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# The Effect of Fishing on the Evolution of North Sea Cod

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**Submitted for**

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Young boy with two cod fish, Battle Harbour, Labrador ca. 1900
(PANL VA 21-18)

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# Abstract

With the recent collapses of many major fish stocks and North Sea cod seeming to be the next on a long list, it has become apparent that our actions have a great effect on fish populations. This thesis looks at how fishing can not only have an immediate effect such as causing declines, but can also affect the evolution of a stock.

A population model is built which is first examined for stability properties. A comparison is also made of the model under fishing and when fishing is absent. A measure of population fitness in terms of ability to invade other populations is then established. This measure is used to examine the sensitivity of the model to parameter values. This is also done for models which use different functions to model life history in order to determine the importance of model choice. Components of fishing mortality are considered with respect to their impact on the stock, for both the main model and the alternate models. Finally, spatial and seasonal considerations are added in a simple way to check if a single region model can be trusted to model the whole of the North Sea.

It is found that although the model is sensitive to the choice of growth function, generally growth has the most effect on population fitness. It is also shown that the level of fishing has more impact on the fitness and yield of the stock than the initial capture length. Thus, it is more important to reduce fishing effort, than change aspects of the fishery such as mesh size in nets. Furthermore the spatial model shows that the establishment of reservoirs, or no-fishing zones, should be done carefully in order not to favour a decrease in growth rate of the stock.

# Acknowledgments

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It would be remiss of me to forget my colleagues in the department, who during the three years have become friends. Their optimism and encouragement, as well as their willingness to listen to my ponderings on cod, is much appreciated. I also thank Craig for his love and understanding during the peaks and troughs of writing up. Finally, I must thank my family who have always been a source of love, advice, and support.

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# Introduction

# Chapter 1

# The Life History of Cod in the North Sea

## 1.1 Cod and its Place in the World

Cod (Latin name *Gadus morhua* ) is one of the most important fish species in the world both historically and economically. The family of fish to which it belongs, the Gadiformes or codfishes, is one of the three most utilized families in marine fishing (Lindberg 1974). Other members of this family caught by world fisheries are the haddock, pollock (also known as saithe), whiting, hake and Pacific cod. In total 6 million tons of gadiform fish are caught each year and more than half of this is Atlantic cod (Kurlansky 1997).

The cod is so popular due to its abundance and use as a food source. It is the whitest of the white flesh fish, has virtually no fat (.3%) and very high protein levels (18%), even in comparison to other fish (Kurlansky 1997). Almost every body part is used or eaten, including the throat, cheeks, airbladder (also used to make a clarifying agent and in some glues), roe, stomach, tripe, milt (or sperm which is eaten in Iceland and Japan), bones which are softened and eaten in Iceland, and the skin which is eaten in some places and also used to make leather (Kurlansky 1997).

The cod fishery has a long history and has influenced many of the countries bordering the North Atlantic. Perhaps best known for its dependence on cod is Newfoundland, an island province of Canada, which had battles waged for its cod and was settled by fishermen needing land to dry their catch. At one time the richest fishing grounds lay off its shores on the Grand Banks, and fish were so plentiful that the Duke of Milan was told ‘the sea there is swarming with fish, which can be taken not only with the net, but in baskets let down with a stone’ (Harris 1998). The fish has had such an impact on the culture and economic survival of the occupants, that the word ‘fish’ is synonymous with cod. In the 1960’s onward, ships from around the world could be seen in harbours and offshore, with countries such as Spain, Portugal and Russia playing major roles in the development of the fishery.

However, tragically, in the 1980’s overfishing was to devastate the stocks surrounding Newfoundland. A moratorium on fishing was finally declared in 1992, which has still not been lifted in the northern waters, apart from the occasional ‘food fishery’ intended for individuals to fish only enough to provide cod for their own tables. This collapse can be blamed almost completely on overfishing (Myers, Barrowman, Hoenig, and Qu 1996), although at first other hypotheses were made, such as seal predation or climate change. Hyperstability had a role to play in the decline, with cod densities in certain locations increasing while numbers decreased on the stock basis, resulting in misleading assessments of the stocks (Rose and Kulka 1999). The stocks have reached such dire levels that it has been recommended by Dr. K. Bell (a Memorial University of Newfoundland fisheries ecologist) that cod should be added to Canada’s endangered species list (Harris 1998), although they currently have only been listed as vulnerable. There are also serious questions on whether the northern stocks will ever return, as originally their return was forecast in 5 years, and 10 years later there still seems no evidence that the stocks will ever reach their previous levels. This return to former glory has been slower than predicted partly due to the low fertility of the stock (Oosthuizen and Daan 1974).

The problem with drastic declines in numbers is unfortunately not restricted to Newfoundland; in the late 80’s the Barents Sea stock also suffered a serious decline. However, prompt action on the part of Norway and the high fertility of the stock (Oosthuizen and Daan 1974) has seen this stock rebound to levels not seen in 25 years (Harris 1998), and it is still, along with the Icelandic fishery, one of the two most important fisheries of cod (http://www.fishbase.com). The North Sea has also undergone declines, for instance in 1902 the British found that its cod stocks had been depleted (Kurlansky 1997). In 2001, it was decided that a decline in stocks was such that it required a moratorium from February to April (for certain areas) while drastic quota cuts have been implemented in recent years.

The economic power of cod is clearly demonstrated by the fact it is one of the few species that wars have been fought over. To some extent, as previously mentioned, the desire for cod has led to battles over Newfoundland waters. A more recent example, which is certainly remembered in Britain, is the Icelandic cod wars. In the late 1950's till early 70's, Iceland expanded its fishing limits on other countries to 12, then 50 and finally 200 miles offshore (Kurlansky 1997). These increases in limits prompted what have become known as the 'cod wars'. Although no lives were lost, Icelandic boats did cut the trawls of vessels inside the limits with 84 trawlers losing their nets in a year of conflict in 1971 (Kurlansky 1997). Shots were fired during the wars, and on May 26th, 1973 a hole was blown in the hull of a British trawler (Kurlansky 1997).

In the rest of this chapter, we will first examine the area of interest to this thesis, the North Sea, and then look at the life cycle of a cod in this body of water. We will then continue by examining the current state of the North Sea cod stock and the problems the area is experiencing.

## 1.2 The North Sea

The North Sea is a body of water surrounded by Europe: on the west side the United Kingdom, to the north east Norway, with Denmark, Germany, the Netherlands and Belgium all having coast along its edge. It is a fairly shallow basin, varying in depth from 30 to 200 meters (Brander 1994). Its surface area is 575 300 square kilometers and it is influenced by the Atlantic, mainly by flow

Figure 1.1: The North Sea : *The black lines show the limits of what is considered as the North Sea. Speckled areas are spawning grounds used by cod. The map was drawn with the help of http://odin.dep.no/md/html/conf/map and the Atlas of the seas around the British Isles(1981)*

through the northern North Sea (Brander 1994).

Different ages of cod are found in different places in the North Sea. Age 1 cod are most common along the coast of the Netherlands and northeast England as well as in the German Bight, as are age 2 cod, although they also are found in the Northern North Sea. Age 3 cod are mainly in the northern North Sea, while age 4 cod and older are scarce throughout (Brander 1994). Spawning areas are scattered across the North Sea as shown in figure 1.1, where they are the speckled regions.

The North Sea can be divided into six distinct regions using hydrography and biology (more will be mentioned about this in chapter 8). Genetic studies have, however, found no clear sub-stocks which are identifiable within these regions (Brander 1994). Hence, in terms of fisheries assessment, the North Sea is normally considered as a single region, sometimes also including the areas between Sweden and Denmark, known as the Skaggerak and Kattegat.

## 1.3 The Life of a Cod

The life cycle of cod has several different stages (figure 1.2). Cod start as eggs, progress through a juvenile stage which switches level in the ocean, and finally reach maturity. The timing of this life-cycle differs according to region, and the first age at maturity in a stock can range from 2 years to 7 years depending on which region the stock inhabits(http://www.fishbase.org). As such, although the general life history is the same from stock to stock, the differences in duration of life stages means that the reaction of the stocks to fishing pressure can be quite different.

The eggs are extremely small (approximately 1.4 mm (R. Myers, Stock and Recruitment data base, http://www.fish.dal.ca/ myers/welcome.html)), and float on the surface drifting with the current. Cod eggs are spawned between January and April, with latitude affecting the peak time of spawning: for instance, the Southern Bight peaks in February while the northern North Sea peak in spawning is in March (Brander 1994; Daan 1978). There is limited spawning in the autumn, but the main spawning season is during the spring (Brander 1994; Anonymous 1981). Spawning takes place in many different areas of the North Sea and figure 1.1 shows where these areas are found. It should be mentioned that due to the similarity between haddock and cod eggs, it is not known exactly where the cod spawn as both spawn at similar times (Daan 1978; Fox, O'Brien, Dickey-Collas, and Nash 2000).

In order to develop normally the sea temperature to which the eggs are exposed should be between 1.5 and 12 degrees Celsius (Thompson and Riley 1981), so years with exceptional sea temperatures can have an effect on the population. Egg mortality is particularly high, with as few as 3 to 4 % of eggs

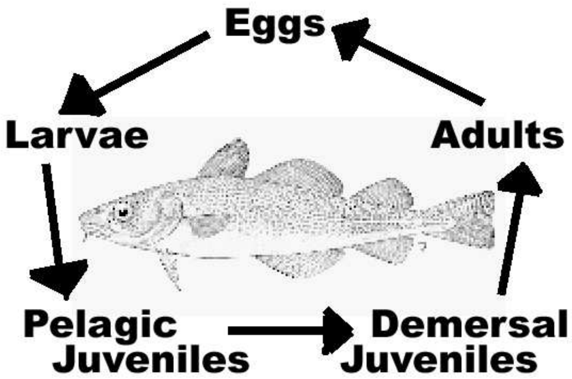


Figure 1.2: The Life Cycle of Cod. *This includes 5 life stages with all cod becoming adults by the age of 6 years (Background image from http://www.fishbase.com)*

hatching (Heesen and Rijnsdorp 1989). Mortality is assumed to be caused mainly by predation, as eggs supply such an easily obtainable food source, and several species eat cod eggs. Herring have been cited as one of the main predators, and the ‘gadoid outburst’ has been suggested to have been caused by a decline in the herring stocks. However, Daan found herring eat only between 0.04% and 0.19% of eggs in the North Sea (Daan, Rijnsdorp, and Overbeeke 1985).

Once cod hatch they become larvae, although according to Brander (1994) very little is known about this stage. This is due to two main reasons. During the early stages of life, the rates of production and mortality of eggs and larvae change rapidly making accurate modelling of this age range very difficult. Secondly there is no assessment of the catching efficiency of gear for fish of this age, preventing good estimates from being made of the percentage caught (Sundby, Bjorke, Soldad, and Olsen 1989). The combination of these two properties makes drawing any conclusions from data on this age risky.

The egg sac does not disappear immediately upon hatching. Larvae live off the egg sac for about 6 days, by which point it has been completely resorbed (Brander 1994), although some larvae do begin to feed at sizes as small as 3.1 mm (Last 1978). After this stage larvae fend for themselves, and many will perish by drifting into areas where food of a suitable size is scarce (Northern Cod Science Project). They feed on phytoplankton and zooplankton, principally eating nauplii and copepodites of calanoid copepods, with prey being determined by the mouth size of the larvae (Last 1978; Thompson and Riley 1981). At this stage mortality is still very high, and as many as 99.9% of fish die in the first 4 months of life(Northern Cod Science Project).

The next stage of life, that of juveniles, can be divided into two parts. A pelagic life stage where fish live towards the top of the water column, and a demersal life stage where fish settle towards the bottom. The pelagic stage differs in duration between areas, being very short or perhaps nonexistent for fish in the southern North Sea (Brander 1994). In other areas, particularly off the coast of Jutland and in the central North Sea, this stage may last as long as 6 months (Anonymous 1981; Daan 1978). However very few pelagic juveniles are found in shallow areas of the North Sea (Daan 1978). Robb and Hislop concluded that competition for food is not great among these juveniles (Robb and Hislop 1981). Cod this age eat mainly copepods until they are 3 centimeters in length, after which their diet is dominated by fish, the largest component being Norway Pout, another gadoid fish (Robb and Hislop 1981).

By 6 months the juveniles have settled to the bottom layer of the ocean, where rocks and weeds give cover to avoid predation, a major consideration for the smallest fish. They are eaten by several other gadoid fish, including cod, whiting, and saithe. At this stage they consume mainly crustaceans although as their size increases fish become a more important component in their diet (Daan 1973). It has been found that juvenile cod (mainly under 15 cm) make a significant contribution to the diet of other cod, being 10% of the diet by weight in the northern North Sea, while only 1% to 2% in the southern North Sea (Daan 1973). My model will start with this life stage, avoiding the difficulty of modelling the extremely high mortality experienced in the previous 3 life stages.

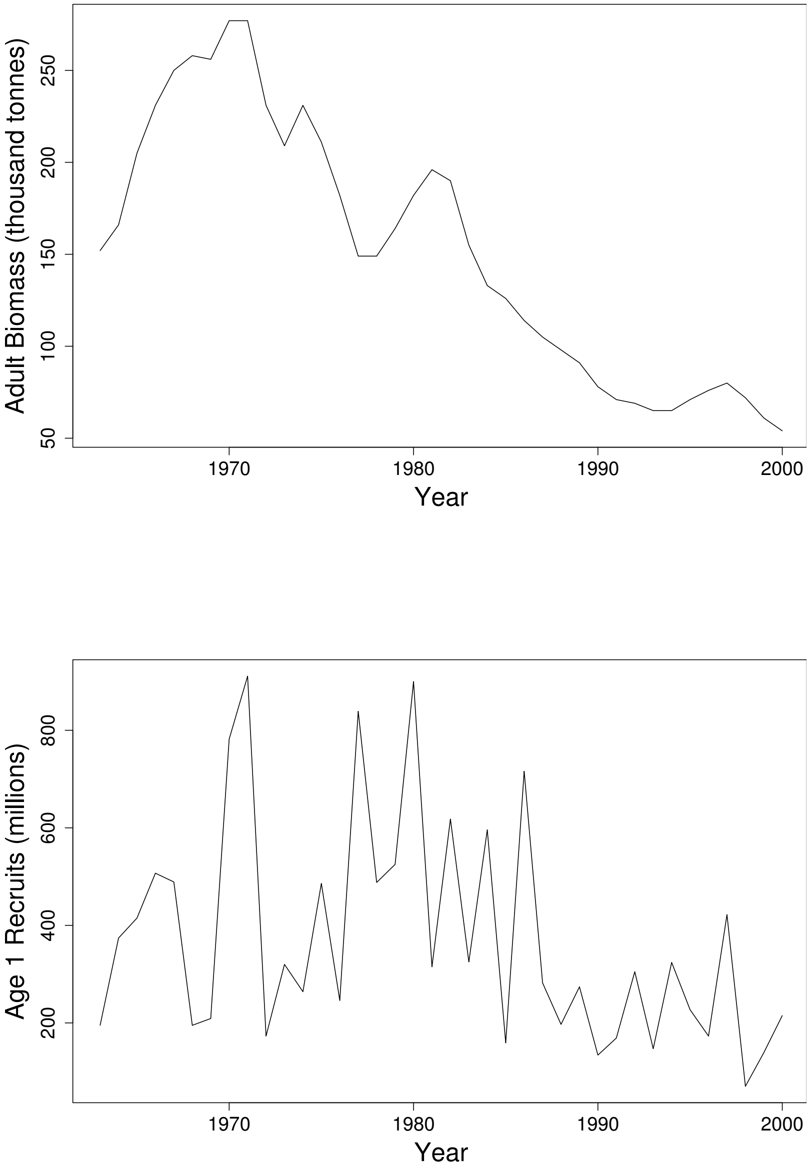
The final stage of a cod's life is adulthood, although very few of the eggs spawned will actually produce adults. Some cod become mature as young as age two, but some cod in the North Sea do not mature until they are six years old. (Oosthuizen and Daan 1974). Males mature earlier than females (Oosthuizen and Daan 1974), although in my model this is not considered as there are not separate models for the two sexes. As adults, the key role of the fish is to reproduce, with older female fish spawning more eggs over a longer time period than their younger counterparts (Harris 1998). The current levels of fishing, however, prevent there being many of these older female fish, and most fish will die before maturation. When stocks are being rebuilt, it is the re-establishment of a healthy population of these older female fish, which will vastly increase the rate of recovery. Fish migrate to spawn, with spawning grounds generally to the south of feeding areas (Brander 1994), although these migrations are relatively short. Adult cod mainly eat fish, including many species used by commercial fisheries including young cod. Mature cod are relatively large fish, and as such do not suffer the same levels of mortality experienced in earlier life stages.

## 1.4 The Recent Past

Historically, the North Sea has not been the most abundant producer of cod; in the 16th through 19th centuries Dutch fishermen sailed to Iceland for cod rather than staying on the North Sea (Brander 1994). There was, however, a large increase in numbers of cod in the 1960's, a phenomenon seen in many gadoid populations, and given the name the 'gadoid outburst' (Holden 1981). This rise in numbers is thought to possibly be linked with the decrease, due to overfishing, of the herring population (Daan, Rijnsdorp, and Overbeeke 1985). For a while afterward, spawning stock biomass (or adult biomass) fluctuated, but from 1981 there has been a steady decrease in the population, and biomass is now at the same levels as before the 1960's (Brander 1994). In fact, levels are so low that the spawning stock biomass is now considered to be well below the safe biological limit of 150 000 tonnes for the stock (Brander 1994). This level (known as MBAL or $B_{pa}$) is believed to be the spawning biomass below which the probability of low levels of recruitment increases. Another reference point used in fisheries management is $B_{lim}$, the lowest value of spawning biomass observed for the population. This value has been set at 70000 tonnes for the North Sea cod stock (ICES 2002). There is great concern for the stock as spawning biomass has hovered around this value for all of the 1990's.

The current situation in the North Sea is definitely worrying. In 2001 forty thousand square miles of ocean were closed to fishing from February to April in order to protect the spawning stock, and the European Union council of ministers has agreed to the lowest total allowable catch (TAC) ever. This quota cut is necessary as there is a lack of large spawning fish due to the long term rise in fishing effort and a decrease in recruiting young cod (Christensen 2001). A fisheries collapse in the North Sea has been predicted for many years, and during the last ten years fishermen have barely managed to catch their quotas, with ever smaller fish being caught (Christensen 2001). Hopefully, the actions of the European Union in closing the grounds and cutting catches will have the desired effect, preventing a disaster such as that which befell the herring stocks

Figure 1.3: The Decline of Adult Biomass in the North Sea (Data from ICES (2002)):*Plots of both adult biomass and recruitment are given. They clearly show that the population levels have dropped in the 1990's*



in the North Sea and the cod stocks off Newfoundland. There is some argument, however, over the level to which it can be hoped the stock will return. It may be unrealistic to expect a return to the levels of the 1960's and 1970's which were exceptional.

# Chapter 2

# A Modelling Background for Fish Stocks

This chapter will examine modelling as a tool for learning about fish populations. It will start by discussing how models can be used to solve problems raised about populations, and then mention the main models used for fisheries assessment in the North Sea. Although these models are not used in this thesis, they are crucial to virtually any work done for populations, as parameters are frequently set using information which has come from such stock assessments.

An important aspect of fisheries assessment is data collection. The different methods are discussed, in order to give a sense of the complexities involved in making an assessment. Upon consideration of the difficulties involved with assessing ocean stocks, much respect is gained for the difficulties faced by both fisheries scientists and managers in trying to assess stocks and set sensible guidelines for fishing.

## 2.1 Modelling Populations

The first question is why should populations be modelled? The simple answer is that models are a tool to help us understand the complexities of the world around us. A good model should be simple to use and understand, give results which are calculable in a short period of time, and increase our knowledge of the field of interest. Models, by necessity, are a simplification of the world. It is impossible to quantify the effect of every part of the environment. Such a model would take so long to create and use that it would not be practical to build. The model would also produce unreliable results as it is not clear how to model many environmental factors and the interactions between factors which affect a population. Hence, models tend to choose a few key factors which are felt to be essential to finding the answer that is sought. These factors will often include ranges of environmental factors grouped into one parameter and thought of as a noise or an environmental effect. Some of the defining characteristics of models and how they will be treated in this thesis will now be discussed.

