_1^f & \frac{1}{2}D^f s_0^f(1-u_0^f)r_0^f b_2^f & & & \frac{1}{2}D^f s_0^f(1-u_0^f)r_0^f b_n^f \\
s_1^f(1-u_1^f)r_1^f & s_2^f(1-u_2^f)(1-r_2^f) & & & \\
& s_2^f(1-u_2^f)r_2^f & \ddots & & \\
& & & s_{n-1}^f(1-u_{n-1}^f)r_{n-1}^f & s_n^f(1-u_n^f)(1-r_n^f)
\end{bmatrix}$$

9.7   Floquet Theory

Consider a system of first order differential equations namely

$$\mathbf{Z}'(x) = \mathbf{A}(x)\mathbf{Z}(x) \qquad\qquad (9.7.1)$$

where $\mathbf{A}(x)$ is periodic with period l or $\mathbf{A}(x + l) = \mathbf{A}(x)$ for $x \in \Re$. Let $\tilde{\mathbf{Z}}(x)$ be a basis of the solution of equation (9.7.1) where

$$\mathbf{Z}(x) = \tilde{\mathbf{Z}}(x)\mathbf{C_0},$$

and $\mathbf{C_0}$ any $n \times n$ matrix.

Note that if $\mathbf{Y}(x) = \mathbf{Z}(x + l)$ then

$$\mathbf{Y}'(x) = \mathbf{Z}'(x + l) = \mathbf{A}(x + l)\mathbf{Z}(x + l) = \mathbf{A}(x)\mathbf{Y}(x), \qquad x \in \Re.$$

Thus $\widetilde{\mathbf{Y}}(x) = \tilde{\mathbf{Z}}(x + l)$ is also a basis for the solution and

$$\tilde{\mathbf{Z}}(x + l) = \tilde{\mathbf{Z}}(x)\mathbf{C}$$

for some invertible $n \times n$ matrix $\mathbf{C}$ of continuous functions. Also, Lukes (1982) proved that for every matrix $\mathbf{C}$ there exists a matrix $\mathbf{S}$ such that

$$\mathbf{C} = e^{\mathbf{S}l} = \tilde{\mathbf{Z}}^{-1}(0)\tilde{\mathbf{Z}}(0).$$

Theorem of Floquet

Each basis $\tilde{\mathbf{Z}}$ for the solution of (9.7.1) can be represented as

$$\tilde{\mathbf{Z}}(x) = \mathbf{P}(x)e^{\mathbf{S}x}, \qquad x \in \mathcal{R},$$

where $\mathbf{P} \in C^1$, $\mathbf{P}(x)$ is invertible, $\mathbf{P}(x + l) = \mathbf{P}(x)$ for all $x \in \mathcal{R}$ and $\mathbf{S}$ and $\mathbf{P}$ are $n \times n$ matrices of continuous functions.

The detailed proof of the Floquet theorem can be found in Coddington (1997).

In order to use the Floquet theorem we need to use the eigenvalues of the matrices properly. That is, if $\lambda_1, \lambda_2, \ldots \lambda_n$ are the eigenvalues of the matrix $\mathbf{S}$ then the eigenvalues of $e^{\mathbf{S}}$ are $e^{\lambda_1}, e^{\lambda_2} \ldots e^{\lambda_n}$. If we now denote the eigenvalues of $e^{\mathbf{S}l}$ by $\sigma_1, \sigma_2, \ldots \sigma_n$ then $\sigma_1 = e^{l\lambda_1}, \sigma_2 = e^{l\lambda_2} \ldots \sigma_n = e^{l\lambda_n}$.

Now when we wish to solve a second order differential equation where $Q_1(x)$ and $Q_2(x)$ are two independent solutions of (9.7.1), use

$$\tilde{\mathbf{Z}}(x) = \begin{bmatrix} Q_1(x) & Q_2(x) \\ Q_1'(x) & Q_2'(x) \end{bmatrix}$$

and we could define matrix $\mathbf{C}$. Say $\mathbf{C} = \mathbf{BJB}^{-1}$ where $\mathbf{J}$ is the diagonal matrix consisting of the eigenvalues of $\mathbf{C}$ and $\mathbf{B}$ consists of the corresponding eigenvectors. When $\mathbf{J} = e^{\Lambda l}$, then

$$\begin{aligned} \mathbf{C} &= \mathbf{B}e^{\Lambda l}\mathbf{B}^{-1} \\ &= \mathbf{I} + \mathbf{B}\Lambda l\mathbf{B}^{-1} + \frac{1}{2!}\mathbf{B}(\Lambda l)^2\mathbf{B}^{-1} + \frac{1}{3!}\mathbf{B}(\Lambda l)^3\mathbf{B}^{-1} + \ldots \\ &= e^{\mathbf{S}l} \end{aligned}$$

and the solution for (9.7.1) is

$$\mathbf{Z}(x) = \theta e^{\lambda_1 x}\mathbf{p}_1(x) + \phi e^{\lambda_2 x}\mathbf{p}_2(x)$$

for a second order system where θ and ϕ are constant. Here $p_i(x + l) = p_i(x)$, for $i = 1, 2$ and λ_1 and λ_2 are the diagonal element of matrix Λ. Note that the solution $\mathbf{Z}(x)$ is only periodic when λ_1 and λ_2 is zero. That is when the eigenvalues of the matrix $\mathbf{C}$ are one.