One key aspect of modelling is to decide which questions the model will be answering. For example, is the interest in modelling an entire ecosystem, a sub-community of the ecosystem, a particular species, or how an individual copes with living in its environment. In each case the model produced will be substantially different. This thesis will focus on cod at the species level. Therefore, although we recognize that the population consists of a number of individuals whose weight and maturation are modelled, a general maturation and growth scheme for the population as a whole shall be used. An alternative approach would be to assume that individuals follow a general growth and maturation scheme, but that for each individual this scheme differs slightly. By tracking individuals the picture of the general population can be constructed. This method, often referred to as individual based modelling, has the advantage that it is a more accurate depiction of the population, as not all individuals will grow identically. It was felt, however, that as we are interested in examining the impact of fishing on the population as a whole, this was a complication to the model which was unnecessary. Furthermore, the entire ecosystem will not be modelled. It will be assumed that food is distributed so that all cod have equal supplies, mortality affects the population as a whole and does not have a spatial term (although in chapter 8 this assumption will be changed), and that human fishing is not affecting food supply for the cod at the same time as it affects mortality. These are large assumptions, however they simplify the model, while still allowing us to examine the impact of fishing on the population.

The next key point is how time should be modelled. Fishery models frequently make use of discrete time models, where time is considered as moving forward in chunks, often using a spacing of a year. Simulations of the population are then easy and data collected for the growth, maturity and mortality of the stock can be used without having to make assumptions of the functions underlying the life history. In this thesis, however, a continuous time model will be used, as growth and fertility are modelled as gradually occurring processes for the population, as opposed to processes which occur in sudden leaps and bounds. Although this is more realistic, the impact the function chosen for a certain aspect of life history will have on any results must be considered. Using a continuous time model implies that when simulations are run, a different discrete time step model shall be used, however, by using small time steps for the simulations, differences in results can be minimized.

It is also important to recognize that random events have an impact on the behaviour of populations. There are two ways to approach this random behaviour when modelling. The first, deterministic modelling, ignores the random behaviour and instead is aimed at finding the main trend. It necessarily assumes that the random behaviour is insignificant in comparison to the underlying trend. When the results of such a model are compared to what is seen in the environment, it is expected that model results will not be an exact replica of the real world. Instead it is hoped that, on average, a deterministic model is accurate. This requires that environmental fluctuations will not take a regular pattern with respect to the deterministic solution, and secondly, that these fluctuations will not be so large that they hide the deterministic effects. Another approach to treating random effects, is stochastic modelling. Instead of the model giving, for instance, the decrease in population over a time period, the stochastic model gives a probability of a certain decrease in population over the time period. As such stochastic modelling can sometimes be thought of like an experiment, where several realizations can be averaged to give an idea of the general behaviour. A good stochastic model will give an idea of how the real world situation can change, and if enough realisations are run there should be some which resemble what has happened in the environment. The main trend found by a stochastic model may be the same as the trend found by a deterministic model, but there exist situations where there is little resemblance between the two. I have chosen to use a deterministic model, as it was felt to be the simpler of the two methods and would let me solve problems numerically as well as through simulation.

A final consideration is the inclusion of spatial dynamics into a model. I shall begin by not including spatial considerations, assuming instead that the North Sea is uniform in its distribution of food, mortality, and numbers and weight of fish. However in chapter 8 a glimpse of what can happen when the North Sea is divided into different spatial regions shall be given. Only two regions shall be used, but even with such a small change, the complexity of the model increases as now immigration and migration have a role to play.

These are some of the main considerations when building a model. It must then be determined which individual aspects should be included, for example, numbers, weight, length, maturity, condition, toxicity levels, or a combination of factors in the model. These same basic tools can build models to answer a variety of questions about a population, such as the effect of temperature, sunlight, pollution, food levels or fishing.

## 2.2 Stock Assessment Models

One of the initial questions frequently asked in fisheries is ‘how many fish are there and how many can we safely catch?’. Since it has been realized that the oceans have their limits, and are not an inexhaustible source of fish, several different models for stocks have been used. In this section several of these models shall be introduced.

There is no standard model which is used for all fisheries assessment. For instance a survey done by the National Marine Fisheries Service in the United States found for 212 of the US stocks, that 39.2 % were assessed with age-structured models, 28.3% with abundance models, 8.0% with production models, 6.1 % with stock reduction models and further stocks were either not assessed, or assessed using professional judgement or other means (Committee on Fish Stock Assessment Methods et al. 1998). In section 2.2.2 I shall discuss in detail the age-structured models which are generally used for North Sea cod (such as extended survivor analysis), however I note that there are many other models which are found to be appropriate for other regions and species.

We start with a rather obvious question, but one that must be answered, ‘Why should fish stocks be assessed?’. The clear answer is that whatever the state of a fishery, there are always inherent problems or dilemmas which must be solved. For developed fisheries these are quite obvious questions, such as ‘how many fish can be caught next year safely?’ or ‘is the fishery reducing the population to unfishable levels?’. For underdeveloped fisheries, questions such as ‘How much can this stock yield?’ and ‘How can we best plan to exploit the fishery?’ are important (Gulland 1983).

The second question is how accurately can populations be assessed. Accuracy of fish assessments is indeed a serious problem. In the collapses of both North Sea herring and Newfoundland cod stocks, assessments did not show that the populations were crashing until stock levels had already decreased considerably (Hilborn and Walters 1992). This was compounded in both cases by the management of the stock. In the case of North Sea herring quota cuts were recommended in 1970, yet in 1974 managers of the fishery agreed to a TAC which was larger than the total population (Hilborn and Walters 1992). There are many worries about the catch data which is frequently used in analysis, as many scientists are skeptical of the ability to detect stock trends using such data (Hilborn and Walters 1992). It is also known that such data can have serious biases. Some stocks can become easier to catch at low numbers due to increased shoaling. If old values are used to estimate the ability to catch a stock this can have profound consequences. Catch records may also ignore discards and in the worst case scenario have been falsified. There are further worries as most stock assessment is done with single population models, ignoring the interactions with other populations. The North Sea is one area in which multi-species analysis is used periodically, however, Daan (quoted in Hilborn and Walters 1992) has pointed out that such models are very data intensive and that the tools for doing multi-species models properly don't exist as of yet. A final difficulty with assessing fish populations is that population numbers are difficult to assess, in that although some acoustic and sonar methods are used, fish cannot be counted or observed as easily as animals living on the surface. Instead they must generally be caught in order for assessments to be made, adding the extra difficulty of assessing how well equipment catches the population and if it catches a representative sample.

A quick run down of different data collection methods will now be given, followed by a brief summary of different assessment models.

### 2.2.1 Data Collection Methods

There are four main ways to collect data, by using commercial fishery data, research vessel surveys, tagging data and lab experiments. Each of these different methods has different relative costs, advantages, and uses for fishery scientists. Upon examining the different methods of data collection it becomes apparent that this is a major area of consideration in fisheries assessment. Without good data on which to base models, there is little hope that accurate assessments of populations can be achieved or that any model of population behaviour can be accurate.

#### Commercial Fishery Data

Commercial fishery data has the advantage that it examines exactly how fishermen are interacting with stocks, and if unbiased and truthfully reported will give an accurate picture of the mortality inflicted on a stock. In terms of ecosystem management, commercial data is grossly biased. Fishermen will only target fish which are financially rewarding, and hence not give an accurate idea of stock levels for all species in the oceans (Gulland 1988). The most important data which can be obtained this way is the magnitude of the total catch, observations on the amount of fishing and corresponding catch, and the size and ages included in the catch (Gulland 1988).

Catch and effort data is best collected by on-board observers. These observers can give accurate accounts of when and how the fishery is conducted, as well as giving information on bycatch, discarding and violations of conservation measures (Hilborn and Walters 1992; Committee on Fish Stock Assessment Methods et al. 1998). All of this information is very difficult to obtain without having an impartial observer on board boats. These observers can also take information on the specifics of the catch, such as species, age and sex distribution caught. However, the problem with obtaining data in this manner is that observers are expensive, in that they must be well trained before being used and sometimes constitute (in terms of the economics of a fishing boat) a useless member of the crew. Careful assumptions must be made when extrapolating observer data to the full fishing fleet as it can be expected that observers will affect fishing practices in many cases, rules are more likely to be strictly followed and gear maintained properly.

Another method for using commercial data is on shore observations of catch. During the sale of fish catches, records are kept on size and weight as a matter of course, and these records can be used by scientists to assess the catch. Furthermore there are programs which sample catches as they come in for age and sex distribution (Committee on Fish Stock Assessment Methods et al. 1998). Of course such methods are not capable of assessing discards of undesirable species or fish too young to be caught in legal mesh sizes, and hence lose some of the data an observer can provide. This collection method is, however, much cheaper.

A third method used in commercial fisheries is examination of logbooks of fishermen. For instance, in Australian trawl fisheries, notes on the start and end locations and the size of the catch are made in the logbook, allowing spatial maps of the population to be created (Hilborn and Walters 1992). Unfortunately, this method rarely gives information on age and species caught, and depends on the fishermen giving an accurate report of what has happened at sea. Once again this is an inexpensive method of gaining data, however, an onboard observer tends to produce the most accurate data.

### Research Survey Data

The second method of data collection is by using research surveys. These surveys are very expensive as a boat must either be owned or hired to do the survey, and is unable to catch fish in a competitive commercial manner. The main advantage of such surveys is that they can use good sampling designs and study the ability of different gear to catch fish. Furthermore, as they are used for research purposes, not commercial purposes, an accurate picture can be built of the proportions of different species in the oceans. Three different ways of obtaining data from research surveys shall now be discussed.

For some populations visual observation can be adequate, if the species surfaces frequently. Assumptions must then of course be made about frequency of surfacing and also observer reliability (Hilborn and Walters 1992) in order to estimate numbers. This method of observation will only provide data on numbers and is unlikely to allow observers to collect any data on sex or age of the population. As such it is rarely used.

Electronic and hydro-acoustic surveys can also be performed. The advantage being that this method does not harm the fish. In order to collect good data, however, certain problems do need to be solved. For instance, the strength of the signal received from targets must be calibrated with the number of individuals, and there is also the problem of species identification (Hilborn and Walters 1992). Many aspects of the population will not be measured in such a survey, including individual size, sex and age of the species monitored. Such methods have been used for tracking migrations of populations, and discovering where in the water column populations live at particular times of the day, year or migratory route.

The most frequent use of research vessel surveys is using commercial fishing gear in imitation of the commercial fishery. Whatever is caught can be fully documented, for all important characteristics such as weight, length, age, sex and species. Sampling can be planned so as to cover the entire region of interest, rather than targeting only areas where fish are known to congregate as in commercial fisheries. The exact configuration of the gear will also be known, allowing for an accurate assessment of its performance. The only assumption which needs to be made is the proportion of fish captured by the gear and its selectivity (Hilborn and Walters 1992). This can be assessed by using a combination of gears (for instance with different mesh sizes) to evaluate the ability of the larger mesh size to catch fish.

### Tagging Data

The third method of data collection which is in standard use is tagging. This is done by putting a tag on the fish through a fin or embedded in flesh. This method allows for the survival, movement, mortality and abundance of fish to be estimated by using the recovered tags to estimate how the population lives. Some tags send radio or acoustic signals, so that the fish can be tracked continuously by boats on the surface. This is generally used to examine daily migrations, changes in depth, or eating patterns. Other types of tags must be recaptured in order to allow assessments of migration or movement, and likely abundances and mortalities to be estimated. Recovery of tags can be difficult sometimes, as many will not be returned when the fish is caught. Thus estimates need to be made for tags not recovered as to how many are due to tag loss, natural mortality, and lack of reporting. Further assumptions must then be made on whether the tags have any effect on the fish carrying them. As such it is often difficult to obtain accurate results through tagging, or even sometimes to estimate how accurate results are (Gulland 1988).

### Laboratory Experiments

A final method of data collection which can be useful to the fisheries scientist is laboratory experimentation. It has both the weakness and strength that conditions can be strictly controlled. This is an advantage in that life-history parameters such as growth can be measured accurately knowing the true age of the fish, temperature and environment in which they have lived. However, laboratory results can not be expected to translate fully to life in the wild where conditions alter from hour to hour and region to region. Furthermore, there are size limits on how large and deep a laboratory tank can be, making it difficult to truly replicate a wild environment. The difficulty of observation in the ocean, makes this a very attractive method for gaining data on virtually every aspect of life-history and behaviour.

### 2.2.2 Assessment Models

The models for assessment, which depend on these data, will now be introduced. Assessment models are frequently based mainly on commercial data, however other types of data, such as tagging data are essential for their information on natural mortality. Tests are also being made of models using only research survey data to see if there is any advantage in excluding fisheries data and if these models could act as a check on the normal assessments (Cook 1995).

There are several different assessment models used for commercial fisheries. The type of fish being examined and the method of fishing affect which model will be used. I will examine in detail only two models, as these are the models which are used most often for North Sea cod.

Many other simple assessment models do exist. Stock-recruitment models are perhaps the most simple as they are generally used for stocks where age effects are not important (Hilborn and Walters 1992). Thus the spawning stock is thought of as a single group which reproduces in the same manner for all ages. Hence this model is frequently used for species which spawn only once in their lifetime. Tretyak (1999) has expanded this model to use age-classes for North-Eastern Arctic cod.

Production models are another type of model which do not require that the population is broken into age-classes. Under this model the manager sets a level of biomass which should be maintained and which, by setting the catch to be less than the growth and new recruits contribution to the population biomass, should either remain constant or increase. This is frequently used by tuna agencies and for finfish stocks. Sometimes this method can provide better estimates of management parameters than age structured models, as shown by Ludwig and Walters(cited in Hilborn and Walters (1992)). Furthermore for populations which are difficult to age, such as many tropical stocks (Jones 1984), these methods are the best available.

However, when fish reproduce over a long lifetime and change how well they spawn with age, a model which breaks the population into age-classes can often provide better advice. In the North Sea two such models, XSA and MSVPA are used.

### Age-Structure Models

The first age-structure model we shall discuss assesses a single species, and is often known by the name virtual population analysis (VPA), although there are many more models, similar in approach, such as ADAPT, CAGEAN and Stock Synthesis (Committee on Fish Stock Assessment Methods et al. 1998). The extended survival analysis model (XSA) is the version which is currently used in the North Sea. Each cohort or year class of fish, is treated separately under these models. The basic premise used is that

$$N_{t,a} = N_{t+1,a+1}e^{M} + C_{t,a}e^{\frac{M}{2}} \tag{2.1}$$

where $N_{t,a}$ is the number of fish of age $a$ in year $t$, $M$ is natural mortality and $C_{t,a}$ is the catch of age $a$ fish in the year $t$ (Hilborn and Walters 1992; Myers, Hutchings, and Barrowman 1997). Generally this method is used to estimate backwards in time, and thus, only estimates numbers for cohorts which are no longer in the population. Also, fish are only considered once they reach the age of entry into the fishery, avoiding tracking the population for ages where natural mortality is high. In order to estimate forwards, natural mortality rates are assumed to be constant and assumptions are made about the fishing mortality on the oldest age class (Hilborn and Walters 1992; Myers, Hutchings, and Barrowman 1997). One way to do this is to assume

$$F = Eq$$

where $F$ is fishing mortality, $E$ is effort and $q$ is catchability. Parameter estimates are made for $q$ from previous cohorts and then adjusted using data on cohorts which have not completed their life cycle. For the North Sea an XSA iteration begins with an initial guess at how many fish will survive past the oldest age group for which records are kept. A standard VPA is then used and catchability and an exponent linking numbers to the CPUE index of abundance estimated. A series of iterations is then repeated until convergence is obtained for the estimates of sizes of cohorts (for more information see Lassen and Medley (2001)).

Although VPA has many advantages, in that it can use full age data, it is not a perfect assessment model. For instance, collecting the age data required can be very expensive (Committee on Fish Stock Assessment Methods et al. 1998). The heavy dependence of this assessment method on catch data can cause problems when catchability of a stock or age class changes with declining stock numbers. This is a particular danger for clupeoid stocks, which have a tendency to increase their catchability when stock numbers are low (Hilborn and Walters 1992). Further difficulties become apparent if there is immigration into a population or two stocks are assessed as one. The VPA model could show a decrease in fishing mortality while one of the substocks was completely fished out (Daan 1991). Similarly misreported landings can have a serious effect on this method (as well as the methods previously mentioned) as this can lead to numbers or fishing mortality be estimated incorrectly (Patterson 1996). As a final note, it is important that aging is done accurately. If a certain percentage of fish are thought to be mis-aged every year, then if a weak cohort is preceded by a strong cohort, it is possible that numbers in the weak cohort are overestimated (Hilborn and Walters 1992).

A further extension to the VPA modelling idea has been implemented in the North Sea, that of Multi-Species Virtual Population Analysis (or MSVPA). Under this method, stock assessments for more than one population are made by separating mortality into three components: fishing mortality, mortality inflicted by other cohorts included in the analysis, and natural mortality not otherwise included. Although this method does give the possibility of looking at the interactions between stocks, for instance giving a possible answer to the question of whether one stock will increase if another is fished down, the quantity of data required for an assessment is overwhelming. For each age class of each species considered, stomach data must be found in order to estimate predation rates on the species and age classes in the model. Only the computer advances of the last few years have meant that such a model can be used. Daan's message that we 'don't really have the tools for multi-species analysis though single species analysis is inadequate' perhaps best summarizes the current situation (Hilborn and Walters 1992).

# Chapter 3

# Thesis Plan

The main aim of this thesis is to examine the impact fishing has on a population. As cod is fished heavily in the North Sea, fishing is one of the most important factors in the natural selection of cod. If it is possible to ensure that the yield obtained from the fishery is sustainable in the short term (or on the ecological time scale), it would be even more valuable to show that it is sustainable on the evolutionary time scale. Thus we wish to discover if the results of the high level of fishing now, will be a population in a hundred or two hundred years which is unfishable, due to the decreased size or fertility of the population, or if there will be relatively little effect. Although of interest from a modelling point of view, if the impact of fishing is not felt within at most 500 years, it may not be worth changing fishing practices, as environmental changes may swamp such an effect.

Knowing what pressures fishing can have on a population, can also help us to understand what may happen in such environmental changes. For example, if water temperature was to change such that fish grew more slowly and fishing favored fish which grew quickly, this would be an indication that the environmental change would have a serious effect on the fishery. If this was the case, it would be worth lowering the level of fishing in order to give the population some resiliency to environmental change.

If it is found through modelling that we can expect fishing to have a large impact on the population it should then be considered when fisheries assessments are performed and managing guidelines created. Rochet (1998) suggests that the maturity schedule incorporated into fisheries assessments should be updated on a regular basis, as fishing is likely to decrease size and age at maturity. Blythe and Stokes (1991) find that there has indeed been a pressure on North Sea cod to decrease size at maturity, further supporting Dr. Rochet's calls for diligence in assuring maturity ogives used are accurate. Their work demonstrates clearly that we cannot expect fish stocks to remain stationary, they will react to the pressures that we exert, and in assessing stock levels we should always remember this.

The model in this thesis is strongly based on the model of Blythe and Stokes (1991) and works to expand the complexity of their model. They assume that all fish become adults at the same time, age $\tau$, where as the model in this thesis assumes a gradual change in proportion mature over a span of six years. It shall be shown that a model allowing a gradual increase in proportion mature will also favor changes in the life history parameters which decrease the age at maturity. Another difference between the two models is that I have only modelled from age six months upwards as I wished to avoid trying to model the life stages where natural mortality is extremely high and changeable. The results found are quite similar to the result found in Stokes and Blythe (1991) where they discovered that harvest levels are now high enough to cause pressure for the weight at first maturity to decrease.

The impact of finding that fishing is having a serious effect on growth and maturity of cod could be important. If such effects are likely to become apparent in the short term, it is certainly of consideration whether fishing practices should be changed in order to lessen these effects. Assessing the importance of different elements of fishing mortality is crucial, we shall try to do this by looking at three different aspects of the fishing curve namely: the initial age of fishing, the peak age for fishing mortality, and the overall level of mortality. If it is possible to assess which of these factors is most important, it is possible to advise fishery managers on how pressure on the stocks should best be reduced.

Cod is currently caught in a mixed fishery with a species which is much smaller, Whiting (*Merluccius capensis* L.). Whiting are mature by age one and are about 23 centimeters at maturity, about a third of the size of a cod at their average age at maturity of four years (Alverson, Freeborg, Murawski, and Pope 1994). However the current mesh size catches fish at about size 30 centimeters, with the legal limit for cod being 35 centimeters, obviously these sizes being far too small as most cod are not yet mature at this age. Ideally cod would not be caught until an age where a significant percentage of the population had been given the opportunity to spawn at least once (Alverson et al. 1994), in order to ensure that there was a resistance to extinction built into the population. It has been shown that if a fished population has a sufficiently high maximum annual reproductive rate and a policy of fishing was followed such that all fish were allowed to spawn at least once, then fishing mortality could be increased to any level without causing the population to become extinct (Myers and Mertz 1998). If the initial size of capture is the most important determinant of the pressure on the stock, then obviously the mesh size with which fisheries are practiced should be increased so that only older cod are caught. This is a controversial issue however, with Norway already advocating such an increase, while countries such as Britain which catch large numbers of whiting resisting such an increase due to the decrease the whiting catch would experience (Oliver 2001).