9.8 Data

In this section the data sets available on the Cape Rock Lobster resource (*Jasus la-landii*), that are used in this thesis, are listed.

The total commercial catch data series that was used in this thesis is listed in Table 9.8.1. The data from 1900 to 1995 is from Cruywagen (1995b) and those numbers since 1996, were personally communicated by the South African Marine and Coastal Management. Note that the percentage data at some years are interpolated, as was done by Cruywagen (1995b).

In Table 9.8.2 the catch per unit effort (CPUE) data series is listed, as it is available since 1975 (Cruywagen, 1995). The minimum size limit was dropped from 89 mm to 80 mm carapace length during the 1992 season, which influences the effort measurement. Therefore the 1992 season is not considered.

The Ford-Walford model (see Chapter 3), intercept parameter could be modified significantly each year while the slope parameter remains constant. Table 9.8.4 shows the male and female intercept parameters, α_m and α_f at each year. For years prior to 1967 the parameter values are taken the same values as that of 1967. The negative values, or shrinkage, for the females at 1990 etc. is an indication that the species uses all available energy to recover from extreme circumstances.

Typical experimental results as was used by Cruywagen (1995b) is shown in Table 9.8.5.

Table 9.8.6 shows an experimental sample of female length versus number of eggs. Such data were used in Chapter 4 to fit a linear relation between female size and the number of eggs produced per female.

Year	Total Catch (kg)	% Males in Catch	Year	Total Catch (kg)	% Males in Catch
1900	1 434 910	72	1950	18 317 690	83
1901	1 268 130	72	1951	18 926 346	83
1902	922 183	72	1952	14 582 537	84
1903	531 378	72	1953	13 679 449	84
1904	396 131	72	1954	12 336 899	84
1905	718 299	72	1955	7 896 653	84
1906	249 047	72	1956	7 896 653	85
1907	610 012	72	1957	7 896 653	85
1908	1 142 105	72	1958	6 856 249	85
1909	1 993 303	72	1959	11 224 531	85
1910	1 880 813	72	1960	11 224 531	86
1911	2 731 426	72	1961	10 471 379	86
1912	5 177 476	72	1962	10 320 748	86
1913	6 718 648	72	1963	10 622 009	86
1914	6 864 268	72	1964	10 622 009	87
1915	8 879 652	87	1965	10 622 009	87
1916	8 596 338	81	1966	9 188 454	87
1917	9 511 503	71	1967	7 079 628	88
1918	5 504 349	81	1968	6 175 846	69
1919	8 705 144	56	1969	7 556 934	86
1920	8 206 635	62	1970	5 600 000	88
1921	6 485 792	70	1971	5 290 000	86
1922	9 097 975	61	1972	5 541 000	80
1923	6 849 515	68	1973	5 722 000	81
1924	8 148 065	81	1974	6 288 000	85
1925	9 803 356	72	1975	6 297 000	86
1926	7 480 653	75	1976	6 297 000	91
1927	7 794 046	76	1977	6 297 000	90
1928	9 492 865	70	1978	5 352 000	90
1929	9 643 231	78	1979	5 352 000	92
1930	10 621 084	88	1980	4 548 000	93
1931	9 931 129	81	1981	3 700 000	94
1932	13 180 169	78	1982	3 700 000	93
1933	15 069 512	79	1983	3 730 000	93
1934	7 609 377	79	1984	3 730 000	95
1935	7 510 018	79	1985	3 805 000	97
1936	9 493 712	79	1986	3 965 000	98
1937	11 436 398	80	1987	3 834 000	97
1938	9 942 930	80	1988	4 000 000	99
1939	11 148 713	80	1989	3 491 000	99
1940	11 567 330	80	1990	2 996 000	100
1941	10 860 976	81	1991	2 509 000	100
1942	9 239 794	81	1992	2 125 000	93
1943	5 555 824	81	1993	2 155 000	88
1944	4 057 856	81	1994	2 155 000	97
1945	5 742 694	82	1995	1 517 790	95
1946	9 634 026	82	1996	1 679 740	92
1947	12 301 077	82	1997	1 916 879	94
1948	13 022 801	82	1998	1 792 703	97
1949	12 578 312	83	1999	1 720 503	

Table 9.8.1: *Total catch per year and the percentage males in the catch for the Cape Rock Lobster fishery.*

Year	CPUE (kg/trap-day)
1975	5.34
1976	6.72
1977	5.2
1978	5.41
1979	4.43
1980	3.29
1981	4.47
1982	6.21
1983	7.51
1984	7.92
1985	8.57
1986	6.46
1987	8.17
1988	7.82
1989	5.72
1990	3.06
1991	3.04
1992	
1993	6.06
1994	3.81
1995	6.2

Table 9.8.2: *Catch per unit effort data series for the Cape Rock Lobster fishery.*

Year	Area 1 Port Nolloth	Area 3 Doring Bay and Lambert's Bay	Area 4 Elands Bay	Area 5 St Helena Bay	Area 6 Saldanha Bay	Area 7 Dassen Island	Area 8 Cape Peninsula	Reserve Hout Bay	Total
1969							168 (87.9)		168 (87.9)
1970						286 (88.1)	557 (85.7)		843(86.5)
1971						272(86.8)	142(85.4)		414(86.3)
1972						205(84.1)	113(88.0)		318(85.5)
1976		128(91.9)	108(90.5)						236(91.3)
1977	19(80.4)	83(89.7)	57(90.2)						159(88.8)
1978		20(89.1)							20(89.1)
1979				71(89.5)	53(90.8)				124(90.1)
1980				160(88.6)	35(89.3)				195(88.8)
1981						828(87.5)			828(87.5)
1982			292(88.5)	273(89.0)	96(90.5)				661(89.0)
1983			192(92.1)				655(88.6)		847(89.4)
1984		260(94.1)		148(87.7)		146(89.5)			554(91.2)
1985								95(103.1)	95(103.2)
1986		6(99.6)						169(106.8)	175(106.6)
1987		12(94.5)	10(94.1)				98(93.0)	167(103.8)	287(99.3)
1988	214(84.7)	17(90.1)	57(92.5)	23 (89.4)		75(89.5)	192(90.2)	517(98.9)	1095(93.3)
1989	159(83.1)	26(92.2)	102(92.5)	9(90.8)		83(89.1)	276(90.1)	104 (97.8)	759(90.0)
1989	159(83.1)	26(92.2)	102(92.5)	9(90.8)		83(89.1)	276(90.1)	104(97.8)	759(90.0)
1990	45(80.8)	23(94.7)	30(90.3)	10(89.1)		84(89.3)	236(90.5)	29(92.3)	457(89.6)
1991	130(81.0)	50(91.2)	21(88.5)			45(87.6)	216(92.5)	32(95.2)	494(88.9)
1992	128(84.1)	10(90.2)	178(89.5)			77(87.9)	210(88.6)	105(92.9)	708(88.6)
1993	101(83.4)	49(88.0)	205(83.4)	236(81.2)		171(80.6)	500(82.1)	311(86.1)	1573(83.1)
1994	265(84.0)			114(78.1)	39(83.0)	99(82.1)	156(81.2)	98(84.1)	771(82.3)
1995	131(82.2)		236(83.8)			208(9.8)	268(80.2)	243(82.9)	1086(81.7)
Total	1192(83.2)	556(92.2)	1380(88.4)	1044(85.9)	223(89.1)	1816(86.2)	2807(86.9)	1870(94.7)	

Table 9.8.3: *A summary of the number of tagging returns, for the Cape Rock Lobster fishery, available for each area and year used by Cruywagen(1997) for fitting the Ford Walford model. The mean lengths of the rock lobsters tagged are given in brackets in mm. This table is from the article by Cruywagen (1997).*

Year	α_m (g)	α_f (g)
1967	63.4	11.4
1968	57.3	11.4
1969	62.8	11.4
1970	64.8	11.4
1971	68.7	11.4
1972	66.7	10.8
1973	64.7	10.2
1974	62.7	9.6
1975	60.7	9.0
1976	51.6	6.2
1977	47.8	5.0
1978	62.9	9.6
1979	70.8	12.1
1980	50.9	6.6
1981	59.4	8.6
1982	57.4	8.0
1983	64.4	10.1
1984	80.5	15.0
1985	48.8	5.3
1986	35.4	1.2
1987	54.0	6.9
1988	47.6	4.9
1989	40.7	2.9
1990	30.8	-0.2
1991	32.3	0.3
1992	30.9	-0.2
1993	33.7	-0.9
1994	34.5	0.6
1995	34.5	0.6

Table 9.8.4: *Male and Female Ford-Walford growth parameters for the Cape Rock Lobster fishery.*

Area	Year	Mean Male Lengths (mm)	Mean Female Lengths (mm)
Dassen Island	1967/68	88.0	78.0
Cape Point	1967/68	83.0	77.0
Port Nolloth	1973/74	79.0	73.0
Lambert's Bay	1974/75	82.0	78.0
Eland's Bay	1974/75	83.0	77.0

Table 9.8.5: *The average carapace lengths of the mature male and female populations of the Cape Rock Lobster fishery, as calculated from size structure information obtained from various experimental studies. The results are for exploited populations (Cruywagen, 1995b).*