If it is found that the peak age of capture should be changed, i.e. the shape of the fishing curve, then different measures are called for. This could be done by examining selectivity of gear and trying to change the amount of each type of gear used in the fishery, or by changing such things as mesh size in nets. Lowering the overall level of fishing would perhaps be the easiest change to make, as this could be changed by reducing quotas and effort in the North Sea, or using less efficient methods for catching fish.

As a result, I will look at not only which life history parameters are likely to change under current levels of fishing, but also which fishing parameters are most likely to relieve such pressure if altered. I shall start by creating a model for a single population and examining its stability properties, establishing whether the population is viable in the long-term, and the type of behavior exhibited. This model will then be expanded into a two population model in order to examine competition. A measure of fitness will then be found, enabling the two populations to be compared in their ability to cope with the environment. In chapter 7 I will look at a sensitivity analysis of the model which will help answer the two main questions posed in this thesis. Finally I shall examine the effect of two more additions to the model. First reproduction will be changed to a seasonable variable, to see if this will have a noticeable effect on the population. Secondly a very simple spatial model will be introduced to check if changes in results are likely to be obtained.

# Part II

# Single Population Models

# Chapter 4

# Construction of a Model

## 4.1 Creating a Single Population Model

### 4.1.1 Age Structured Model

In this chapter I shall build the model which will be the basis for all work in this thesis. The thesis characterizes a deterministic model for North sea cod and hence the lack of goodness of fit tests in this chapter does not detract from the usefulness of the model. Fertility and mortality have been modelled as depending on age (and for later chapters size), rather than using blanket values across the whole population. Growth and maturation are modelled as continuous processes rather than as step functions as in many fisheries models.

After some consideration a standard model was adopted, the McKendrick-von Foerster equation as described in Ecological Dynamics (Gurney and Nisbet 1998). The notation of Gurney and Nisbet will be used in the following discussion.

This model is built by assuming that $f(a,t)$ is a continuous age distribution of the number of age $a$ fish at time $t$ of the population, having the property that $f(a,t)da$ is the number of individuals at time $t$ that are in the age range $a$ to $a + da$. Notice that under conditions where there is no immigration or emigration the change in f(a, t) with respect to time, in other words $\partial f(a,t)/\partial t$, is given by

$$\frac{\partial f(a,t)}{\partial t} = -\frac{\partial f(a,t)}{\partial a} - \delta(a,t)f(a,t) \tag{4.1}$$

where $\partial f(a,t)/\partial a$ is the change in $f(a,t)$ with respect to age and $\delta(a,t)f(a,t)$ gives the mortality rate at time $t$. This model assumes that all cod which join the population at the same time grow in exactly the same manner. An unrealistic simplification, but one that was felt necessary to avoid complications which would make analytic work with the model impossible.

Clearly there must also be a mechanism for adding fish to the population and as the model is of a closed population, this mechanism is the birth rate. Fish will only be modelled from age six months, thus there is a six month delay term in reproduction. Fish younger than this live in a different ocean layer (Anonymous 1981), and thus experience a different environment making it sensible to separate out this group. Furthermore, mortality rates for very young fish and eggs are extremely high and changeable due to natural causes making them difficult to model as mentioned in chapter 1. As the production of fish obviously depends on the population numbers and fertility of the population this leads to

$$f(0.5,t) = R(t) = \int_{0.5}^{\infty} B(a,t-0.5)f(a,t-0.5)da \tag{4.2}$$

where $B(a,t-0.5)$ is the production of half year old fish.

A changing environment is not used for the first part of this thesis, thus mortality can be assumed to be independent of time. Hence the probability that a fish will survive to age $a$ ($S(a)$) is simply

$$S(a) = exp\left[\int_{0.5}^{a} -\delta(x)dx\right] \tag{4.3}$$

and $f(a,t)$ can be calculated for any age using $R(t)$ and $S(a)$ as

$$f(a,t) = S(a)R(t-a).$$

Notice that this now means using equation 4.2, the Lotka renewal equation (Gurney and Nisbet 1998)

$$f(0.5,t) = R(t) = \int_{0.5}^{\infty} B(a,t-0.5)S(a)R(t-a-0.5)da, \tag{4.4}$$

holds true.

Now that the model form has been established, the two key components, mortality and fertility, will be examined. The functions for both will be fitted in sections 4.2 and 4.3. The mortality function is divided into two parts, natural mortality and fishing mortality. Fishing mortality is defined as the mortality imposed by human fishing, while natural mortality includes all other mortality such as predation by birds, mammals and other fish, cannibalism, and death due to human causes other than fishing. All fish are assumed to die by age 50 in the case of a population with no fishing and age 25 in a fished population as survival rates are essentially zero for these ages (as will be seen in section 4.2).

The fertility function at age $a$ and time $t$ is

$$B(a,t) = \beta c(t) w(a) p(a) \tag{4.5}$$

where $\beta$ is the production parameter, $c(t)$ is the competition function, $w(a)$ is the weight at age, and $p(a)$ is the proportion mature. Notice that by using the proportion mature in the fertility function, the average fertility at age is used as mature and non mature fish are not separated into different groups. The competition function $c(t)$ gives a limit on how successful breeding is, and has the form $c(t) = exp(-A/K)$ where $A$ is the adult biomass and $K$ is a limiting factor. The form of the competition function ensures that at very high population levels fertility is low, possibly as there is higher mortality of very young fish due to crowding and increased predation. This competition function does not lower fertility at low population levels. Weight is included in the fertility function as the number of eggs produced by fish is a linear function of body weight (Oosthuizen and Daan 1974), hence fertility can be expected to rise with body weight.

### 4.1.2 Finding Equilibrium States

The equilibrium values of a population provide important information. For any real population there is always an equilibrium value of zero, such that if this equilibrium is obtained the population is then extinct. This equilibrium is often labelled the trivial equilibrium of the population, as it is obvious that if there are no fish in the population there can obviously be no fish in the future, unless they migrate into the area from another region. Furthermore, if the only nontrivial equilibrium values are negative, it is a clear indication that the population is not viable, and will in a matter of time become extinct. Hence, the next step is to find the general form of the equilibrium for the population, under the assumption that mortality and fertility are time independent.

If the population is assumed to be at equilibrium then

$$R^\star = \int_{0.5}^{\infty} B^\star(a) S^\star(a) R^\star da \tag{4.6}$$

and canceling $R^\star$ gives the renewal condition

$$1 = \int_{0.5}^{\infty} B^\star(a) S^\star(a) da. \tag{4.7}$$

The fertility $B$ from equation 4.5 is now substituted into equation 4.7 to give

$$1 = \int_{0.5}^{\infty} \beta p(a) w(a) c^\star S^\star(a) da \tag{4.8}$$

hence

$$\frac{1}{c^\star} = \int_{0.5}^{\infty} \beta p(a) w(a) S^\star(a) da. \tag{4.9}$$

Using the form of the competition function,

$$e^{(A^\star/K)} = \int_{0.5}^{\infty} \beta p(a) w(a) S^\star(a) da \tag{4.10}$$

then

$$A^\star = K \ln \left( \int_{0.5}^{\infty} \beta p(a) w(a) S^\star(a) da \right) \tag{4.11}$$

giving an easy way to calculate the equilibrium adult biomass. Using equation 4.6 it is seen that

$$R^\star = \beta c^\star \int_{0.5}^{\infty} p(a) w(a) S^\star(a) R^\star da. \tag{4.12}$$

But as adult biomass is simply

$$A^\star = \int_{0.5}^{\infty} p(a) w(a) S^\star(a) R^\star da \tag{4.13}$$

this gives

$$R^\star = \beta e^{-A^\star/K} A^\star. \tag{4.14}$$

## 4.2 Fitting Mortality Parameters

As mentioned in section 4.1 mortality has been divided into two different components. This is a natural thing to do in fisheries, mainly as one type of mortality is uncontrollable (natural mortality) while the second (fishing mortality) depends purely on the actions of fishermen, and is governed by the regulations and quotas set by fisheries scientists and governments. Discard mortality, which includes mortality caused by unwanted fish (due to age, size, species etc) being caught during the fishery and thrown back, has not been specifically included. Such mortality is difficult to estimate (Alverson, Freeborg, Murawski, and Pope 1994) and it is certainly possible that mortality rates are underestimated, especially for young fish.

### 4.2.1 Natural Mortality

The data for natural mortality comes from Cook (1998) and was given at age as in the following table 4.1. These are standard natural mortality estimates for the North Sea which can be found in many other papers.

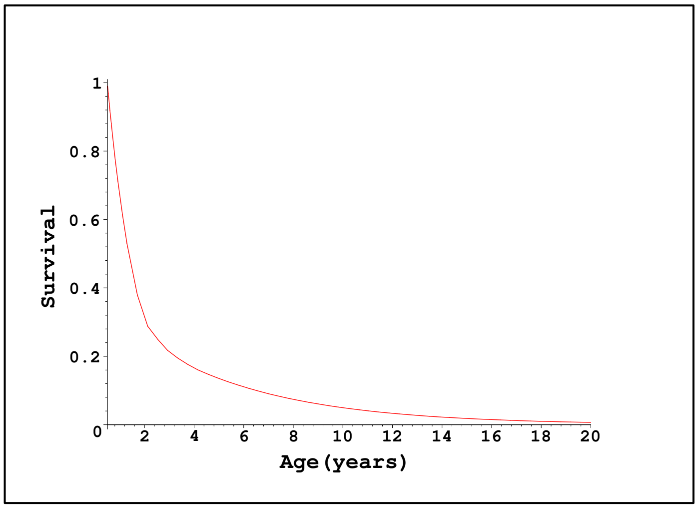
Table 4.1: Natural Mortality at Age

| Age | 0.5-2 | 2-3 | 3-4 | 4+ |
|---|---|---|---|---|
| Mortality | 0.8 | 0.35 | 0.25 | 0.2 |

The corresponding survival curve, when considering natural mortality alone (figure 4.1), shows that by age 20 very few fish will still be alive. This is what we would expect the survival curve for the North Sea to look like if the population were not fished.

The form of natural mortality has been changed in part 3 of the thesis when more than one population is under consideration. For a single population having natural mortality depend on age as opposed to size causes no problems as weight is a function of age. However, as soon as a second population is introduced there is a strong argument that natural mortality should no longer depend on age as

Figure 4.1: Natural Mortality Survival Curve: *Ages plotted from age 6 months. This shows that when a stock suffers from only natural mortality, there will be many fish of age 6 and over, which are mature and capable of producing vast numbers of eggs.*

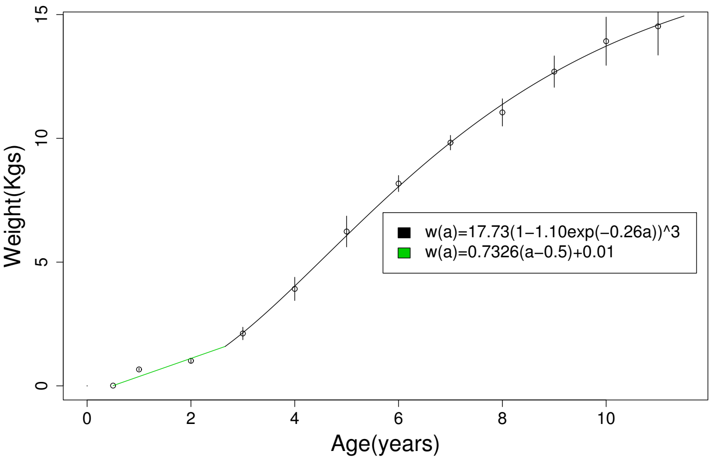


it is unlikely that time alive is the main determination of mortality. Instead natural mortality will then depend on weight, as the size of a fish determines whether it is an attractive food source for another creature and if it is catchable by another species. The function will be transferred from a function of age to a function of weight at age using the weight function in the next section. This is done as in part 3 of this thesis, the population parameters established in this chapter will be those of the resident population in the North Sea. Hence, as a next step, the function for weight at age will be examined.

### 4.2.2 Weight

The data used to fit weight at age was taken from the paper by Cook (1998) previously mentioned, where weight was given as the average over ten years from 1986 to 1995. An additional forced data point of ten grams is used as the weight at age half a year to ensure a sensible starting weight. The fitting of the data was done using a Pascal program using the down-hill simplex method, more details on this method can be found in Appendix A. After some exploration of the fitting it was decided that the data should be divided in two, as a better fit was acquired by fitting with separate growth curves for young and old fish. There are two disadvantages to this decision. First, that it complicates the model by requiring two growth curves, which although continuous are not continuously differentiable. This gives an intersection point which must always be considered. This being admitted, there is some justification for having different growth curves for young fish (where the population is dominated by immature fish) and older fish where most fish are mature. This is due to different growth priorities in the two groups: for older fish the key aim is to reproduce while for younger fish it is to grow enough to survive to the age to reproduce. In an individual based model it would be sensible to have separate growth curves before and after maturation. This model, however, is population based and does

Figure 4.2: Weight at Age: *Young cod are modelled with linear growth while older cod are modelled using von Bertalanffy weight growth*



not keep mature and immature fish separate, hence the border between the two types of growth is due to fitting, rather than biology.

For young growth three types of growth were considered: linear, power, and exponential growth. The last two were suggested as growth curves in Peters (1983), however the latter provided a very bad fit and was not used. Although linear growth is less realistic than power growth, it shall be used in the main model as it is the simpler of the two and allows more model manipulations. The power growth curve will be used as a test of model assumptions and will be mentioned again shortly. For older growth three different types of growth from Peters (1983) were considered: von Bertalanffy, Gompertz and Logistic. All three gave similarly good fits as expected (Ricklefs 1967), however the von Bertalanffy fit had the smallest sum of squares. The other two shall once again be used as tests of robustness of the assumptions.

A Pascal program was then written which fitted intersecting linear and von Bertalanffy growth curves. The linear growth curve $w(a) = g_1 * (a - 0.5) + 0.01$ had best fit $g_1 = 0.7326$, while the von Bertalanffy curve $w(a) = w_\infty(1 - be^{-g_2 a})^3$, had best fit $w_\infty = 17.7252$, $g_2 = 0.2603$, and $b = 1.1034$. The intersection point of the two curves is at age 2.66 years. Figure 4.2 shows the fits for old and young fish on the same graph. Note that in this model the maximum weight for a cod will be 17.7 kg, $g_2$ is the exponential rate of growth for old fish, while a function of $b$ gives the minimum age the growth curve could be applied to (Peters 1983).

The power growth curve, used to test the importance of assuming linear growth, was fitted using the von Bertalanffy curve which had already been fitted for older growth. Hence, as it is used for only three date points, the first of which is forced, and has only two parameters, it is a simple matter of solving a system of two equations for two unknowns. Thus the power curve is $w(a) = g_{1_p} * (a - 0.5)^{g_{1_{p2}}} + 0.01$ with $g_{1_p} = 0.8565565323$ and $g_{1_{p2}} = 0.3892578309$. A comparison of the linear and power fit is given in figure 4.3.

The two alternate growth curves for older fish have been fitted using the same linear fit for the young fish as given above. The Gompertz function is $w(a) = w_{0_G} \exp(G^{(1-e^{-g_G a})})$ with best fit (using the Downhill simplex method) to 3 digits of $w_{0_G} = 0.0927$, $G = 5.14$ and $g_G = 0.407$ and intersection point 1.82. Here once again $g_G$ is the exponential rate of constant growth, while $w_0$ is the minimum size the curve could be applied to and $w_{0_G} \exp G = 15.8$ is the maximum size in kilograms(Peters 1983), and is somewhat less than in the von Bertalanffy fit.

The Logistic fit has the form $w(a) = w_{\infty_L} w_{0_L} e^{g_L a}/(w_{\infty_L} - w_{0_L} + w_{0_L} e^{g_L a})$ with best fit $w_{\infty_L} = 14.5$, $w_{0_L} = 0.311$ and $g_L = 0.667$ and intersection point 2.12. Once again $g$ is the exponential rate of constant of growth and $w_{0_L}$ and $W_{\infty_L}$ are respectively the minimum and maximum sizes for the cod (Peters 1983), notice that the maximum size is once again smaller than in the von Bertalanffy fit. In figure 4.4 the three functions for older fish are plotted together to show the differences in weight at age. This graph shows that the von Bertalanffy fit and Gompertz fit are very similar, and one would expect that results using these growth models would also be similar. The Logistic fit on the other hand, gives a higher weight between ages six and nine and a lower weight outside of this region.

Now that the weight at age of the population has been established, the natural mortality is transformed to depending on weight rather than age. In figure 4.5 the graph of natural mortality at weight is given.

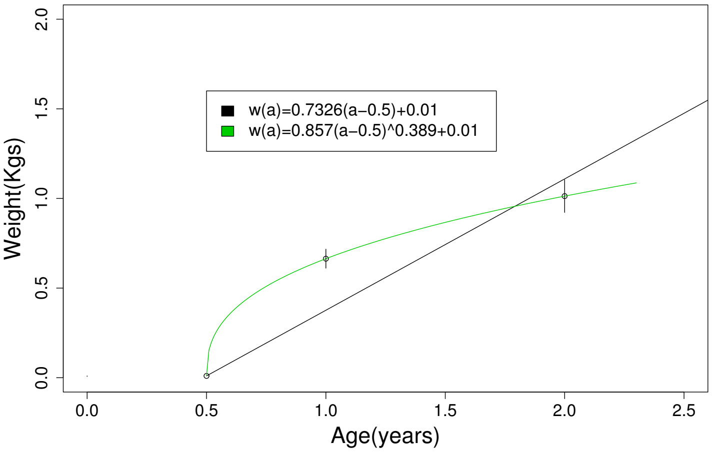


Figure 4.3: Comparison of Linear and Power Growth for Young Cod: *The power fit (green) is a perfect fit. Fish of age less than two have a much higher weight under the power growth curve, and a much smaller weight for fish aged more than two.*

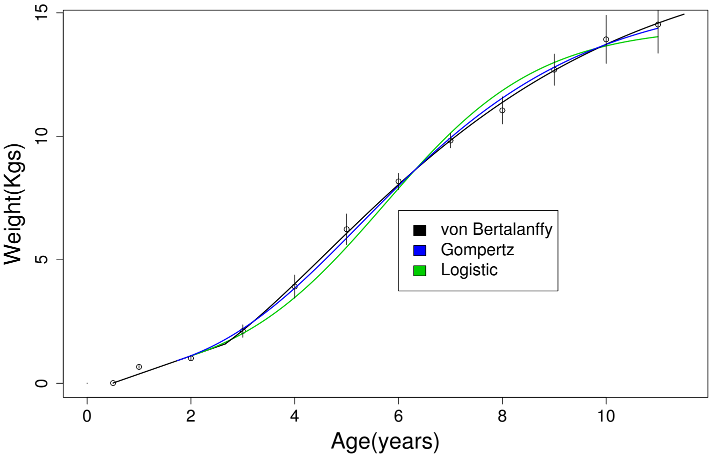


Figure 4.4: Weight at Age under Different Models: *Three different weight models are shown for older cod. The green logistic growth curve is noticeably different from the Gompertz and von Bertalanffy growth curves.*

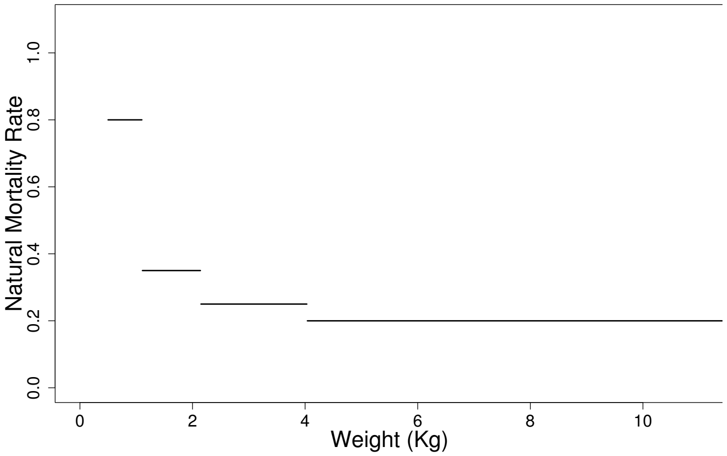


Figure 4.5: Natural Mortality at Weight: *Natural mortality is measured as a step function with fish over the weight of 4 kilograms being large enough that they suffer little natural mortality, mainly due to their lack of predators.*

### 4.2.3 Fishing Mortality

Fishing mortality will also depend on weight, but this data has been extracted through length, as this is a standard way in which fishing mortality is presented. Rather than fitting length as a separate aspect of growth, a weight-length transformation has been used which was found on Fishbase (http://www.fishbase.org) from Dorel (1985) and Daan (1974) which gives $w = l_a L^3$ where $l_a = 0.0104$ and $L$ is length. As the model uses the von Bertalanffy growth curve the cubed relationship is already implicitly assumed, due to the derivation of the von Bertalanffy weight curve. Using this and the weight functions, the equations for length at age are $l = 119.6625(1 - 1.1034e^{-0.2603a})$ and $l \approx (70442a - 34259)^{1/3}$. This gives the maximum length of a fish to be just less than 120 cm.

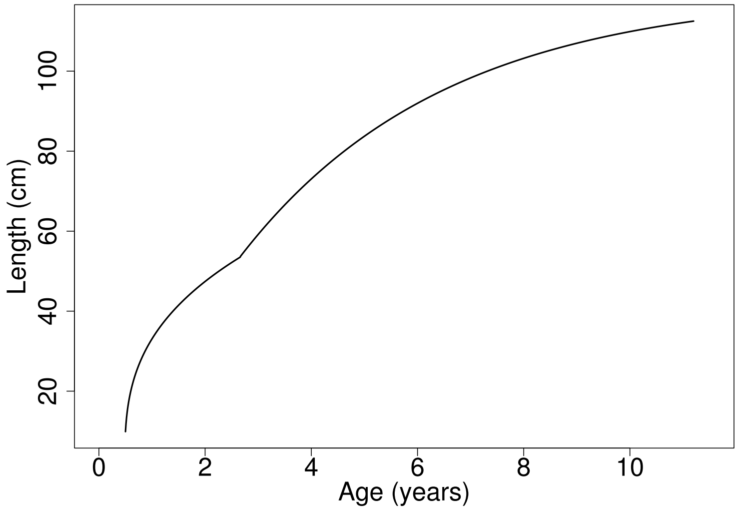


Figure 4.6: Length at Age: *The length is plotted using the weight length conversion* $w = 0.0104L^3$. *The anomalous cusp is due to the change in weight growth.*

The graph of length at age is shown in figure 4.6 giving an initial length of 9.87 cm. It should be mentioned that the weight conversion is given in Daan (1974) as being valid for fish of length 22 cm and larger. It is however only of concern when fishing mortality is in effect. As fishing mortality will be modelled as starting at

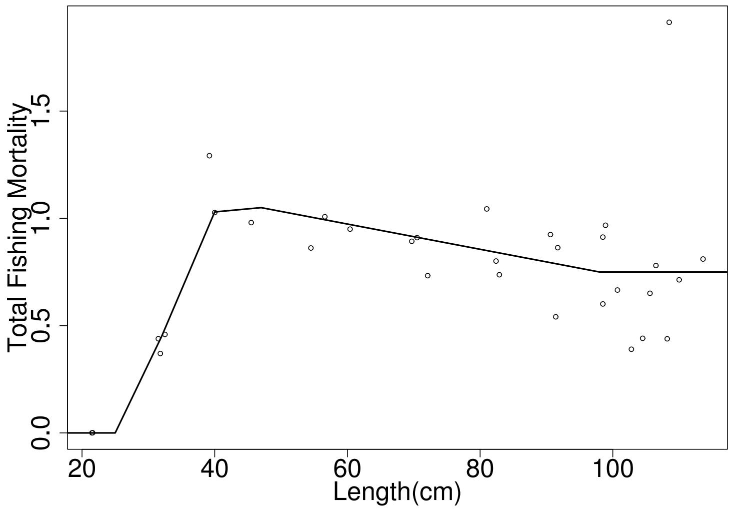


Figure 4.7: Fishing Mortality at Length: *The points on the graph and rough curve shape are taken from Cook and Reeves (1996).*

Table 4.2: Defining Points for Fishing Mortality

| Length | 0 | 25 | 32 | 40 | 47 | 98 |
|---|---|---|---|---|---|---|
| Total Fishing Mortality | 0 | 0 | 0.45 | 1.03 | 1.05 | 0.75 |

25 cm, I will not worry about finding an alternate length transformation for the younger fish. It should be mentioned that it is likely that I am underestimating length at a young age given the estimates in (Daan 1974) for fish from length 5cm to 22cm. The anomalous cusp in figure 4.6 is an artifact from having two growth curves for young and old fish. This cusp however is not close to a point where the mortality changes and there is no obvious carry over effect.

The curve used for fishing mortality in this thesis is a very rough curve taken from Cook and Reeves (1996). It is based on data for fishing mortality for all gears and cod mean lengths from 21.5 cm to 113.6 cm for the years 1990-1992 for the Scottish Demersal trawl fishery. The graph from Cook and Reeves (1996) is reproduced in figure 4.7, with the curve being the fishing mortality used in this thesis, rather than the curve given in their paper (which is very similar).

The fishing mortality at length is estimated as straight lines joining the points given in Table 4.2 where the points were roughly estimated from the graph in the report. The fishing mortality is converted to fishing mortality at weight using the weight conversion given above, with the results being presented in table 4.3.

Table 4.3: Fishing Mortality at Weight

| Lower Limit (Kg) | Upper Limit (Kg) | Fishing Mortality |
|---|---|---|
| 0 | 0.1625 | 0 |
| 0.1625 | 0.3407872 | $0.0642857((\frac{1000w}{0.0104})^{1/3} - 25)$ |
| 0.3407872 | 0.6656 | $0.0725((\frac{1000w}{0.0104})^{1/3} - 32) + 0.45$ |
| 0.6656 | 1.453522 | $\frac{2}{700}((\frac{1000w}{0.0104})^{1/3} - 40) + 1.03$ |
| 1.453522 | 9.7883968 | $-\frac{3}{510}((\frac{1000w}{0.0104})^{1/3} - 47) + 1.05$ |
| 9.7883968 | - | 0.75 |

Now that fishing mortality has been set for the population, a survival curve for the fished population can be found (figure 4.8). Notice that in comparison to the non-fished population (figure 4.1), fish die much earlier and most are dead by age 6. Thus in a fished population many fish die before they have the chance to reproduce, creating a strong natural selection force on the population.

## 4.3 Fitting Parameters for Fertility

As stated in subsection 4.1 fertility is modelled using equation 4.5

$$B(a,t) = \beta c(t)w(a)p(a).$$

The weight function has been fit in the previous section and I will now set functions for proportion mature, the production parameter $\beta$, and $K$ the competition parameter.

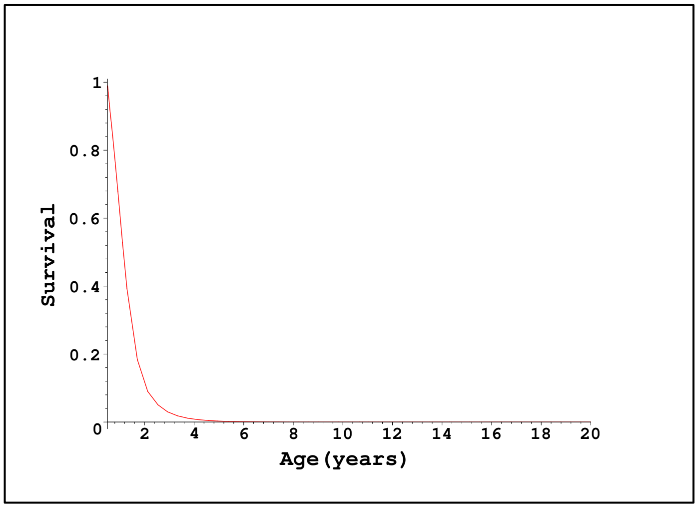


Figure 4.8: Survival Under Natural and Fishing Mortality: *We see that fishing mortality causes a much shorter expected life span than Natural mortality alone (see figure 4.1).*

### 4.3.1 Proportion Mature

The proportion mature was also fitted using data from Cook (1998) using the downhill simplex method (Appendix A). The cumulative Weibull distribution $p(a) = 1 - \exp(-p_x a^{p_y})$ gave a good fit with the parameters $p_x = 0.003581546$ and $p_y = 3.98385$. The fit is shown in figure 4.9. Increasing the $p_x$ or $p_y$ parameter will decrease the length of time till all fish are mature, although for fish under age 1 decreasing $p_y$ will increase the proportion mature at age.

In order to consider the effect of choosing the Weibull distribution to model proportion mature, four other functions were fitted, each having their own strengths and weaknesses. A graph of these functions can be seen in figure 4.10. Originally these functions were used to help predict behaviour in the main model which was difficult to analyse, and hence were chosen to be simple functions which allowed numerical analysis to be performed easily.

The first of these alternate functions assumes all fish mature at the same age. The age was chosen to be $p_{x_1} = 3.75$ as this is the age where 50 percent of fish are mature under the Weibull distribution. Hence for this model

$$\begin{aligned} p(a) &= 0, a \leq p_{x_1} && (4.15) \\ &= 1, a \geq p_{x_1} && (4.16) \end{aligned}$$

This model has the advantage of simplicity, allowing for more manipulations to be carried out analytically. As this assumption is one used frequently by fishery scientists, it also permits us to examine the effect of a common assumption.

The second function is the cumulative of the exponential distribution where $p(a) = 1 - e^{-p_{x_2}a}$. This function does not fit the data particularly well, but was used as it is a fairly simple model. It is also related to the Weibull distribution in that it is the same distribution only with the parameter $p_y$ set to be 1. The best fit value for $p_x$ was found to be 0.252926. From figure 4.10 it is noticeable that many more young fish are mature than under the Weibull distribution, hence we expect results under the two models to differ substantially.

The third and fourth functions used are both cumulative distributions of the gamma distribution

$$\frac{1}{\Gamma(\alpha)p_{x3}^{\alpha}} y^{\alpha-1} e^{-y/p_{x3}}$$

with $\alpha = 3$ and $y = a + p_{x_3}$ and in the second case $\alpha = 4$. When the cumulative distribution is written for $\alpha = 3$ we have

$$\frac{1}{2p_{x3}^{3}}(-p_{x_3}e^{-\frac{a-p_{y3}}{p_{x3}}}(a-p_{y_3})^2 - 2p_{x3}^{2}e^{-\frac{a-p_{y3}}{p_{x3}}}(a-p_{y_3}) - 2p_{x3}^{3}e^{-\frac{a-p_{y3}}{p_{x3}}} + 2p_{x3}^{3}).$$

with best fit $p_{x_3} = 0.6070$ and $p_{y_3} = 2.017$ to four significant figures. Hence under this maturation scheme no fish matures prior to age 2.017 and thus the function underestimates the proportion mature for young fish. When the cumulative distribution is written for $\alpha = 4$ we have

$$-1/6\frac{a^3e^{-\frac{a}{p_{x4}}} + 3a^2p_{x_4}e^{-\frac{a}{p_{x4}}} + 6ap_{x_4}^2e^{-\frac{a}{p_{x4}}} + 6p_{x_4}^3e^{-\frac{a}{p_{x4}}} - 6p_{x_4}^3}{p_{x_4}^3}$$

where the best fit was found to be $p_{x_4} = 0.9497$. Under this model the proportion mature at young age are slightly overestimated.

### 4.3.2 $\beta$

The $\beta$ parameter is a production parameter which is the number of offspring produced per kg of body weight under ideal conditions. An estimate is made using data from Myers, Bridson, and Barrowman (1995), using the survival curve for a fished population from the section 4.2.3.

Dr. R. Myers' data base stores data on number of recruits per kilogram of spawner for many world stocks, including North Sea Cod. For the North Sea stock it uses an age of recruitment of 1 year and gives the corresponding number of recruits to be 9.82 per kilogram of spawner. Calculating backwards using the survival function in the previous section 4.2.3, a value for $\beta$ of 15.9 was obtained. This has been used as a baseline value throughout the thesis.

### 4.3.3 $K$

The competition function $c(t)$ is $e^{-A/K}$ where $A$ is the adult biomass. The value for $K$ is somewhat arbitrary, and will determine the level of the population. When stability is looked at in the next chapter it will be seen that this parameter has no effect on whether the equilibrium for the population is stable or not. However in order to generate a reasonably realistic population level, having adult biomass from 80 to 300 thousand tonnes (Serchuk, Kirkegaard, and Daan 1996), I used a value of $K = 10^9$ which in the fished model gives an equilibrium adult biomass of approximately 155 thousand tonnes. This value is slightly above the reference point $B_{pa}$ =150 thousand tonnes mentioned in section 1.4, and puts the population in a region where it would be much healthier than the current stock.

Next a short word on the assumptions made about competition. It is sensible to assume that competition should increase as population increases, i.e. that for large populations it is difficult to reproduce numerously. Large numbers of fish can cause food shortages and attract predators. Although there is not an increase in competition for small population size there is the argument that for very low numbers finding mates may be a problem and hence reproduction will not be as successful as for larger groups. To have competition depend on adult biomass is also fairly sensible, although it may well depend on a history of adult biomass rather than just a single value. I use biomass rather than just numbers, as larger fish use more resources and are capable of eating more small fish.

## 4.4 Models

Having introduced how different components of life history will be modelled, the models used through the thesis can now be introduced. The main model includes fishing and will be known as the fished model. The growth of older fish takes the von Bertalanffy form while young fish grow linearly and fish mature following the Weibull distribution.

As a comparison we shall also look at a model which is identical to that above, only fishing has not been included as a source of mortality. Thus fish only die due to natural mortality. This model shall be referred to as the unfished model.

There are also two sets of alternate models. The first set change how the proportion mature is measured, but keep fishing mortality and growth the same as in the fished model. These alternate models use respectively concurrent maturation, an exponential distribution, a gamma(3) distribution, and a gamma(4) distribution to model proportion mature.

The final set of models is the group which models growth in alternate ways. The first of these, the power model, uses a power growth curve for young fish and a von Bertalanffy curve for older fish. The the Gompertz model has linear growth for young fish and a Gompertz growth curve for older fish. Finally Logistic model has linear growth for young fish with a logistic growth curve for the older fish.

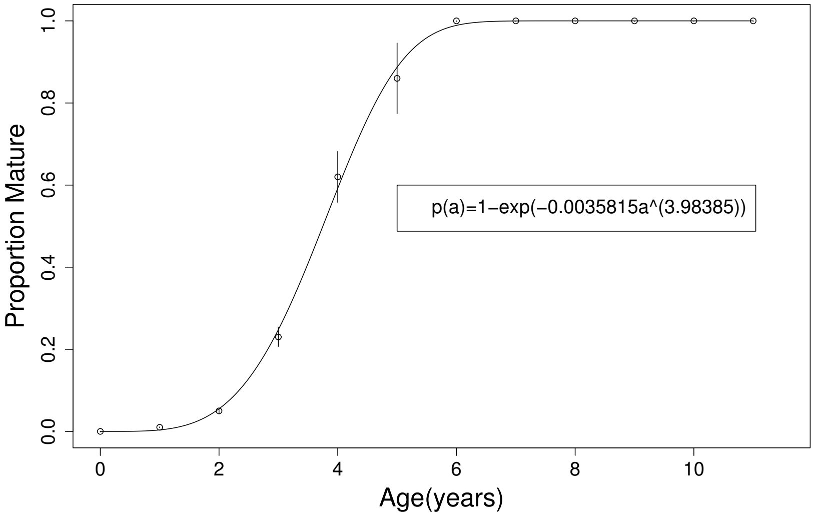


Figure 4.9: Proportion Mature at Age : *The Weibull distribution gives a good fit to the data*

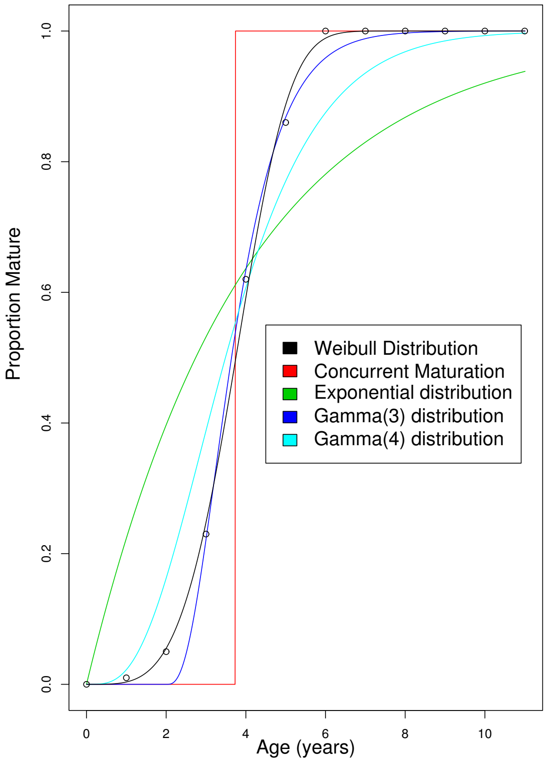


Figure 4.10: Approximations for Proportion Mature

# Chapter 5

# Behaviour of the Population

In the previous chapter I established the models which shall be used throughout this thesis. The next step is to look at their behaviour. A method for finding the equilibrium of a population under any set of parameters has been found, the next question to ask is, how does the model behave under different parameter values. By examining the type of equilibrium found for a particular parameter set, the type of behaviour expected can be determined. For example, a negative result for equilibrium adult biomass must correspond to ultimate extinction. If the equilibrium is found to be an attractor (i.e. if the population is close to the equilibrium it tends to get closer) then we will find that either the population settles to the equilibrium value in a steady manner, or else that it will oscillate around the equilibrium value, with smaller and smaller oscillations until it settles to the equilibrium. If the equilibrium value is unstable, the population will not settle to equilibrium and will follow one of two patterns. Either the population gradually decreases until it becomes extinct or oscillates continually around the equilibrium possibly taking on a chaotic behaviour. All these types of behaviour can have an impact on how the population reacts to patterns of fishing. Thus this chapter will concentrate on observing how the population behaves for different parameter values, particularly the fertility parameter ($\beta$).

## 5.1 Stability of the Model

### 5.1.1 Finding Stability Equations

The stability of the model can be found by linearizing around the equilibrium. This will allow us to examine what happens if the population deviates from the equilibrium by a small amount. As we are looking at small quantities, the linear approximation of the model will give a true picture of the dynamic behaviour. Thus the simpler linear equations for the population, will allow us to determine broad patterns of behaviour, and indicate if we should expect quick returns to equilibrium, oscillations, or limit cycles where the population cycles in a set way permanently. Simulations will then show us the exact behaviour (i.e. limit cycles, chaos etc) as perturbations of the equilibrium are allowed to become large.