Year	Area	SubArea	Sample	Length	Total Weight (g)	Egg Weight (g)	Number of Eggs
1987	8	2	1	68	7.914	6.555	107 066
1987	8	2	2	87	11.595	10.237	167 194
1987	8	2	3	72	7.925	6.567	107 251
1987	8	2	4	65	7.012	5.653	92 330
1987	8	2	5	69	7.426	6.068	99 100
1987	8	2	6	85	8.812	7.453	121 728
1987	8	2	7	68	7.937	6.578	107 435
1987	8	2	8	76	7.466	6.108	99 754
1987	8	2	9	76	8.547	7.188	117 402
1987	8	2	10	84	10.724	9.365	152 955
1987	8	2	11	68	7.930	6.571	107 324
1987	8	2	12	78	8.950	7.591	123 990
1987	8	2	13	74	8.291	6.932	113 225
1987	8	2	14	86	10.186	8.827	144 175
1987	8	2	15	86	10.218	8.859	144 697
1987	8	2	16	69	8.452	7.093	115 850
1987	8	2	17	75	8.777	7.418	121 165
1987	8	2	18	83	9.201	7.842	128 080
1987	8	2	19	90	9.501	8.142	132 987
1987	8	2	20	74	9.288	7.929	129 506
1987	8	2	21	86	10.945	9.587	156 576
1987	8	2	22	81	10.232	8.873	144 921
1987	8	2	23	80	8.654	7.296	119 157
1987	8	2	24	74	8.428	7.069	115 463
1987	8	2	25	81	7.718	6.359	103 860
1987	8	2	26	73	6.320	4.961	81 028
1987	8	2	27	75	8.935	7.576	123 742
1987	8	2	28	76	8.347	6.988	114 130
1987	8	2	29	84	9.680	8.321	135 910
1987	10	1	1	73	8.889	7.531	122 997
1987	10	1	2	91	11.352	9.993	163 222
1987	10	1	3	86	11.254	9.895	161 615
1987	10	1	4	69	6.722	5.363	87 599
1987	10	1	5	79	9.214	7.855	128 292
1987	10	1	6	76	9.199	7.840	128 046
1987	10	1	7	97	11.947	10.588	172 935
1987	10	1	8	91	11.473	10.114	165 195
1987	10	1	9	89	10.494	9.135	149 207
1987	10	1	10	96	12.511	11.152	182 149
1987	10	1	11	83	9.977	8.618	140 763
1987	10	1	12	72	7.295	5.936	96 949
1987	10	1	13	83	9.392	8.033	131 198
1987	10	1	14	95	11.607	10.248	167 277
1987	10	1	15	76	9.142	7.783	127 121
1987	10	1	16	89	12.684	11.326	184 979

Table 9.8.6: *A 1987 data sample from the experimental records of the South African Marine and Coastal Management on egg production.*
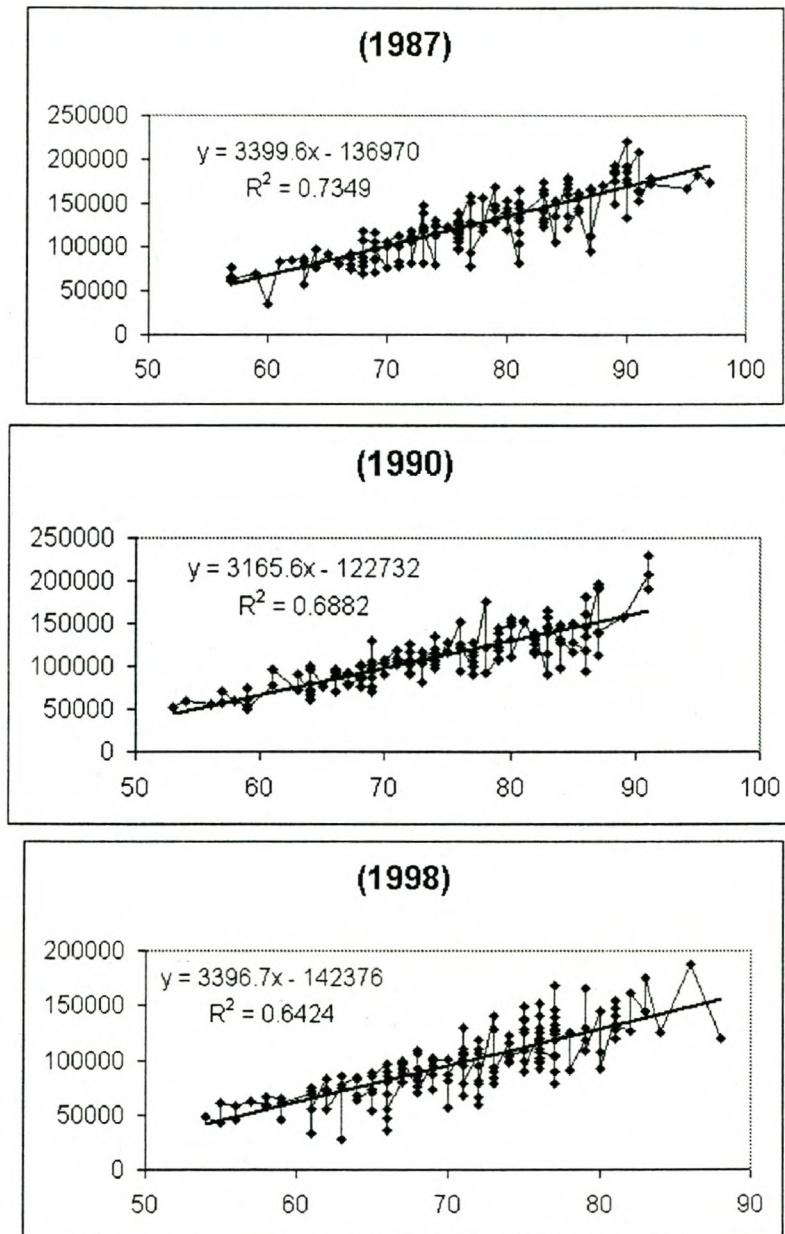
Figure 9.8.1: *Linear fit to diving-data giving the number of eggs at lengths of a certain year. A sample of such a data set is given in Table 9.8.6.*

Year	intercept	slope	R^2
1985	-153238	3643	0.67
1986	-16056	1554.3	0.22
1987	-136970	3399.6	0.73
1988	-160781	3716.2	0.75
1989	-140469	3478.0	0.73
1990	-122732	3165.6	0.69
1991	-164067	3789.6	0.71
1992	-142546	3527.2	0.75
1993	-128293	3231.5	0.68
1994	-138869	3318.2	0.66
1995	-152928	3524.4	0.70
1996	-122913	3235.5	0.79
1997	-273790	5118.6	0.63
1998	-142376	3396.7	0.64

Table 9.8.7: *Linear fit to experimental records for egg production, (as given in Table 9.8.6, per year).*

Bibliography

[1] Arnason, R., 1989. *Minimum Information Management with the help of Catch Quotas*. In: Proceedings of workshop of Scientific foundations for Rights Based Fishing, (eds. Neher, P.A., Arnason, R., Mollet, N.), 215-245, Kluwer Academic Press, Dordrecht.

[2] Barkai, A., Bergh, M.O., 1992. *A New Management Strategy for Optimal Utilization of the South African Cape Rock Lobster (**Jasus lalandii**) resource*. Unpublished document: Sea Fisheries Research Institute, South Africa WG/01/92/WCL1.

[3] Bell, G., 1980. *The Costs of Reproduction and Their Consequences*. Am. Nat. **116**, 45–76.

[4] Bergh, M.O., 1991. *Population and Harvesting Theory for Nonlinear Sex and Age-structured Resources*. Natural Resource Modeling **5**(1), 91–134.

[5] Bergh, M.O., Getz, W.M., 1988. *Stability of Discrete Age-structured and Aggregated Delay-difference Population Models*. J. Math. Biol. **26**, 551–581.

[6] Bergh, M.O., Johnston, S.J, 1992. *A Size Structured Model for Renewable Resource Management, with Application to Resources of Rock Lobster in the South -East Atlantic*. S. Afr. J. Mar. Sci. **12**, 1005-1016.

[7] Beverton, R.J.H., Holt, S.J., 1957. *On the Dynamics of Exploited Fish Populations*. Fisheries Investment Series 2, **19**, U.K Ministry of Agriculture and Fisheries, London.

195

[8] Beyers, C.J. De B., 1979. *Stock Assessment and some Morphometric and Biological Characteristics of the Rock Lobster Jasus lalandii on Marshall Rocks, its Main Commercial Fishing area off South West Africa, 1971 – 1974.* Invest. Rep. Sea Fish. Brch. S. Afr. **117**, 1-24.

[9] Botsford, L.W., 1992. *Further Analysis of Clark's Delayed Recruitment Model.* Bulletin of Mathematical Biology **54**, 275-293.

[10] Caswell, H., Weeks, D.E., 1986. *Two-Sex Models: Extinction, and Other Dynamic Consequences of Sex.* The American Naturalist **128**(5), 707-735.

[11] Clark, C.W., 1976. *A Delayed-Recruitment Model of Population Dynamics, with an Application to Baleen Whale Populations.* J. Math. Biol. **4**, 101-147.

[12] Clark, C.W., 1990. *Mathematical Bioeconomics. The Optimal Management of Renewable Resources.* Second edition, John Wiley & Sons, Inc: New York.

[13] Christensen, S., Vestergaard, N., 1993. *A Bioeconomic Analysis of the Greenland Shrimp Fishery in the Davis Strait.* Marine Resource Economics **8**, 345-365.