The stability question is examined from the perspective of number of 6 month fish entering the population. Let

$$R(t) = R^\star + r(t)$$

where $R^\star$ is the equilibrium level of fish at age 6 months and $r(t)$ is assumed to be small with respect to $R^\star$. I then let $u(a) = p(a)w(a)S(a)$ to simplify notation. From equation 4.14 we obtain

$$R(t) = \beta e^{-A/K} A = \beta e^{\left(-\frac{1}{K}\int_{0.5}^{50} u(a)R(t-a)da\right)} \int_{0.5}^{50} u(a)R(t-a)da$$

thus

$$\begin{aligned} R^\star + r(t) &= \beta e^{\left(-\frac{1}{K}\int_{0.5}^{50} u(a)[R^\star + r(t-a)]da\right)} \int_{0.5}^{50} u(a)\left[R^\star + r(t-a)\right]da \\ &= \beta e^{\left(-\frac{R^\star}{K}\int_{0.5}^{50} u(a)da\right)} e^{\left(-\frac{1}{K}\int_{0.5}^{50} u(a)r(t-a)da\right)} \times \\ &\quad \left[R^\star \int_{0.5}^{50} u(a)da + \int_{0.5}^{50} u(a)r(t-a)da\right] \end{aligned}$$

As $r(t-a)$ is very small the exponential expression can be replaced with the first two terms of the Taylor approximation, namely

$$1 - \frac{1}{K}\int_{0.5}^{50} u(a)r(t-a).$$

Thus,

$$\begin{aligned} R^\star + r(t) &= \beta e^{\left(-R^\star \frac{\int_{0.5}^{50} u(a)da}{K}\right)} \left[1 - \frac{1}{K}\int_{0.5}^{50} u(a)r(t-a)\right] \\ &\quad \times \left[R^\star \int_0^{50} u(a)da + \int_{0.5}^{50} u(a)r(t-a)da\right] \\ &= R^\star - \frac{\beta}{K} e^{\left(-\frac{R^\star}{K}\int_{0.5}^{50} u(a)da\right)} R^\star \int_{0.5}^{50} u(a)da \int_{0.5}^{50} u(a)r(t-a)da \\ &\quad + \beta e^{\left(-\frac{R^\star}{K}\int_{0.5}^{50} u(a)da\right)} \int_{0.5}^{50} u(a)r(t-a)da \end{aligned}$$

getting rid of second order $r(t-a)$ terms. Cancelling $R^\star$ from both sides we obtain

$$r(t) = \beta e^{\left(-\frac{R^\star}{K}\int_{0.5}^{50} u(a)da\right)} \left[-\frac{R^\star}{K}\int_{0.5}^{50} u(a)da + 1\right] \int_{0.5}^{50} u(a)r(t-a)da \tag{5.1}$$

which is linear in $r(t)$. We define

$$Z = \beta e^{-\frac{R^\star}{K}\int_{0.5}^{50} u(a)da} \left[-\frac{R^\star}{K}\int_{0.5}^{50} u(a)da + 1\right]. \tag{5.2}$$

Using the definition of the competition function and equation 4.13

$$Z = \beta c^\star \left[1 - \frac{A^\star}{K}\right]. \tag{5.3}$$

When the competition and adult biomass are then substituted using equations 4.9 and 4.11

$$Z = \frac{1}{\int_{0.5}^{50} u(a)da}\left(1 - \log\left(\beta \int_{0.5}^{50} u(a)da\right)\right). \tag{5.4}$$

Setting $r(t) = r_0 e^{\lambda t}$, we obtain from equation 5.1

$$r_0 e^{\lambda t} = Z \int_{0.5}^{50} u(a) r_0 e^{\lambda t - \lambda a} da \tag{5.5}$$

$$1 = Z \int_{0.5}^{50} u(a) e^{-\lambda a} da. \tag{5.6}$$

Solving this equation will determine the stability of the system. If $\lambda$ is positive and real then the equilibrium diverges exponentially. If $\lambda$ is negative and real then the equilibrium converges exponentially. If the root is complex, then the sign of the real part will signal if we have divergence or convergence, and in the case of convergence the population will oscillate towards the equilibrium (Gurney and Nisbet 1998).

### 5.1.2 The Boundaries of Stability Behaviour

Note that for both models, $\int_{0.5}^{50} u(a)$ and $Z$ can be calculated given a value for $\beta$, the fertility parameter. Hence we can ascertain which type of behaviour will arise as $\beta$ varies.

We begin by examining the region where $\lambda$ in equation 5.6 is real. Note that if $\lambda$ is real then $\int_{0.5}^{50} u(a)e^{-\lambda a}da$ will be non-negative as $u(a)$ is non-negative. Hence if

$$Z > \frac{1}{\int_{0.5}^{50} u(a)da} \tag{5.7}$$

then $\lambda > 0$ otherwise

$$1 < Z \int_{0.5}^{50} u(a)e^{-\lambda a}da.$$

But this in turn allows us to find the region with respect to $\beta$ as from equations 5.4 and 5.7

$$\beta = \frac{1}{\exp(Z \int u(a)da - 1) \int u(a)da}. \tag{5.8}$$

Thus from 5.7

$$\beta < \frac{1}{\int_{0.5}^{50} u(a)da}. \tag{5.9}$$

However using the equation for equilibrium adult biomass

$$A^* = K\left(\ln\left(\beta \int_{0.5}^{50} u(a)\right)\right) \tag{5.10}$$

then upon substitution of 5.9

$$A < 0$$

as the logarithm in 5.10 is less than 1. But if adult biomass has an equilibrium value which is negative and hence impossible in the real world, then the only option is that the population will tend to the trivial equilibrium, the zero state. Hence in the region where

$$\beta < \frac{1}{\int_{0.5}^{50} u(a)da} \tag{5.11}$$

the population is not viable.

Now note that if

$$0 < Z < \frac{1}{\int_{0.5}^{50} u(a)da}$$

$\lambda$ is still a real root, however, it must now be negative in order for

$$1 = Z \int_{0.5}^{50} u(a) e^{-\lambda a} da.$$

The point where $Z$ is zero corresponds to

$$\begin{aligned} 0 &= \frac{1}{\int_{0.5}^{50} u(a)da} \left(1 - \log\left(\beta \int_{0.5}^{50} u(a)da\right)\right) && (5.12) \\ 1 &= \log\left(\beta \int_{0.5}^{50} u(a)da\right) && (5.13) \\ \beta &= \frac{e}{\int_{0.5}^{50} u(a)da}. && (5.14) \end{aligned}$$

Thus for

$$\frac{1}{\int_{0.5}^{50} u(a)da} < \beta < \frac{e}{\int_{0}^{50} u(a)da} \qquad (5.15)$$

there is a negative real root.

The region where

$$\beta > \frac{e}{\int_{0}^{50} u(a)da}$$

is a region where stability is governed by a complex root and simulations have shown oscillatory behaviour in this region. For values of $\beta$ just above this boundary value there is a negative complex root as populations settle to an equilibrium value. However, solving for the boundary between a negative complex and positive complex root unfortunately is not quite as easy. An attempt was made in Maple (Waterloo Maple Inc ) to solve the problem numerically, however the form of the function for proportion mature makes this too difficult to solve. Even when simpler proportion mature models (such as the concurrent maturation model) were used there were difficulties in solving this problem. Often the solutions found were due to numerical error and missed the true solution. Hence a new method of solving this problem had to be found and this is shown in the next section.

## 5.2 Finding Stability in Complicated Models

### 5.2.1 Fourier Transforms

A new method was used to solve

$$1 \;=\; Z\int_0^{50} u(a)e^{-\lambda a}da \tag{5.16}$$

for the boundary between oscillatory convergence and divergence. I begin by letting $u(a) = 0$ when $a < 0$, as fish cannot have negative age. When $a > 50$ (or 25 in the fished model) all fish are assumed to be dead (i.e. S(a)=0), as the survival curves indicate it is unlikely that any fish are alive past this age(figures 4.1 and 4.8). The limits of integration can then be changed so that

$$1 \;=\; Z\int_{-\infty}^{\infty} u(a)e^{-\lambda a}da. \tag{5.17}$$

Furthermore, the boundary between a complex root with negative real part and a complex root with positive real part, will be the first complex root which is entirely imaginary. Hence we are solving the equation where $\lambda$ is replaced with $I\omega$ where $\omega$ is real:

$$\frac{1}{Z} \;=\; \int_{-\infty}^{\infty} u(a)e^{-I\omega a}da. \tag{5.18}$$

The right hand side is now the Fourier transform of $u(a)$ so the problem can be rewritten as

$$\frac{1}{Z} = \;=\; \Re(U(w)) \tag{5.19}$$

$$0 \;=\; \Im(U(w)) \tag{5.20}$$

where $U(\omega)$ is the Fourier transform of $u(a)$. This set of equations can be solved first by finding the smallest positive value of $\omega$ which satisfies the imaginary equation 5.20. By substituting this into the real equation 5.19 the value of $Z$ can be found. To find the corresponding value of $\beta$ the value of $Z$ can be simply transformed as earlier using equation 5.4.

This method, however, will only work if an analytically tractable transform exists. Maple was unable to calculate such a transform for any of the models, thus an alternate method was chosen. I now show how to deal with this problem through Discrete Fourier transforms implemented through Fast Fourier Transforms (FFT's).

### 5.2.2 Fast Fourier Transforms

In order to examine the relationship between the FFT and Fourier transform we will follow the explanation in James (1995). We begin with the discrete Fourier transform pair of the sets of numbers $[x_n]$ and $[X_m]$ each with $N$ elements,

$$\begin{aligned} X(m) &= \sum_{0}^{N-1} x(n)e^{-2\pi inm/N} && (5.21) \\ x(n) &= \frac{1}{N}\sum_{0}^{N-1} X(m)e^{2\pi inm/N}. && (5.22) \end{aligned}$$

Note that the exponent term has changed from the Fourier transform given earlier in equation 5.18. The $2\pi$ term is included for the discrete transform and not the continuous form in order to match the form for the two transforms in Maple (Waterloo Maple Inc ).

I will now show the link between the continuous and discrete transforms.The Dirac function, $\delta(x-a)$, is 0 unless $x=a$. The Dirac Comb $III_a(x)$ is defined as an infinite set of equally spaced (with spacing of $a$) Dirac functions such that

$$III_a(x) = \sum_{n=-\infty}^{\infty} \delta(x-na).$$

The Fourier transform of this function is another Dirac comb namely $III_{\frac{1}{a}}(\omega)/a$[1].

The Fourier transform of $f(t)III_a(t)$ is

$$\int_{-\infty}^{\infty} f(t)III_a(t)e^{-it\omega}dt = \frac{1}{a}F(\omega) * III_{1/a}(\omega) \qquad (5.23)$$

where $*$ is the convolution of the two functions.

It is now assumed that f(t) is 0 outside the limits $(0, N)$, that there are $N$ teeth in the Dirac Comb and that f(t) extends over a range $\leq Na$. The notation is then changed so that the form of the exponential term in the integral is correct:

$$\int_{-\infty}^{\infty} f(t)III_a(t)e^{-it\omega}dt = \int_{-\infty}^{\infty} f(t)III_a(t)e^{-2\pi it\omega_1}dt \qquad (5.24)$$

---

[1] For more information on Fourier transforms see James (1995), Bracewell (1978), and Appendix F in Nisbet and Gurney (1982).

where

$$\omega_1 = \frac{\omega}{2\pi}.$$

Then using the properties of the Dirac function

$$\begin{aligned}\int_{-\infty}^{\infty} f(t) III_a(t) e^{-2\pi i t\omega_1} dt &= \int_{-\infty}^{\infty} \sum_{n=-\infty}^{\infty} f(t) e^{-2\pi i t\omega_1} \delta(t - na) dx &(5.25)\\ &= \sum_{n=-\infty}^{\infty} \int_{-\infty}^{\infty} f(t) e^{-2\pi i t\omega_1} \delta(t - na) dx. &(5.26)\end{aligned}$$

Due to the assumption that there are only N teeth in the comb we can write

$$\int_{-\infty}^{\infty} f(t) III_a(t) e^{-2\pi i t\omega_1} dt = \sum_{n=0}^{N-1} f(na) e^{-2\pi i\omega_1 na}, \qquad (5.27)$$

thus from 5.23

$$\sum_{n=0}^{N-1} f(na) e^{-2\pi i\omega_1 na} = \frac{1}{a}\left(F(\omega) * III_{\frac{1}{a}}(\omega)\right). \qquad (5.28)$$

Hence given the discrete Fourier transform of a function which suits the necessary requirements, the Fourier transform can be estimated for a point $\omega = 2n\pi/(Na)$ by multiplying the value for the $n^{th}$ point by $a$.

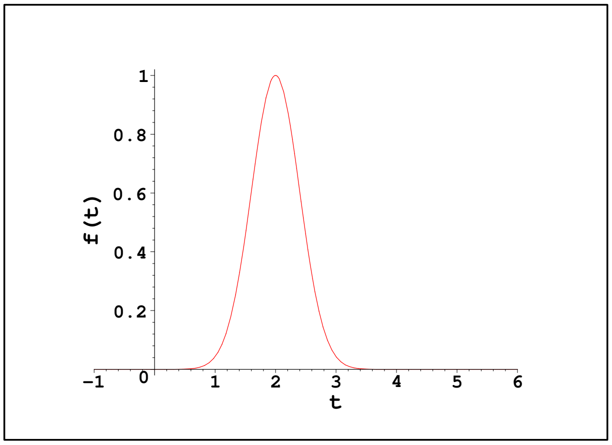
An FFT is a very efficient way of estimating a discrete Fourier transform using a number of points equal to a power of two. An explanation of how the Fast Fourier transform works is given in James (1995). Its key advantage is that it reduces the number of multiplications needed for a transform of length N from $N^2$ to $2N \log_2(N)$, a significant saving of time even for very fast computers. A good estimate of the Fourier transform can be made using the FFT under certain conditions. A range of points must be chosen such that the function extends over a range less than the range chosen on which to perform the FFT. Within the range chosen, points are selected at even intervals and the value of the function evaluated at these points is used to calculate the Fast Fourier transform.

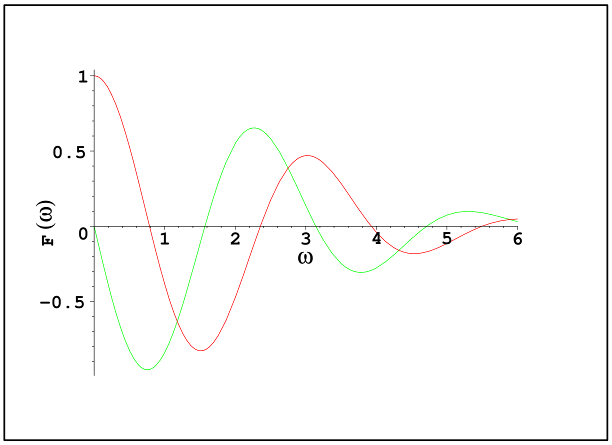
To show that the FFT finds the correct results we examine a simple exponential function namely $f(t) = \exp(-\pi * (t-2)^2)$ which has Fourier transform

$$F(w) = e^{-2i\omega - 4\pi} e^{\frac{1}{4}\frac{16\pi^2 - \omega^2}{\pi}}.$$

In figure 5.1, the plot of the function is seen as well as a plot of the real (red) and imaginary (green) parts of the Fourier transform of the function.

Figure 5.1: A Simple Exponential Function and its Fourier Transform: *A simple exponential function* $f(t) = \exp(-\pi * (t-2)^2)$ *is plotted with its Fourier transform divided into real (red) and imaginary(green) parts. The value of the real part of the Fourier transform when the imaginary part is zero for the first time, gives the value of Z for which the stability changes to non-converging oscillations.*





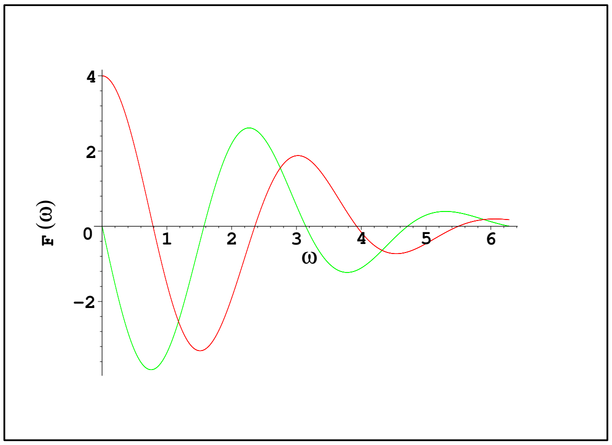
A fast Fourier transform was then calculated using $2^{14}$ points with an interval of 1/4 and starting at time 0. Figure 5.2 gives the plot of the real and imaginary parts of the FFT as well as the error of the scaled FFT with respect to the Fourier Transform. Ideally the value of $w$ where the imaginary part of the Fourier transform is zero would be estimated by finding the $n^{th}$ point for the FFT where the imaginary part is zero, and multiplying by $8\pi/2^{14}$. However, the FFT does not include the first point where the imaginary part becomes zero. Hence I estimate the true zero point by fitting a line between the smallest negative and positive values of the imaginary part of the FFT where the imaginary part first changes sign. Then by fitting a line between the corresponding values of the real part this zero can be used to estimate the true value of the real part of the Fourier Transform. We then observe that for the Fourier transform the first zero of the imaginary part occurs at 1.57 and the real part has value $-0.8217$. For the FFT the corresponding real value is $-3.2867$ which when multiplied by 0.25 gives four decimal point accuracy. From figure 5.2, the error in estimating the Fourier transform is always quite small, if rather systematic. In the case of my model, the value of $-0.82$ would be the estimate of the value of $Z$ and then the corresponding value of $\beta$ could easily be found. This method will be used to find the boundary value of $\beta$ which divides converging and diverging oscillatory behavior in the results section of this chapter.

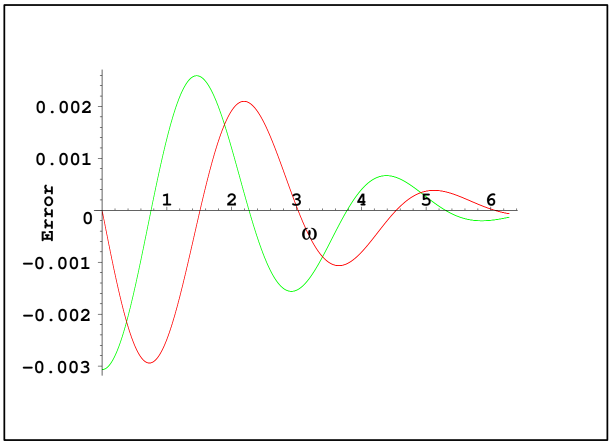
### 5.2.3 Simulation Method

To run a simulation of a population governed by the equations in section 4.1 the package Solver(Gurney et al. 1998a) is used, with a program implementing the Escalator Boxtrain method. This method is detailed in Gurney and Nisbet (1998) and an accompanying program titled EBT1 has been modified for my model (see Appendix B).

To give a brief description, the key idea is to divide the population into several cohorts of equal time interval $\Delta a$. Having done this, cohorts can now be numbered such that cohort $i$ contains all fish which were born between time $i\Delta a$ and $(i+1)\Delta a$. As cohorts will become empty as fish age, it is sensible to have a

Figure 5.2: FFT of an Exponential Function: *The FFT of* $f(t) = \exp(-\pi * (t-2)^2)$ *is plotted below, the red line being the real part and green line the imaginary part. The second graph gives an estimate of the error between the Fourier transform and the scaled FFT, with the red line showing the error for the real part, and green line for the imaginary part.*





cut off age, $a_D$, such that when the fish reach age they are no longer included in calculations. Of course this age must be chosen so that the number of fish above this age is insignificant in terms of the general population, hence in my model $a_D = 50$ for unfished populations and $a_D = 25$ for fished populations. Thus only cohorts containing some fish of age less than equal to $D\Delta a$ (where $D = a_D/\Delta a$) will be included in the model, thus letting us keep only $D+1$ cohorts in the model at any time. The model at time $t$ will therefore have cohorts $M(t) - D$ to $M(t)$ where $M(t) \equiv \text{trunc}(t/\Delta a)$. The computer program is then written so that only the active cohorts are kept by recycling cohorts as they reach the maximum age.

It is necessary to keep track of age, size and numbers in each cohort. We first notice that the number of fish of age 6 months at time t can be written as

$$R(t) = \sum_{i=M(t-0.5-a_D)}^{M(t-0.5)} B(\bar{w_i}, \bar{a_i}, t) N_i$$

where $\bar{w_i}$ and $\bar{a_i}$ are the average weight and age in the cohort, while $N_i$ gives the number of fish in each cohort.

Now consider the number of fish in each cohort, $N_i$. The change in numbers over time is affected by the mortality rate, $\delta(\bar{w_i}, t)$. Hence

$$\frac{dN_i}{dt} = R(t) - \delta(\bar{w_i}, t) N_i \tag{5.29}$$

where $R(t) = 0$ unless $i$ is the new cohort, i.e. $i\Delta a < t \leq (i+1)\Delta a$.

Next looking at total age of a cohort, $A_i$, notice that this quantity increases through the aging process but is decreased as fish die. Also as the model begins with fish of age 6 months there is a term depending on the initial addition of fish to the population. Hence

$$\frac{dA_i}{dt} = 0.5R(t) + N_i - \delta(\bar{w_i}, t) A_i \tag{5.30}$$

where we have as above $R(t) = 0$ unless $i\Delta a < t \leq (i+1)\Delta a$.

Finally the weight of the population must be considered. This again is kept as the total weight for the cohort $W_i$, with the average weight being

$$\bar{w_i} = \frac{W_i}{N_i}.$$

The total weight of the cohort increases as new fish are born into the cohort and with the aging process, but decreases as fish die. Let $g_w(\bar{w_i}, \bar{a_i}, t)$ be the growth rate of an individual and $w_r$ the weight at age 0.5. Then

$$\frac{dW_i}{dt} = R(t)w_r + g_w(\bar{w_i}, \bar{a_i}, t)N_i - \delta(\bar{w_i}, t)W_i. \tag{5.31}$$

Again $R(t) = 0$ unless $i\Delta a < t \leq (i+1)\Delta a$.

This method is implemented using a Solver program with the functions defined in chapter 4. A key step in running these programs is that the output interval and time step must always be integer sub-multiples of the cohort width (Gurney et al. 1998b). As such, the programs were run with a fixed time step and the output interval was chosen to be the cohort width. When cohort width and time step are decreased the accuracy of the simulation is increased. The basic program used for all models is included in Appendix B.

## 5.3 Results and Robustness

### 5.3.1 Results

Having now established methods for finding equilibrium values, determining stability, and running simulations of the populations, the results for the model can be examined. As a first step the equilibrium values for the fished and unfished models are given in table 5.1 using the parameters set in chapter 4.

Table 5.1: Equilibrium Values: *Equilibrium values are given for when the fertility parameter is 15.9. Notice that fishing mortality has a significant effect on the equilibrium values found. In the unfished model, the number of half year fish is much smaller, while the adult biomass is much larger.*

| Population characteristic | Unfished model | Fished model |
|---|---|---|
| Adult Biomass(thousand tonnes) | 4959 | 155.0 |
| Half year old fish (millions) | 553.4 | 2111 |

Table 5.2: Stability Boundaries with Respect to Fertility ($\beta$)

| Stability Boundary | Unfished Model | Fished Model |
|---|---|---|
| Point of Viability | 0.1116 | 13.62 |
| First Oscillatory Behaviour | 0.3033 | 37.01 |
| Non Convergence | 7.359 | 260.2 |

Notice that, as expected, the adult biomass is much higher for the unfished model as this population suffers much less mortality. The equilibrium level for 6 month old fish is, however, smaller. This is because in the unfished model reproduction is limited due to high levels of competition and thus not as many new fish are produced as in the fished model where crowding is not a factor. Although less fish are produced in an unfished population, due to the increased expected life span, more will survive to become part of the adult biomass.

We next examine the stability in the fished and unfished models for different levels of fertility. From equations 5.11 and 5.15 it is possible to establish the two boundaries between non-viability, exponential convergence, and oscillatory convergence. Using the FFT method the third boundary, between oscillatory convergence and limit cycles can be found.

In figure 5.3 the plots of $u(a) = p(a)w(a)S(a)$ are presented for the unfished and fished models. The graph for the unfished model is skewed, and shows that $u(a)$ is noticeably different from 0 for ages less than 35. For the fished model the graph is more symmetrical, and $u(a)$ is virtually zero for all ages above 15. Hence, it is expected that there should be different results for the stability boundaries for the two models as they are found using functions of $u(a)$. The FFT's for these models were calculated using $2^{14}$ points and an interval between points of 1/8. For the unfished model the imaginary part of the FFT is first zero at $\omega \approx 0.4$ where the real part is approximately $-22.5$, producing a value of $\beta \approx 7.36$. For the fished model this occurs when $\omega \approx 0.76$ with the corresponding real value of $-0.55$ giving a value of $\beta \approx 260$.

Notice, from table 5.2, that fishing has a profound effect on stability, as the production parameter $\beta$ must be much higher for a fished population to survive. Similarly higher values of the $\beta$ parameter are needed before limit cycles, or oscillations of any type can be expected to occur. The actual behaviour under these two models, within different stability boundaries, is shown in figures 5.4 and 5.5 produced using solver simulations. These graphs highlight that the same basic behaviours occur in both situations, only for different parameter values.

For the unfished model (figure 5.4) the population is viable for very low values of $\beta$. As the fertility term includes mortality before 6 months, as new fish only enter the population at this age, the population is quite resilient with respect to increased mortality for this very young stage. As such several years of conditions which promote high juvenile mortality are unlikely to cause extinction. There is a narrow parameter region in which an exponential approach to equilibrium is found, but in such a region this equilibrium can be obtained quite quickly in less than 100 years (see figure 5.4). For higher values of $\beta$ there is an oscillatory decay to equilibrium, with large oscillations being possible. Finally note that the value of 15.9, used for the fertility parameter, lies in the region where limit cycles appear. As a result the population will not achieve the equilibrium adult biomass, instead it will oscillate around this value continuously.

For the fished model, there is a different situation. The value of $\beta$ which gives limit cycles in figure 5.4 for the unfished model would not even lead to a viable population in the fished model (see figure 5.5). With $\beta = 12$ the fished population becomes extinct. The region in which the population converges exponentially to equilibrium is large, with the graph for $\beta = 15.9$ being shown in figure 5.5. Within two hundred years the population manages to settle. It is unlikely that the fertility level could be high enough for the population to undergo limit cycles or even oscillatory behavior, considering that this would require that the fertility level was more than doubled. Additionally the fished model will not have the same resilience to mortality on larvae and pelagic juveniles that the unfished model has. This is because the current fertility level is only just higher than the minimum value for a viable population. Hence several years of high juvenile mortality which lowered the production of 6 month fish, could have a very serious effect on the population. Certainly there would be a more dramatic effect than if fertility were lowered for an unfished population.

On comparison of the results for the fished and unfished model, it is not surprising that stocks which have a low fertility rate can become extinct extremely quickly, even under low levels of fishing pressure. Such an effect is seen in many deep sea species as well as larger fish with few offspring, such as sharks. Ideally, before such species were fished, an analysis of the stability of the population should be performed in order to assure that the addition of extra mortality would not cause the population to go from a stable situation to one where the population declines to extinction.

Note, that stability boundaries have only been found with respect to the fertility parameter. The reason for this is that the fertility parameter $\beta$ is likely to be one of the parameters which is most changeable. This is due to its dependence not only on the egg producing ability of fish, but on the mortality rates during the first six months of life. All other parameters which have an effect on stability are included in the function $u(a)$. In the equations which are solved for the third stability boundary (see 5.19 and 5.20), this function is involved in both sides of the equation. Thus as we must use FFT's to estimate the value of the Fourier transform, the set of equations is no longer easily solved. Instead a point by point examination is necessary in order to find this stability boundary for any parameter other than the fertility parameter.

An estimate of where these boundaries lie can, however, be made by examining individual values for parameters and finding the stability limits for these points. By plotting these values against $\beta$, the stability boundaries with respect to the parameter of interest can be estimated taking $\beta = 15.9$. This has been done for two parameters, one maturation parameter, $p_y$, and one weight parameter, $w_\infty$. In figure 5.6, the proportion mature parameter $p_y$ has been considered, with $\beta$ plotted on a log scale on the y axis. The dotted line gives the value of $\beta$ used in the model. We observe that the population will be extinct if $p_y$ is less than approximately 3.7. However the population will not take on an oscillatory behaviour until $p_y$ is much larger than any value included in the graph, which would be unrealistic. It is also clear that increasing $p_y$, and thus the proportion mature, lowers the level of $\beta$ needed for the different types of behaviour. Thus, as expected, a population which matures early (i.e. $p_y = 4.4$) does not need to be as fertile as a population where maturation occurs more slowly ($p_y = 3.6$) in order to be viable.

In the second figure (figure 5.7), the maximum weight parameter ($w_\infty$) has been used instead. A very similar situation arises. The dotted line again gives the set value of $\beta$ of 15.9, giving that the population will become extinct if $w_\infty$ is less than approximately 15.4. Again, $w_\infty$ must be much larger before it is possible for the population to show oscillatory behaviour if $\beta$ is kept at the set value. Increasing the value of $w_\infty$ will lower the stability boundaries with respect to $\beta$.

### 5.3.2 Robustness

An important question is how dependent the results above are on the particular model chosen. It would be hoped that the system is fairly resilient to changes in the model. Thus if data is modelled incorrectly wrong conclusions about the model would not be made.

We will start by observing the difference that changing the function for proportion mature has on the equilibrium adult biomass values in both the fished and unfished model, and the values of $\beta$ which determine the behaviour of the model around the equilibrium. In table 5.3, $\beta = 15.9$ when equilibrium adult biomasses are calculated.

In the unfished case the equilibrium biomass levels given, with one exception, are in a parameter region where the population experiences limit cycles. These values were found to be very similar in all cases, and with environmental noise would be indistinguishable. This was also discovered to be true for values of $\beta$ which give a stable equilibrium as well, and as such it would be difficult to determine which function was governing proportion mature purely from the equilibrium adult biomass found in the population. With the exception of the distribution for exponential maturation, stability boundaries are also fairly sim-

| | Main Model | 1 | 2 | 3 | 4 |
|---|---|---|---|---|---|
| Without Fishing | | | | | |
| Adult Biomass | 4959 | 4969 | 4902 | 4952 | 4938 |
| Point of Viability | 0.1116 | 0.1105 | 0.1182 | 0.1123 | 0.1139 |
| First Oscillatory Behaviour | 0.3033 | 0.3004 | 0.3213 | 0.3054 | 0.3097 |
| Limit Cycles | 7.359 | 6.980 | 21.35 | 7.228 | 9.064 |
| With Fishing | | | | | |
| Adult Biomass | 155 | 0 | 1010 | 30.0 | 429.7 |
| Point of Viability | 13.62 | 17.4 | 5.788 | 15.43 | 10.35 |
| First Oscillatory Behaviour | 37.01 | 47.31 | 15.73 | 41.94 | 28.12 |
| Limit Cycles | 260.2 | 166.6 | 2083 | 198.3 | 753.0 |

Table 5.3: Equilibrium Adult Biomass under Different Maturation Schemes: *The columns correspond to the proportion mature being modelled with the Weibull distribution, concurrent maturation, a cumulative exponential distribution, a cumulative Gamma ($\alpha = 3$) distribution and a cumulative Gamma ($\alpha = 4$) respectively.*

ilar with tiny regions where different types of behaviour depending on the model chosen. The exponential model is quite different, with a much higher fertility level needed in order for limit cycles to appear in the population. This model has a much longer period during which fish mature (see figure 4.10) and hence will not experience the same increase in competition when fertility increases as the other models.

However, with the heavy fishing mortality that is included in the fished model it becomes easier to distinguish between the different functions. The equilibrium adult biomasses are quite different, with the model where all fish mature at the same time actually being extinct when $\beta = 15.9$. The exponential model has more than twice the biomass of any other model, while the third model has a fifth of the biomass of the Weibull distribution model which has a third that of the other gamma distribution model. Differences can also be seen in the stability boundaries, particularly for the exponential model which has wildly different values from the other four. These differences are explained by the high level of mortality, under such mortality the ability to reproduce at a very young age becomes very important. Thus the exponential distribution, which allows many fish to mature at very young ages (see figure 4.10), is more resilient to the level of mortality. Hence it has a higher equilibrium adult biomass, and a lower minimum fertility level than the other models. This provides a startling example of why accurate data is needed for fisheries stocks. If we cannot be certain of the exact progression of maturation, this can have a significant effect on the biomass predicted to be in the oceans as well as the expected behaviour of the stocks. It should be noted that for the Weibull and Gamma distributions, the same type of behavior occurs in the region where we expect $\beta$ to lie.

Table 5.4: Stability Boundaries for the Models under Different Growth Schemes

| | Main Model | Power | Gompertz | Logistic |
|---|---|---|---|---|
| Without Fishing | | | | |
| Adult Biomass | 4959 | 4959 | 4934 | 4903 |
| Point of Viability | 0.1116 | 0.1116 | 0.1144 | 0.1179 |
| First Oscillatory Behaviour | 0.3033 | 0.3034 | 0.3109 | 0.3206 |
| Limit Cycles | 7.359 | 7.340 | 6.328 | 5.314 |
| With Fishing | | | | |
| Adult Biomass | 155 | 0 | 145 | 63.52 |
| Point of Viability | 13.62 | 19.80 | 13.75 | 14.90 |
| First Oscillatory Behaviour | 37.01 | 53.82 | 37.38 | 40.56 |
| Limit Cycles | 260.2 | 388.7 | 277.6 | 328.3 |

We now look at what would happen if growth were modelled using one of the alternate functions from chapter 4. It should be noted that for the alternate growth models we have set the boundaries for different types of mortality using the weight function in question in the method of the previous chapter. This is in order to compare the differences between choice of model rather than difference in value for weight at a particular age. For the calculation of adult biomass $\beta = 15.9$ even though the calculation used in chapter 4 would set $\beta = 20.9$ for the power model.

The first thing we notice is that for the unfished model results are very similar for equilibrium adult biomass, with just over a 1 % difference between all models. Stability boundaries are also quite similar, especially between the linear and power growth models which are virtually indistinguishable. The Logistic model begins limit cycles at a smaller value of $\beta$ than the other three models in this case. However for all four models the value of $\beta$ used to calculate adult biomass is well within the region of limit cycles

For the fished model values of adult biomass are quite different with the $\beta$ value being too low to have a viable population when young growth is modelled with the power model (using $\beta = 20.9$ gives a value of 54 thousand tonnes). Examining the linear and power growth functions, we notice that fish which grow according to the latter scheme put on weight much more quickly and therefore suffer fishing mortality from a much earlier age. Hence, with the increased mortality the population experiences and no increase in the proportion mature at such a young age, the fertility parameter $\beta$ needs to be larger in order to ensure a viable population. The Gompertz rate of growth for older fish gives very similar results to the von Bertalanffy, with slightly higher values of $\beta$ for the boundaries between behaviour regions. The equilibrium adult biomass is also quite similar. It is suspected that with the addition of environmental noise, it would be very difficult to distinguish which of the two models was in effect. The Logistic growth for older fish differs more substantially from the von Bertalanffy growth curve (see figure 4.4), although stability regions are fairly similar. The equilibrium adult biomass, however, is half that of the main model.

## 5.4 Summary

In this and the previous chapter we have examined a single population model for cod in the North Sea. We have looked at how equilibrium values can be found as well as the stability of these equilibriums, and have considered seven possible changes to functions in the model as well as a fished and unfished model.

### 5.4.1 An Unfished Population

For an unfished population, the results were fairly robust. Model changes had a fairly small effect on the population, with the exception of switching to exponential maturation. Due to the low mortality in the model, fish have long life expectancy. Thus small differences between populations for young ages will not be noticeable due to the overwhelming influence of older fish. In an unfished population most of the reproduction of the stock is due to fish aged 4 to 15, with younger fishing being a small percentage of the adult biomass and hence having little effect on reproduction. Therefore any changes to the model which affect mainly fish under age 4, will have few effects on the population. Hence the power model, which changes life history only below the age of two and a half, has virtually no effect on stability and equilibrium values.

This conclusion is further supported by the effect of changing the model for proportion mature. The function which requires higher values of fertility in order to be viable and before limit cycles begin, is the exponential function. When referring back to figure 4.9, we see that with this model 100% maturity is still not achieved by age ten even though the proportion mature is higher for young ages. This means that the adult biomass is dominated by comparatively young fish, which weigh less, and therefore are less able to reproduce than a similar number of older fish.

The changes to the older growth curve affected stability more than the change of the young growth curve. Both functions reduce the maximum weight achievable by a fish. Hence reproductive ability of an individual fish has been comparatively lowered. This difference is most apparent in the level of $\beta$ at which limit cycles begin to appear, while the equilibrium values found for adult biomass are very similar in all three cases.

### 5.4.2 The Addition of Fishing

Once fishing is added to the model the situation changes considerably. Fishing provides a major source of mortality, and significantly decreases the life span of the fish. Thus young fish contribute more to the population while older fish become rare, diminishing the importance of how fish grow and mature at an older age.

This pattern is clearly observed in the table for changes in functions of growth (table 5.4). For the unfished model, changing the linear growth of young fish to power growth had virtually no effect, whereas for a fished population it has a significant effect. The population with power growth has a higher minimum value of $\beta$ in order for it to be viable. This is directly attributable to the fact that under such growth young fish gain weight much more quickly (see figure 4.3), and therefore become susceptible to fishing mortality at an earlier stage in life. The model with Gompertz growth for older fish, which is more similar to the von Bertalanffy curve at a young age than an old age, has proportionally closer values for stability boundaries in a fished population than in an unfished population. The Logistic model has a similar discrepancy in both fished and unfished populations as it differs more noticeably than the Gompertz model for ages three through six (see figure 4.4).

A similar effect is observed in the table for proportion mature. When all fish mature at the same age (3.75), there is an increase in minimum value of the fertility parameter. This is not surprising as this model is alone in preventing reproduction till such an old age. Conversely, for the exponential model a much lower minimum value is found, as under this model the proportion mature at young ages is relatively high.

### 5.4.3 Discussion

The fished model used in this thesis gives an equilibrium adult biomass of approximately 155 thousand tonnes. This value is realistic when considering the population between 1965 and 1985 (see figure 1.3). For the last fifteen years, however, when biomass has declined to less than 100 thousand tonnes it seems, at best, optimistic. Thus, if the value of $\beta$ were estimated using only recent data it would be lower. This is worrying as the minimum value of $\beta$ needed for a viable population is not much lower than the value used in the model.

For the fishery it is important to establish which type of stability is being shown in the population. As cycles can have long periods, it is crucial to realise when the fishery is involved in a periodic oscillation, or whether there is a decline towards a lower equilibrium biomass or perhaps even extinction. The correct course of action will differ depending on the situation, and following the wrong course of action may have disastrous consequences. For instance, management plans for pacific salmon have used fishing to increase cyclic behaviour as these populations undergo steady oscillations, although it has been suggested that this is not a wise course of action (Welch and Noakes 1990). The same fishing plan for a population which was declining towards a lower biomass, could cause it to become extinct. Furthermore, in the case of a population which was exhibiting limit cycles, timing of fishing could either increase the range of cycles, perhaps making the population unfishable at times, or could remove the cycles from the population, perhaps lowering overall yield. Hence, the stability of the population can indeed affect how the fishery should be managed. The current trend in the North Sea seems to be a decline in biomass, possibly towards extinction. It is thought that the biomass levels of the sixties and seventies were an aberration (Holden 1991), in which case this may be a decline towards a lower biomass level. Either way, it is generally felt (see chapter 1) that a decrease in fishing mortality would help the population, allowing it either to stabilize or perhaps increase its biomass level.

This model's parameters are in a region where there is an exponential approach to equilibrium with no oscillatory behaviour. However, if the fishery were to stop, the unfished model suggests that the population would undergo limit cycles. One would expect that, as long as biomass has not been decreased low enough for stochastic effects to play an important role, the population would rebound quickly. This would be a drastic action for the E.U. to take however, as it would require shutting not only the cod, but also closing the joint whiting and haddock fisheries and would cause many job losses.

We have shown in this chapter that model choice does affect what is seen, particularly when a fished model is considered. Frequently the type of behaviour expected will be the same for all models for reasonable parameter values, however the equilibrium adult biomass varied substantially between models. Some of these differences will become far less apparent once environmental noise is considered (for example El Nino effects, temperature and climate changes). However, there is a clear suggestion that in order to have an accurate picture of what is taking place in the North Sea the growth and maturation of cod should be modelled accurately.

The work in the two previous chapters has highlighted that the rate of growth and speed of maturation can have a large effect on the population. In the following chapters we shall investigate which aspects of these rates are most crucial in determining a populations ability to survive.