[14] Cochrane, K.L., Bross, R., Butterworth, D.S., Hutton, T., Laan, R., Jackson, L., Martin, R., Payne, A.I.L., Penney, A., Roelofse, A., Shannon, L.V., Stander, G., 1995. *Review of International Experiences in Access Rights and their Implications for Fisheries Management in South Africa.* Document prepared on behalf of the sea Fisheries Research Institute, department of Environmental affairs and Tourism, by the Access Rights and Resource Implications Task Group.

[15] Cockcroft, A.C., Goosen, P.C., 1995. *Shrinkage at Moulting in the Rock Lobster* **Jasus lalandii** *and Associated Changes in Reproductive Parameters.* S. Afr. J. Mar. Sci. **16**, 195-203.

[16] Coddington, E.A., Carlson, R., 1997. *Linear Ordinary Differential Equations.* SIAM, Philadelphia.

[17] Cruywagen, G.C., 1995(a). *West Coast Rock Lobster CPUE Series.* Unpublished document: Sea Fisheries Research Institute, South Africa WG/06/95/WCL2.

[18] Cruywagen, G.C., 1995(b). *A Two-sex Delay Difference Model for Estimating Pristine Population Levels. The South African Cape Rock Lobster.* Unpublished document: Sea Fisheries Research Institute, South Africa WG/08/95/WCL1.

[19] Cruywagen, G.C., 1996(a). *A Sex-Structured Delayed Recruitment Model.* Mathematical Biosciences **134**(1), 85-111.

[20] Cruywagen, G.C., 1996(b). *Competition in a Spatial Heterogeneous Environment: Modelling the Risk of Spread of a Genetically Engineered Population.* Theoretical Population Biology **49**(1), 1–38.

[21] Cruywagen, G.C., 1997. *The Use of Generalized Linear Modelling to Determine Inter-annual and Inter-area Variation of Growth Rates: The Cape Rock Lobster as Example.* Fisheries Research **29**, 119-131.

[22] Cruywagen, G.C., 1999. *On the Survivorship and Historical Growth of the South African Cape Rock Lobster.* S. Afr. J. Mar. Sci. **21**, 279-288.

[23] Cruywagen, G.C., Cochrane, K.L, Melville-Smith R., Goosen, P., 1994. *Estimation of the Pristine Biomass of the South African West Coast Rock Lobster.* Unpublished document: Sea Fisheries Research Institute, South Africa WG/06/94/WCL1.

[24] Denn, M.M., 1969. *Optimization by Variational Methods.* McGraw-Hill, New York.

[25] Deriso, R.B., 1980. *Harvesting Strategies and Parameter Estimation for an Age-structured Model.* Can. J. Fish. Aquat. Sci. **37**, 268–282.

[26] Fisher, A.C., 1981. *Resource and Environmental Economics.* Cambridge University Press, Cambridge.

[27] Folmer, H., Gabel, H.L., Opschoor, H., 1995. *Principles of Environmental and Resource Economics. A guide for Student and Decision-Makers.* Edward Elgar Publishing Limited, Cheltenham.

[28] Fox, W.W., 1975. *Fitting the Generalized Stock Production Model by Least-squares and Equilibrium Approximation.* U.S. Fish. Bull. **73**, 23–37.

[29] Getz, W.M., 1980. *The Ultimate-sustainable-yield Problem in nonlinear Age-structured Populations.* Mathematical Biosciences **48**, 279–292.

[30] Getz, W.M., 1988. *Harvesting Discrete Nonlinear Age and Stage Structured Populations.* J of Optimization Theory and Applications **57**(1), 69–83.

[31] Getz, W.M., Haight, R.G., 1989. *Population Harvesting: Demographic Models of Fish, Forest, and Animal Resources.* Princeton University Press, Princeton.

[32] Goh, B., 1980. *Management and Analysis for Biological Populations.* Elsevier Scientific Publishing Company, Amsterdam.

[33] Goh, B.S., Agnew T.T., 1977. *Stability in a Harvested Population with Delayed Recruitment.* Mathematical Biosciences **42**, 187-197.

[34] Goosen, P., 1995. *Comments on the West Coast Rock Lobster Trap CPUE Series 1968/69 to 1993/94.* Unpublished document: Sea Fisheries Research Institute, South Africa WG/04/95/WCL2.

[35] Goosen, P.C., Cockcroft, A.C., 1995. *Mean Annual Growth Increments for Male West Coast Rock Lobster* **Jasus lalandii**. *1969- 1993.* S. Afr. J. Mar. Sci. **16**, 377-386.

[36] Grimshaw, R., 1990. *Nonlinear Ordinary Differential Equations.* Blackwell Scientific Publications, Oxford.

[37] Hannesson, R., 1993. *Bioeconomic Analysis of Fisheries.* Blackwell Scientific Publications Ltd., Oxford.