Figure 5.3: The Proportion of Biomass which is Alive and Mature at age $a$ for the Unfished and Fished Models: *Notice that the scales are different on the two graphs, and u(a) obtains higher values for the unfished model.*

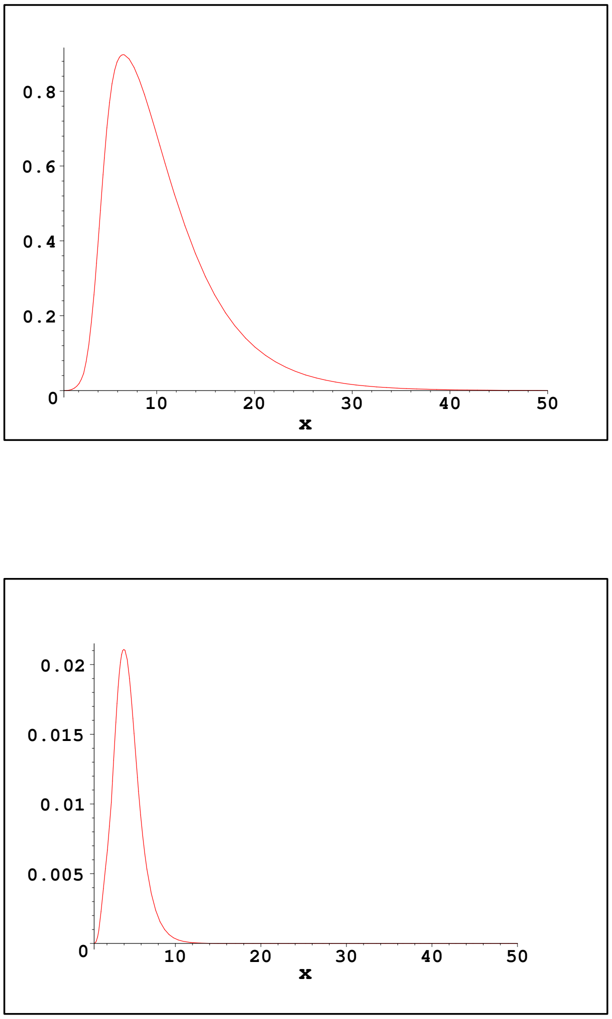


Figure 5.4: Behaviour for Different Fertility Parameter Values in an Unfished Population: *Note the first graph where the population becomes extinct is plotted on a different scale from the other three. Quite small values of $\beta$ are sufficient to have a population with limit cycles and the population is viable even under very low fertility levels.*

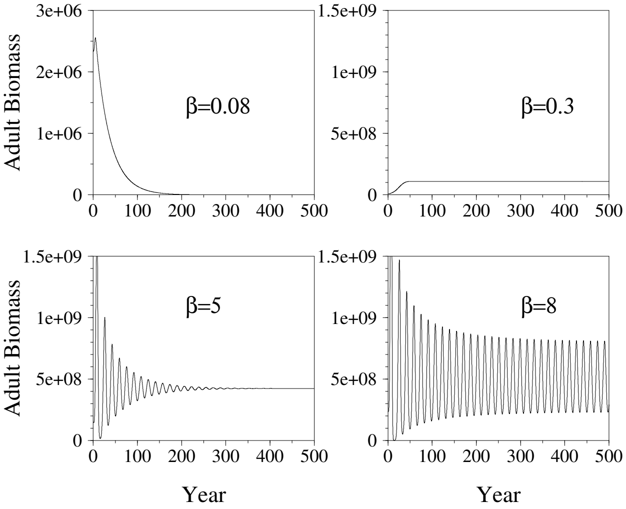


Figure 5.5: Behaviour for Different Fertility Parameter Values in a Fished Population: *Note that the graphs are plotted on different scales. Fertility must be extremely high before limit cycles appear in the population. The value of 15.9, used as the basic value for $\beta$, is only just large enough to provide a viable population, as when $\beta$ is 12 the population becomes extinct.*

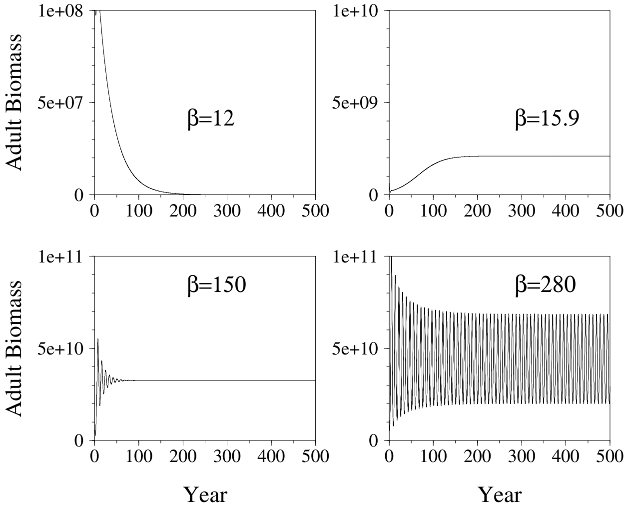


Figure 5.6: Stability Behavior for $p_y$ : *The dotted line gives the set value of* $\beta$*, which is plotted on a log scale. We see that a population with the parameter values of chapter 4, requires that* $p_y > 3.75$ *in order to be viable. There is a steady decrease in the value of* $\beta$ *required for a viable population as* $p_y$ *increases.*

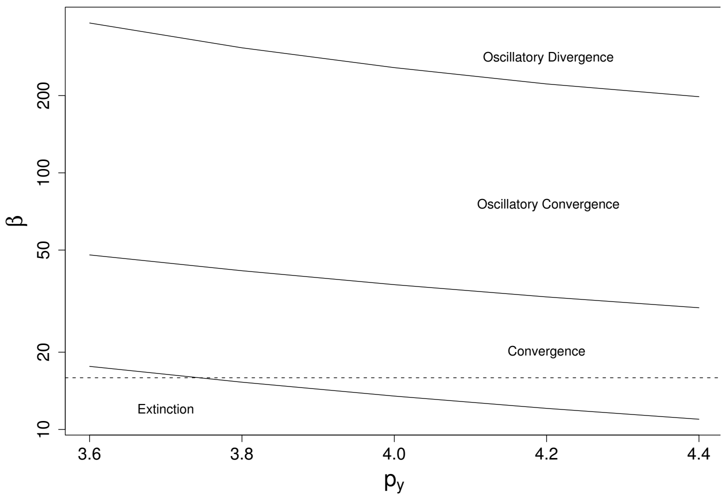
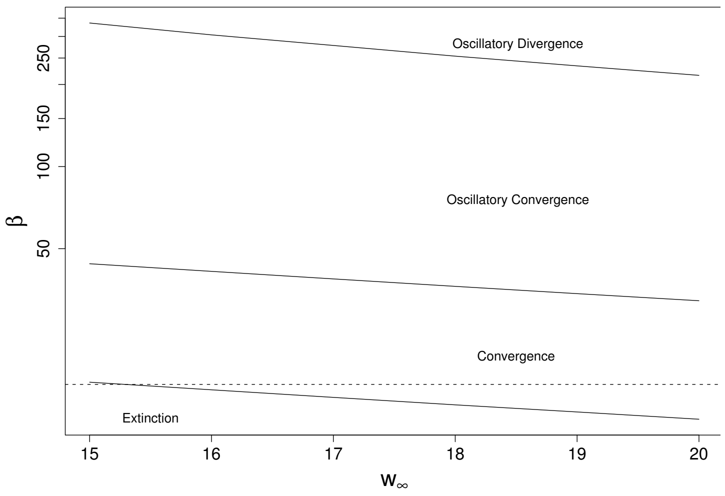


Figure 5.7: Stability Behavior for $w_\infty$ : *The dotted line gives the set value of* $\beta$. *We see that a population with the parameter values of chapter 4, requires that* $w_\infty > 15.4$ *in order to be viable. There is a steady decrease in the value of* $\beta$ *required for a viable population as* $w_\infty$ *increases.*



# Part III

# Competing sub populations

# Chapter 6

# Evolution through competing phenotypes

The previous chapter examined the case of a single population, with set parameters for growth, fertility and mortality. This part of the thesis will study the interactions of a two population model, each population having different parameters controlling its life history. The main question is whether human fishing of cod stocks is capable of exerting a significant influence on the population. This could be by either changing which mutations are favoured or how quickly a mutation is able to increase its numbers.

In this chapter a measure will be found to ascertain the fitness of the population. Once this is established populations can be compared, and it is possible to determine which evolutionary paths are likely to occur. In chapter 7 a sensitivity analysis will be performed in order to assess which parameters affect the fitness of the population the most, and hence which aspects of life history are likely to change. Different aspects of fishing mortality will also be assessed, in order to determine the most effective way of reducing fishing pressure on the population. Finally in chapter 8 seasonal and spatial behaviour will be included in the model. This enables us to examine if a non spatial model can fully capture the complexity of the North Sea, or if future work should concentrate on creating a fully spatial model.

## 6.1 Introduction

In recent decades the question of how populations will evolve has been raised for many different populations, not only cod. Several people have examined methods for judging how evolution will take place for a given model, for example Law and Grey (1989), Nisbet, Gurney, and Metz (1989), Blythe and Stokes (1990), Brown and Parman (1991), and Thompson and Stokes (1996) which will be examined in the following section. Others research has looked at stocks for evidence of change in life history parameters (de Veen (1976), Beacham (1983), Jorgensen (1990), Reznick, Bryga, and Endler (1990), and Rijnsdorp and van Leeuwen (1996)).

The level of mortality imposed by fishing in many of the world's fisheries is extremely high and is often quite selective, imposing a major force of selection on populations. Even without strong age or size selectivity the high mortality inflicted on a population can have a significant effect. Borisov (1979), for example, investigated Arctic-Norwegian cod and discovered that high levels of fishing mortality will select for younger maturing fish (fish in this population mature from age 6 to 15). However, under low mortality levels the reproductive contributions of early, middle, and late maturing fish in the population are balanced. In the case of high levels of fishing mortality it is found that half of all eggs laid during the life of a year-class come from early maturing fish, and the other half virtually all from middle maturing group, with the late maturing group producing almost no eggs. Obviously in a situation of high fishing pressure, late maturing fish will not be able to pass on their genes. In a situation of low fishing pressure, the early maturers are responsible for approximately 16% of eggs, middle maturers 64% and late maturers approximately 21%. Additionally, the population has seen an increase in growth rate and a reduction in average life span.

Dr. Rochet examines the effect of fishing in a more general way. She considers 77 stocks, most of which are commercially used, and finds that populations compensate for fishing by increasing size and decreasing age at maturity (Rochet

1998). Her work concentrates on female traits examining the time to 5% survival, length at 5% survival, age and length at sexual maturity and a measure of fecundity. She suggests that her findings should be considered by managers when assessing stocks and that data on the proportion mature at age should be frequently updated.

Dr. Rowell finds evidence that for cod in the North Sea there has been a trend towards a smaller minimum size at maturation and an increase in range of sizes at which maturation occurs when data from 1893, 1923 and recent years are compared (Rowell (1991), see also Oosthuizen and Daan (1974)). These effects seem most likely to be explained by evolutionary responses, although this could not be determined conclusively. Similarly, the Scotian shelf cod population in the Northwest Atlantic has exhibited signs of significant changes in the last half century. There has been a 50% drop in median length and age at sexual maturity between 1959 and 1979 (Beacham 1983). For instance, by 1978 females in NAFO area 4VN matured at a median length and age of 32cm at 2.6 years, as opposed to 65cm at 6.7 years in 1959. The changes in the population are notable for having occurred in a time period when exploitation has increased dramatically (Beacham 1983).

Finally the growth of Sole (*Solea solea*) in the North Sea has increased since the 1950's in a way which is not correlated to temperature or increased nutrients from river discharge (although it is possible that density dependence effects of stock abundance have played a role (Millner and Whitny 1996)). Evidence has also been given by de Veen (1976) that length at age has increased from the mid 60's, with the main change in length increment being for the 2 and 3 year old year classes.

Evolution may not be the only cause of such changes in population parameters. Fish populations have an ability to change their phenotype (or expression of their genes in an environment) as their environment changes. The extent of the ability of a fish to change its phenotype is also referred to as its reaction norm. So a question which must also be answered is whether changes in the reaction norm and changes in genotype of a population can be distinguished.

This is important as a change of phenotype can be reversed quickly by changing the environment, whereas a reverse in genotype may take longer or never occur if the necessary genes have disappeared from the population and do not mutate again.

Reznick has managed to look at both phenotypic and genotypic change within an experiment. He experimented with guppies (*Poecilia reticulata* L.) in an eleven year study involving thirty to sixty generations. Evolution of the genotype occurred when guppies were placed in an environment where adults were no longer under heavy predation (Reznick, Bryga, and Endler 1990; Reznick 1991). This resulted in a 10 to 20% change in the age and size at maturity and a 25% decrease in the number of young in the first litter. These fish could be distinguished from the original genotype in a common environment. Hence, at least some of the life history differences in the population which had not sufferred adult predation were genetic rather than phenotypic (Reznick et al. 1990). Reznick did find however, that phenotypic effects can be much larger (as much as four to ten times larger) than evolved responses, and hence genetic effects may often be unnoticeable in comparison (Reznick 1991).

An example where phenotypic responses may be large enough to either hide or preclude evolutionary responses is Plaice (*Pleuronectes platessa* L.) in the North Sea. It is believed that many of the changes seen for Plaice are linked to density dependence or other phenotypic effects, although 24% of phenotypic variablility of traits is associated with genotypic variability (Rijnsdorp 1991; Rijnsdorp 1993). There has been a decrease in age and length at maturity since 1990 and a growth increase for size classes larger than 35 centimetres since the 70's (Rijnsdorp 1993; Rijnsdorp and van Leeuwen 1996).

Dr. J. Hutchings also examines both phenotypic and genotypic effects in his paper on brook trout (*Salvelinus fontialis*) in two Newfoundland coves (Hutchings 1991). He summarizes that the ability to react phenotypically to the environment can be expected to evolve when the spatial distribution of individuals across habitat is random with respect to genotype and when the habitat significantly influences fitness. His work finds that size-selective fishing mortality has the greatest effect on the reproductive effort of fish. Although the same results are found whether or not the ability of populations to phenotypically adapt is included in the model, this ability can affect the rate of such changes. For instance, one of the effects found for size-selective harvesting is that there is a reduction in juvenile density due to the sparsity of spawning adults (Myers, Hutchings, and Gibson 1986), upon which increased juvenile growth appears due to density effects. This can result in an immediate change to earlier age and increased effort at first reproduction if phenotypic responses are considered, as the ability to change age at reproduction may be already in existence (Hutchings 1991). However, if no reaction norm response is included any change would take a longer period of time due to the wait for genetic evolution.

So what is required for evolution to take place? Firstly, there must be phenotypic variations based on a heritable genetic variation, i.e. a parameter of interest must be heritable and not solely based on environmental reactions. Secondly, mortality (or other factors inhibiting reproduction) of the population must result in different genotypes reproducing different amounts (Policansky 1991). Hence in order for evolution to occur, the population must undergo enough pressure that not all genotypes in the population can react sufficiently by altering their phenotypic response to the environment. If this is the case then some genotypes may increase their occurrence in their population while others remain constant or decrease. It should be noted at this stage that an unsuitability to the environment does not require that a gene will disappear from the population. An illustration of this is sickle-cell anaemia in humans, where one of the homozygous genotypes results in sickle-cell anaemia while the heterozygous genotype provides increased resistance to malaria (Hammerstein 1996). This increased fitness of the heterzygote prevents sickle-cell anaemia disappearing from the population.

### 6.1.1 Clonal versus Genetic Models

Ideally when examining the evolution of a stock one would include a model of the species' genes, studying what happens as spawning or mutation occurs, and looking at several different traits in terms of many different genes. However, in practice this is very difficult to do. In many cases it is not yet known which genes are responsible for certain aspects of traits and secondly the genetical component of selection is also generally unknown (Weissing 1996). Furthermore, such models, even if the necessary background data was known would present many problems for a mathematical solution, or even computer simulation due to their complexity. Hence a simpler, and less realistic situation is generally modeled.

The two standard approaches are to use a simplified genetic model or to use a clonal model. The first is to use a simplified genetic framework. One example includes Mendelian genetics with a two-allele single-locus genetic model. In this type of model the two alleles can be represented by $A$ and $a$, and the result is three different genotypes which arise, namely $AA$, $Aa$, and $aa$. If the different genotypes have frequencies $P$, $Q$, and $R$ then the frequencies of the alleles are

$$p = P + Q/2 \quad \text{and} \quad q = 1 - p$$

respectively (Nisbet et al. 1989). Frequently it will be assumed that there is random mating and non overlapping generations, with survival prior to reproduction being the only selective force. This allows the Hardy-Weinberg equilibrium to be used to give the frequencies of the genotypes as

$$P = p^2, Q = 2pq, \quad \text{and} \quad R = q^2.$$

Simple tracking of genotypes is now possible as knowledge is only required on either p or q (Nisbet et al. 1989). More complicated models can easily be formulated by altering assumptions slightly, for instance having non random mating, or overlapping generations. This implies, however, that the Hardy-Weinberg equilibrium can no longer be used (Nisbet et al. 1989). A model can also use multiple loci, or have more than two alleles per locus, each expansion leading to extra complexity of the model, but also adding realism. One paper which uses a genetic approach to examine North Sea cod is by Thompson and Stokes (1996). They use the one-locus and two allele model, assuming that the allele $A$ codes for fast growth while $A'$ codes for slow growth. The heterozygote ($AA'$) gives a growth rate midway between that of the two homozygotes, as neither allele is assumed to be dominant. They then keep track of the proportion of each gene ($A$ or $A'$) to see which is favored in the population. Their paper finds the fast growing gene increases in frequency over a 50 year simulation.

Another standard approach, which shall be applied in this thesis, is to use a clonal model. This assumes that offspring are exact replicas of their parents, and that different populations do not interbreed. Although this is obviously unrealistic, it allows other aspects of the model to be more complicated and can suggest what may happen under a genetic model. Several authors have used clonal models including Blythe and Stokes (1991), whose model served as a base for the model in this thesis. Under such models, if new populations with different phenotypes are added to the model the most common result is that there is mutual exclusion with one population becoming extinct. There are cases where two populations can coexist but this is a rare situation as there is no interbreeding.

Studies have been carried out on the results found by the two modeling approaches. Nisbet et al. (1989) examined a model for Nicholson's blowflies under both such strategies and found the results to be the same although initial invasion is faster in the clonal case. Similarly Getz and Kaitala (1991) and Geritz et al. (1998) have discovered that generally ecologically stable strategies (or populations such that small groups of mutants using other strategies cannot invade) can be found using a model without explicit genetic structure. It is hoped that adding genetic structure to the model I use will similarly not affect the general conclusion, although it is an avenue for further research.

### 6.1.2 Different Methods of Examining at Evolution

A key question now is how fish are likely to evolve under the model? By simulation it is possible to observe what will happen to mutant populations as they are added to the system. However, examining the model purely through simulations is unsatisfying, a more general answer is desired to avoid case by case testing of each situation. The question of how to look at evolution under a model has been treated by several authors. Two methods have been used by people doing similar work, one using the resident population and the other using the invading population. The latter method, as introduced by Blythe and Stokes (1990), will be used in this thesis

The 'streetcar theory' of evolution provides basic concepts which are useful to ponder. A streetcar has many temporary stops before it reaches a final destination at which it will stop for a long time. The same idea can be used to think about evolution. Stages where certain genetic mutations take over can be thought of as the temporary stops (as the streetcar waits for the next advantageous mutation before moving), whereas the final destination is when the population has a uninvadable genotype (Hammerstein 1996). Hammerstein argues that the temporary stops on the evolutionary streetcar depend strongly on the genetic details of the population while the final destination is determined mainly by forces on the phenotypic level. It is possible that this final destination may never be reached. There may be no genotype which is resistant to invasion by all others, or the time needed to evolve to such a genotype may be so long that the environment has time to change such that the fictional 'streetcar' must change route.

There are two different ways to think about evolution. In order for a new genotype to take over a population it must increase in numbers when at small population size and secondly, once established it must resist invasion from less fit genotypes. These ideas generate different approaches to modeling evolutionary changes in fish stocks. Two papers on the effect of size and age specific harvesting exemplify this difference and shall now be discussed.

Law and Grey use the idea of an ESS (an evolutionary stable strategy defined by Smith and Price (1973)). An ESS is a strategy which, given a particular environment, will not permit invasion by any evolutionarily feasible strategy (Brown and Parman 1991). This idea is further expanded by finding the ESS which will give the maximum total yield after evolution, or finding the ESOHS, the evolutionarily stable optimal harvesting strategy (Law and Grey 1989). They use a female's expected lifetime production of female offspring as a measure of fitness for the Arctic-Norwegian cod population. Their model finds, on the assumption that population dynamics are well behaved, that in the presence of fishing mortality earlier maturation is favored. They suggest that high fishing rates should be restricted to the spawner fishery and pressure decreased on the feeding grounds, as this will cause late-maturing life histories to be selected, giving increased yields (Law and Grey 1989).

I shall, however, follow the method of Blythe and Stokes (1990). They approach the problem by searching for a strategy which when rare will be able to invade any other evolutionarily feasible strategy. Hence, it is essential to find which life history strategies allow a population to increase at small numbers whatever the strategy of the resident population. This will be done by finding a measure of fitness which can be calculated for a population without consideration of any competing population. Then, in any situation, a population with a higher level of fitness will successfully invade another population with a lower fitness level. Blythe and Stokes (1990) find that equilibrium adult biomass is one of the population characteristics which acts as such a measure. They originally concluded that fitness increases with increased size at maturity when harvesting efficiency is low, and that high harvesting efficiency will eventually result in extinction (Blythe and Stokes 1990). Their follow up papers, which added natural mortality and an initial neonate size to the model, find that currently there is pressure for a reduced size at maturity, and that reducing the harvesting rate would increase yield (Blythe and Stokes 1991; Stokes and Blythe 1991).

The ESS approach has been used on Blythe and Stokes' model by Brown and Parman (1991). Their results differed from the original results in Blythe and Stokes (1990) but agreed with the results of the later papers. This demonstrates that the additions to the Blythe and Stokes model, mentioned in the previous paragraph, were essential. An advantage of the invasion approach is that the invasibility criteria can be extended to cases where the resident population is not at equilibrium when the invading population arrives (Blythe and Stokes 1991).

I follow the invasibility strategy of Blythe and Stokes, finding a measure of fitness which after a simple calculation determines which of two populations is capable of invading the other. A population which is capable of invading another will not always succeed, however, in the real world. Stochasticity at low numbers may prevent the invasion, and as genetic mutation is random the genes required to produce a population with certain characteristics may not arise.