[38] Heydorn, A.E.F., 1969. *Notes on the biology of* **Pamulirus homarus** *and on length/weight relationships of* **Jasus lalandii**. Invest. Rep. Div. Sea Fish. S. Afr. **69**, 1–27.

[39] Hilborn, R., Walters, C.J., 1992. *Quantitative Fisheries Stock Assessment : Choice, Dynamics & Uncertainties*. Chapman & Hall, New York/ London.

[40] Johnston, S.J., 1996. *West Coast Lobster: Updated Size Structured Model and Preliminary 1996/97 Replacement Yield TAC Estimates*. Unpublished document: Sea Fisheries Research Institute, South Africa WG/07/96/WCL1.

[41] Johnston, S.J., Bergh, M.O., 1993. *Size-based Estimates of Survivorship for the South African Rock Lobster* **Jasus lalandii.** Fisheries Research **18**, 277-304.

[42] Johnston, S.J., Butterworth, D.S., 1995. *A West Coast Rock Lobster Stock Assessment Model: Model Description and Results, and Preliminary Biomass Projections*. Unpublished document: Sea Fisheries Research Institute, South Africa WG/04/95/WCL1.

[43] Johnston, S.J., Butterworth, D.S., 1997. *The Operational Management Procedure for West Coast Rock Lobster*. Unpublished document: Sea Fisheries Research Institute, South Africa WG/07/97/WCL29.

[44] Kuronuma, Y., Tisdell, C.A., 1994. *Economics of Antarctic Minke Whale Catches: Sustainability and Welfare Considerations*. Marine Resource Economics **9**, 141-158.

[45] Levin, S.A., May, R.M., 1976. *A Note on Difference-Delay Equations*. Theoretical Population Biology **9**, 178–187.

[46] Leslie, P.H., 1945. *On the Use of Matrices in Certain Population Mathematics*. Biometrika **33**(3), 183 -212.

[47] Luenberger, D.G., 1979. *Introduction to Dynamic Systems: Theory, Models, & Applications*. John Wiley & Sons, New York.

[48] Lukes, D.L., 1982. *Differential Equations: Classical to Controlled.* Mathematics in Science and Engineering **162**. Academic Press, New York.

[49] Maly, E.J., 1970. *The influence of Predation on the Adult Sex Ratios of Two Copepod Species.* Limnol. Oceanogr. **15**, 566–573.

[50] Magnus, W., Winkler, S., 1966. *Hill's Equation.* Interscience Publishers, New York.

[51] Mantel, J., 1999. *A Marine Fisheries Policy for South Africa - White Paper.* http://www.gov.za/sfri/white.htm

[52] Mantel, J., Matthews, S., 1998. *Sea Fisheries Research Institute of South Africa.* http://www.gov.za/sfri/sf.htm

[53] Mather, D., Sauer, W., 1999. *Economic Organisation and Redistribution: The Case of the Squid Fishing Industry in South Africa (Discussion Document).* Workshop on Bio-Economic Modelling as an Input to Fisheries Management by Chief Directorate: Marine & Coastal Management South Africa in collaboration with The Nansen Program, Cape Town, August.

[54] May, R.M., 1974. *Biological Populations with Nonoverlapping Generations: Stable Points, Stable Cycles, and Chaos.* Science **186**, 645-647.

[55] McKoy, J.L., Esterman, D.B., 1981. *Growth of Rock Lobster (**Jasus edwardsii**) in the Gisborne Regions, New Zealand.* N.Z. J. Mar. Freshwater Res. **15**, 121-136.

[56] Melville-Smith, R., Stewart, P.C., Kittaka, T.J(ed)., 1993. *The Spiny Lobster* **Jasus lalandii** *(H. Mine Edwards, 1837) off the South African Coast: Interannual variations in male growth and female fecundity. Proceedings of the fourth international worksop on Lobster biology and management.* Crustaceana **68(2)**, 174-183.

[57] Munro, G.R., 1992. *Mathematical Bioeconomics and the Evolution of Modern Fisheries Economics.* Bulletin of Mathematical Biology **54**(2/3), 163-184.

[58] Murray, J.D., 1989. *Mathematical Biology.* Springer-Verlag, Berlin.

[59] Nagylaki, T., 1974. *Conditions for the Existence of Clines.* Genetics **80**, 595 - 615.

[60] Newman, G.G., 1973. *Assessment and Management of some Marine Stock in Southern Africa.* PhD thesis. University of Stellenbosch. South Africa. 268pp.

[61] Newman, G.G., Pollock, D.E., 1974. *Biological Cycles, Maturity and Availability of Rock Lobster,* **Jasus lalandii***, on two South African Fishing Grounds.* Investl. Rep. Sea Fish. Branch S. Afr. **107**: 16pp.

[62] Okubo, A., 1980. *Diffusion and Ecological Problems: Mathematical Models.* Biomathematics **10**, Springer-Verlag. Berlin.

[63] Pacala, S.W., Roughgarden, J., 1982. *Spatial Heterogeneity and Interspecific Competition.* Theoretical Population Biology **21**, 92 - 113.

[64] Pascoe, S., Mardle, S., 1999. *Optimal Fleet Size in the English Channel: a Multi-Objective Programming Approach.* Resource Modelling Association Annual Conference Halifax, Canada, 23-25 June.

[65] Pella, J.J., Tomlinson, P.K., 1969. *A Generalized Stock Production Model.* Bulletin Inter-Am. Trop. Tuna Comm. **13**, 419–496.

[66] Pollock, D.E., 1982. *The Fishery for and Population Dynamics of West Coast Rock Lobster Related to the Environment in the Lambert's Bay and Port Nolloth Areas.* Investl. Rep. Sea Fish. Branch S. Afr. **124**: 57pp.

[67] Pollock, D.E., 1986. *Review of the Fishery for and Biology of the Cape Rock Lobster* **Jasus lalandii** *with notes an Larval Recruitment.* Can. J. Fish. Aquat. Sci. **43**, 2107-2117.

[68] Pollock, D.E., 1997. *Egg-production and Life-history strategies in Some Clawed and Spiny Lobster Populations.* Bull. of Mar. Sci. **6(1)**, 97-109.

[69] Pollock, D.E., Beyers, C.J. De B., 1979. *Trap Selectivity and Seasonal Catchability of Rock Lobster* **Jasus lalandii** *at Robben Island sanctuary, near Cape Town.* Fish Bull. S. Afr. **12**, 75-79.

[70] Pollock, D.E., Beyers, C.J. De B., 1981. *Environment, Distribution and growth rates of West Coast Rock Lobster* **Jasus lalandii** *(H. Milne Edwards.).* Trans. R. Soc. S. Afr. **44**, 379-400.

[71] Press, W.H., Flannery, B.P., Teukolsky, S.A., Vetterling, W.T., 1989. *Numerical Recipes in Pascal.* Cambridge University Press, Cambridge.

[72] Punt, A.E., 1988. *Model Selection for the Dynamics of Southern African Hake Resources.* M Sc-thesis. University of Cape Town, South Africa.

[73] Reed, W.J., 1980. *Optimum Age-Specific Harvesting in a Non-linear Population Model.* Biometrics **36**, 579–593.

[74] Rektorys, K., 1969. *Survey of Applicable Mathematics.* Iliffe Books Ltd. London.

[75] Ricker, W.E., 1954. *Stock and Recruitment.* J. Fish. Res. Bd. Can. **11**, 559–623.

[76] Ricker, W.E., 1975. *Computation and Interpretation of Biological Statistics of Fish Populations.* Fisheries Research Board of Canada, Bulletin no. 191.

[77] Rorres, C., Faires, W., 1975. *Optimal Harvesting Policy for an Age-Specific Population.* Mathematical Biosciences **24**, 31-47.

[78] Sandal, K.L., Steinshamn, S.I., 1995. *A General Approach for Optimal Management of Renewable Resources.* World Conference on Natural Resource Modelling, Pietermaritzburg, South Africa, 5 - 10 July, 1995.

[79] Sandberg, P., Bogstad, B., Røttingen, I., 1998. *Bioeconomic advice on TAC - the State of the Art in the Norwegian Fishery Management.* Fisheries Research **37**, 259-274.

[80] Samuelson, P.A., Nordhaus, W.D., 1989. *Economics.* MacGraw-Hill, New York.

[81] Schaefer, M.B., 1954. *Some Aspects of the Dynamics of Populations Important to the Management of Commercial Marine Fisheries.* Bulletin Inter-Am. Trop. Tuna Comm. **1**, 27–56.

[82] Schumann, C.G.W., Franzen, D.G., De Kock G., 1964. *Ekonomie, 'n Inleidende Studie.* Universiteit Uitgewers en Boekhandelaars Bpk., Stellenbosch.

[83] Scott, R.H., Nigro, N., 1982. *Principles of Economics.* Macmillan Publishing Co., Inc., New York.

[84] Shigesada, N., Kawasaki, K., Teramoto, E., 1986. *Traveling Periodic Waves in Heterogeneous Environments.* Theoretical Population Biology **30**, 143 - 160.

[85] Stewart, G.W., 1973. *Introduction to Matrix Computations.* Academic Press, New York.

[86] Smith, G.D., 1978. *Numerical Solution of Partial Differential Equations.* 2nd ed. Oxford Applied Mathematics and Computing Series. Oxford University Press, London.

[87] Waicent (United Nations website managers), 1999. *FAO Fisheries Department: Number of Fishers Doubled Since 1970.* http://www.fao.org/fi/highligh/fisher/c929.asp

[88] Winston, W.L., 1994. *Operations Research: Applications and Algorithms.* Duxbury Press, Belmont.