## 6.2 Competing Populations

The model used for competing populations is essentially the same as the model for a single population. The main differences are that natural and fishing mortality are now weight dependent so that sensible comparisons between the populations can be made. Both types of mortality are size dependent as natural mortality tends to affect small fish to a greater extent, due to predation, while human fishing preferentially catches larger fish. The competition function now depends on the total adult biomass of the population as it is assumed that, although populations do not interbreed, they use the same resources and intermingle. Hence for the resident population

$$f_r(0.5,t) = R(t) = \int_{0.5}^{\infty} \beta p_r(a) w_r(a) e^{-(A_r+A_i)/K_r} S_r(a) R_r(t-a) da \tag{6.1}$$

and

$$f_r(a,t) = S_r(a) R_r(t-a)$$

and similarly for the invading population.

Next consider the possible equilibria of the system. There are three trivial equilibrium points. Both populations may become extinct, or either the residents or invaders may die out, leaving a single population which behaves as it would under the single population model. The only other possibility is a coexistence equilibrium. If such an equilibrium exists

$$\begin{aligned} R_r^\star &= \int \beta_r w_r(a) p_r(a) e^{-(A_r+A_i)/K_r} S_r(a) R_r^\star da &(6.2)\\ R_i^\star &= \int \beta_i w_i(a) p_i(a) e^{-(A_r+A_i)/K_i} S_i(a) R_i^\star da &(6.3) \end{aligned}$$

requiring the system of renewal equations

$$\begin{aligned} 1 &= \int \beta_r w_r(a) p_r(a) e^{-(A_r+A_i)/K_r} S_r(a) da && (6.4) \\ 1 &= \int \beta_i w_i(a) p_i(a) e^{-(A_r+A_i)/K_i} S_i(a) da && (6.5) \end{aligned}$$

to be solved. Thus

$$\begin{aligned} A_i + A_r &= K_r \int \beta_r w_r(a) p_r(a) S_r(a) = \frac{K_r \beta_r A_r^\star}{R_r^\star} && (6.6) \\ A_i + A_r &= K_i \int \beta_i w_i(a) p_i(a) S_i(a) = \frac{K_i \beta_i A_i^\star}{R_i^\star}. && (6.7) \end{aligned}$$

Hence, two populations may coexist under the very specific circumstance that

$$\frac{K_r \beta_r A_r^\star}{R_r^\star} = \frac{K_i \beta_i A_i^\star}{R_i^\star}. \tag{6.8}$$

We shall show in the next section that if the competition coefficient $K$ is the same in both populations, then this is equivalent to the equilibrium adult biomasses being the same.

## 6.3 Invasion of the Population

Next we wish to establish a measure of fitness which will determine when a population is capable of successfully invading another population. This is achieved by assuming that the resident population is in equilibrium and then observing what happens for a very small population of invaders. As $\beta$ is infeasibly large when limit cycles appear, this is the only interesting case to be examined. Let the invading populations life history parameters have subscripts 'i' and assume that the competition functions for each population are the same (although the competition coefficient K may be different)[1]. Then

$$f_i(0,t) = \int_{0.5}^{50} \beta_i w_i(a) p_i(a) c_i(t) S_i(a) f_i(0.5, t-a) da. \tag{6.9}$$

If the invading population is very small in comparison to the resident population, then two assumptions can be made. First, that the competition function

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[1] If the competition functions are different but both depend on the Adult biomass variable and are monotonically a very similar result is obtained.

depends only on the resident population as $A_i$ is very small. Secondly that the linear approximation

$$f_i(a,t) \approx e^{\lambda t} \tag{6.10}$$

can be made. Hence,

$$e^{\lambda t} = \int_{0.5}^{50} \beta_i p_i(a) w_i(a) c_i(A_r^\star) S_i(a) e^{\lambda(t-a)} da \tag{6.11}$$

thus,

$$1 = \int_{0.5}^{50} \beta_i p_i(a) w_i(a) c_i(A_r^\star) S_i(a) e^{-\lambda a} da. \tag{6.12}$$

This equation can now be solved for $\lambda$. If $\lambda$ is positive then the invading population will increase, otherwise it will decrease to extinction.

The solution of 6.12 is made easier by noting that all functions involved in the integral are non-negative. Hence, from the second mean-value theorem for integrals,

$$1 = e^{-\lambda h} \int_{0.5}^{50} \beta_i p_i(a) w_i(a) c_i(A_r^\star) S_i(a) da \tag{6.13}$$

where $h$ is some value between 0.5 and 50. Thus if

$$1 > \int_{0.5}^{50} \beta_i p_i(a) w_i(a) c_i(A_r^\star) S_i(a) da \tag{6.14}$$

$\lambda$ is negative and hence the invading population dies out, and vice versa.

This inequality can be rewritten so that if

$$c_i(A_r^\star) < \frac{1}{\int_{0.5}^{50} \beta_i p_i(a) w_i(a) S_i(a) da} \tag{6.15}$$

then

$$A_r^\star > c_i^{-1}\left(\frac{1}{\int_{0.5}^{50} \beta_i p_i(a) w_i(a) S_i(a) da}\right) \tag{6.16}$$

as the competition function $c_i$ is a decreasing function. Thus the invading population dies out. But, from equation 4.11

$$A_i^\star = c_i^{-1}\left(\frac{1}{\int_{0.5}^{50} \beta_i p_i(a) w_i(a) S_i(a) da}\right) \tag{6.17}$$

thus

$$A_r^\star > A_i^\star \tag{6.18}$$

when the invading population is unsuccessful. Similarly if

$$A_r^\star < A_i^\star \tag{6.19}$$

then the invading population will take over. Therefore the equilibrium adult biomass is a fitness function for the model. Any population which maximises equilibrium adult biomass will be uninvadable by other populations.

Note that if two populations have the same competition coefficient and equilibrium adult biomass then a coexistence equilibrium exists as

$$\frac{\beta_r A_r^\star}{R_r^\star} = \frac{\beta_r A_r^\star}{\beta_r c^\star(A_r^\star) A_r^\star} = \frac{1}{c^\star(A_r^\star)} = \frac{1}{c^\star(A_i^\star)} = \frac{\beta_r A_i^\star}{\beta_i c^\star(A_i^\star) A_i^\star} = \frac{B_i A_i^\star}{R_i^\star}.$$

Furthermore, if the competition constants are equal for both populations, then if two populations have a coexistence state, such that

$$\frac{B_r A_r^\star}{R_r^\star} = \frac{B_i A_i^\star}{R_i^\star} \tag{6.20}$$

then as above

$$\frac{B_r A_r^\star}{R_r^\star} = \frac{1}{c^\star(A_r^\star)} = \frac{1}{e^{A_r/K}}. \tag{6.21}$$

Thus

$$\frac{1}{e^{A_r/K}} = \frac{1}{e^{A_i/K}} \tag{6.22}$$

implying the equilibrium adult biomasses are the same. Hence, the populations are equally fit.

Notice that the previous section showed it is possible for a double population equilibrium to exist without the equilibrium adult biomasses being the same, however this requires the competition coefficients to be different. In order for such an equilibrium to be achieved both populations would need to be established at large numbers or the population with larger equilibrium adult biomass would have to be the invading population.

A final consideration is that random noise, or stochasticity, has not been included in the model. Stochasticity has a large effect for small populations, and in the real world, a mutant will often not be able to invade as its population becomes extinct due to stochastic variations. Thus my results will represent best case scenarios for the invading fish, and the phenotype of the population can be expected to change more frequently than if stochastic effects were included.

The next chapter shall use this measure of fitness to analyse which life-history parameters have the most effect on the population. After such an analysis it is possible to predict which evolutionary paths are most likely to be followed, and to gain an appreciation of the impact humans have on the population.

# Chapter 7

# Finding the Best Fishing Policy

## 7.1 Introduction

When examining any model, a natural question to ask is how the parameters affect the outcome of the model. The study of the change in model outcome (or yield) versus the change in parameter is known as sensitivity analysis. There are a variety of methods available to examine the sensitivity of models. The best method may often differ between types of models and the situation in which the model is studied. The rewards of performing a sensitivity analysis are clear. An understanding of the importance of parameters in terms of the yield of the model gives information on which parameters need to be most accurately determined in order to model the real world accurately. Such an understanding also lets us determine which parameters can be changed to improve yield, output or population levels for the situation we are modelling

It is this use of sensitivity analysis which shall be examined in this chapter. If we can discover which elements of the model give the best yield in terms of fitness, we can establish which life history elements most effect the population. In turn this shows which evolutionary paths will be most favourable to the population.

To do this seven of the life history parameters are examined to see which has the biggest impact on the population. The parameters used are the four weight parameters $(b, g_2, w_\infty, g_1)$, two proportion mature parameters $(p_x, p_y)$, and fertility parameter ($\beta$). Following this, the fishing mortality to which the population is subjected is considered, and the aspect of mortality which impacts the population the most is determined. This shall be done by looking at three elements controlling mortality, namely the initial length at entry to the fishery (controlled mainly by mesh size), the overall fishing mortality level (controlled mainly by effort), and finally the length at peak mortality (controlled by the type and mix of gear used for fishing). The results will let us see how fishing pressure can be reduced most effectively, in terms of both increasing fitness and yield of the population.

### 7.1.1 Methods of Sensitivity Analysis

There are many different methods for looking at the sensitivity of models. One general approach is to look at local sensitivities, thus examining narrow bands of values around the given parameter value. This measures the effect of small parameter changes. Classical sensitivity analysis uses $\delta y_i/\delta k_j$ as a measure of sensitivity of the variable or model output $y_i$ to the parameter $k_j$ (Swartzman and Kaluzny 1987). One standard measure used this way, is the normalised local sensitivity matrix which has entries

$$S_{i,j} = \frac{k_j}{y_i}\frac{\delta y_i}{\delta k_j}$$

where the coefficients are the linear estimate of the percentage change in the variable $y_i$ caused by a one percent change in the parameter $k_j$ (Turányi and Rabitz 2000). I, however, am interested in looking at sensitivity to a wide range of values. Thus it is not practical to use such methods, as the number of calculations to cover the full range for each parameter of interest would be excessive. In general, using such a method for sensitivity analysis in an ecological model is untenable (Swartzman and Kaluzny 1987) as many such models have discontinuities in their functions. The models in this thesis are no different, in that the growth rates of the functions used both in the main model and in the alternate models have discontinuities. Thus the standard approach to sensitivity analysis is not useful in our situation.

Global sensitivity analysis, on the other hand, examines the reaction of the model to large changes in parameter values. A standard idea used in global sensitivity analysis is to use OAT (one at a time) designs. In such a design only one variable is changed at a time. These methods are frequently used in screening to establish which parameters should be included or excluded in a model. Generally in such designs a standard value for each parameter is taken (such as the value given in the literature) and two extreme values are chosen. The differences in outputs between the standard and two extreme values are used to discover which parameters have the most importance (Campolongo, Kleijnen, and Andres 2000). One such type of design is the Morris OAT design, labelled a global sensitivity experiment in Campolongo et al. (2000) as they cover the entire space over which factors may vary. To summarize the ideas used in this method, if there are k factors, and if $\Lambda$ is a predetermined value, then the elementary sensitivity of the i'th factor is

$$d_i(x) = \frac{[y(x_1, ..x_{i-1}, x_i + \Lambda, x_{i+1}, ...x_k) - y(x)]}{\Lambda}$$

where $x$ is the vector of parameter values at their normal values, and $y(x)$ is the output of the model. For each factor a range of elementary factors may be computed where $\Lambda$ takes on values $\frac{1}{p-1}, \frac{1}{p-2}, ..., 1$ or a scaled version of this.

It should be noted that for a model with many parameters, such as a weather or global warming model, screening methods should be used before any sensitivity analysis is performed, as there can be hundreds of parameters. By using OAT designs, or other methods such as sequential bifurcation (Bettonvil and Kleijnen 1996) a small group of factors can be found which have the most effect on the outcome of the model. Hence, a relatively small group of factors can be examined fully, without fear that an important factor has not been considered.

The models of this thesis have a relatively small number of parameters hence prescreening is unnecessary. However, the method with which sensitivity is examined could cope with large numbers of parameters, if a small fractional design were used.

### 7.1.2 Introduction to Factorial Design

Factorial design can be thought of as an extension of simple one at a time parameter designs. Instead of testing for the effect of one parameter at a time, several different parameters are considered concurrently. The result is a significant saving in experimental time and potentially cost, especially if error in experiments must be taken into consideration. This method also has the advantage that if any interactions between parameters are important, these effects can be estimated. For OAT designs this is impossible as only one parameter is ever changed at a time.

In order to create a factorial design several questions must be answered. For instance one must know how many parameters (or factors as they will be called in the design) are of interest, and how many different levels of each factor are of concern. In other words, are the effects of just high and low values of a factor important or is it necessary to examine the effect of a range of values? The answers to these questions depend on the model in which the parameters are used and whether a parameter's effect is linear or more complicated. Once these questions have been answered a design can be created which has experimental runs for each possible combination of factor levels.

The most commonly used factorial designs have factors with either two or three levels. This is due to problems with the size of a design. For instance, to have 6 different parameters at 2 levels each, a full design will have $2^6 = 64$ different factor level combinations for which experiments must be run. If each factor were to have 4 levels, this would be 4096 runs, requiring substantially more time and money to complete the experiment. In table 7.1 a design is shown for one of the most simple cases, a design where there are three factors, each tested at two levels. The full design matrix for this experiment has $2^3$ combinations of the factors A, B, and C. We will label high values of a parameter with $+$ and low values with $-$. For each parameter combination a run or multiple runs, when there is a source of error in the results, are performed. The advantage of a full design is that all parameter interactions can be estimated from the results.

The main effect for A is estimated from the table using the average of results

Table 7.1: A Simple 3 factor 2 Level Design: *This design has three factors; A, B, and C. These are each tested at two levels, - and +, giving a total of 8 runs in the design*

| Run | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|
| A | - | + | - | + | - | + | - | + |
| B | - | - | + | + | - | - | + | + |
| C | - | - | - | - | + | + | + | + |
| Yield | 728.45 | 675.75 | 771.85 | 705.5 | 714.5 | 642.05 | 766.75 | 677.25 |

when A is high minus the average of results when A is low (Swartzman and Kaluzny 1987). If the yield is represented by $Y$ and $A-$ and $A+$ used to show the level of $A$ this can be written as

$$\bar{Y}_A = \bar{Y}_{A+} - \bar{Y}_{A-} = 675.1375 - 745.3875 = -70.25.$$

For the interaction AB, the effect is calculated using the effect of A when B is high minus the effect of A when B is low. This gives the following table of effects (table 7.2). Thus factors A and C have negative effects on yield, while BC is the only interaction effect which is positive. Notice also that the main effects are much larger than the two way interaction effects which are in turn larger than the three way effect.

The calculation of effects can also be done by noticing that for the factors, (A, B, C) that the effect is found by multiplying the results row by the row of the factor of interest, summing, and then dividing by the number of plus signs. Similarly the effects of interactions can be found by multiplying the rows of the factors involved times the result row. Thus for interaction AB the row for A is

Table 7.2: Effects of a 2 Level, 3 Factor Design

| | A | B | C | AB | AC | BC | ABC |
|---|---|---|---|---|---|---|---|
| Effect | -70.3 | 40.1 | -20.2 | -7.6 | -10.8 | 3.5 | -0.8 |

Table 7.3: A Simple 2 Level, 3 Factor Fractional Design: *This design is created by using only runs where the level for the interaction ABC is +*

| | A | B | C | AB | AC | BC | ABC | Result |
|---|---|---|---|---|---|---|---|---|
| 2 | + | - | - | - | - | + | + | 675.75 |
| 3 | - | + | - | - | + | - | + | 771.85 |
| 5 | - | - | + | + | - | - | + | 714.5 |
| 8 | + | + | + | + | + | + | + | 677.25 |

multiplied by that for B and then by the results row. The sum is then taken and divided by four to give the interaction effect (Campolongo and Saltelli 2000)

In some cases when the number of factors in a design is large the full design is too big to be used. For example, the resulting experiments may be too costly or the resultant number of data collected might be too great for a computer to handle. In this case fractional factorial designs may be used. These designs assume that all interactions of a certain size have negligible effects. For instance, a half or $2^{3-1}$ design can be created for the design introduced in table 7.1 by confounding interactions with main effects. This is done by dividing the table in two by whether $A \times B \times C$ is positive or negative, essentially confounding this interaction with the overall mean. This gives a new design as shown in table 7.3

If the same logic is followed as above then the effect of A is now found to be -66.675, which is also the effect found for the interaction $B \times C$. In fact, if multiplication under mod 2 is considered such that $A^2 = 1$ then we can calculate which effects are aliased by multiplying by ABC, such that A is aliased with BC and (B,AC) and (C,AB) are also aliased pairs. We also note that these pairs have the same order of signs in table 7.3. Hence the parameters have been aliased with two way interactions which are assumed to be negligible in comparison to the effect of the parameter itself. If the other half of the table had been used for the fractional design, estimates of the effects would be different. The same aliases would be used, only the sign of the effects of the single parameter and its aliased interaction would be different.

The estimates of effects for the fractional design are given in table 7.4. We notice that the signs of effects have remained the same, as has the order of importance. The effect of B is, however, noticeably lower, as the confounding with AC has had a substantial effect.

Table 7.4: Fractional Design Effects

| | A | B | C |
|---|---|---|---|
| Effect | -66.675 | 29.425 | -27.925 |

Some authors have advocated using ANOVA (analysis of variance) methods to assess sensitivity when using fractional design methods (Swartzman and Kaluzny 1987). However, as in the case of deterministic simulation (such as in our model) there is no random component, it makes no sense to perform statistical tests. Furthermore the values computed in an ANOVA table are all monotone functions of the effects calculated earlier (Swartzman and Kaluzny 1987). Thus only the effects shall be considered in this thesis.

### 3 Level Factorial Designs

When designs are expanded to having three levels for each parameter instead of two, a slightly more complicated situation unfolds. Designs become bigger much more quickly as even with only three factors, twenty-seven experiments are required to do a full three level design. If each experimental run or simulation is costly, it is obvious why a design with only eight runs might be preferred. Although designs for two factor levels are well documented, it is more difficult to find designs listed for three level designs. Some authors such as Connor and Zelen (1959), Grove and Davis (1992), Gardiner and Gettinby (1998), and Hicks (1993) do, however, list three level designs.

Fractional designs are also more complicated in their alias structure, as now each interaction consists of multiple parts. For example, for two factors A and B, we can list two AB interactions, AB and $AB^2$, following the practice of including only interactions where the exponent of the first term is one. The interactions which generate the design shall be called generators as in Connor and Zelen (1959) (thus in the earlier case where we looked at a two level design, the generator of the fractional design was ABC). Following the explanation of Connor and Zelen (1959), we denote the generators as $(G_1, G_2, \ldots, G_p)$ and let $(\lambda_1, \lambda_2, \ldots, \lambda_p)$ be a vector of elements which take on the values 0,1, and 2. We call two such vectors $(\lambda_1, \lambda_2, \ldots, \lambda_p)$ and $(\lambda'_1, \lambda'_2, \ldots, \lambda'_p)$ equivalent if they have the property that $(\lambda_1, \lambda_2, \ldots, \lambda_p) = (2\lambda'_1, 2\lambda'_2, \ldots, 2\lambda'_p)$ modulo three. Then all expressions needed to form the alias system are obtained from $G_1^{\lambda_1}, G_2^{\lambda_2}, \ldots, G_p^{\lambda_p}$ using all the nonequivalent vectors $(\lambda_1, \lambda_2, \ldots, \lambda_p)$. As a final step the exponents associated with the generators are reduced modulo 3 such that the first generator has exponent 1 (Connor and Zelen 1959). Hence with $p$ generators, we have $(3^p - 1)/2$ non-equivalent expressions which form the alias structure when 3 factor levels are used. To find the quantities aliased with a particular effect, say A, we multiply each of these expressions and its square by A and reduce modulo three such that the leading letter of every expression has exponent 1 (Connor and Zelen 1959).

For instance, if a design is generated by the expressions $ABCD$ and $BC^2DEF^2$ then the fundamental identity required to create the aliases is

$$I = ABCD = BC^2DEF^2 = AB^2D^2EF^2 = AC^2E^2F.$$

Then the factor A would be aliased with all interactions in table 7.5. In this table we see that A is only aliased with three (or more) way interactions, which normally would mean that the estimates for the effect of A would be reliable even though they are confounded with other interaction effects.

Table 7.5: Alias Creation for Factor A

| | | | | |
|---|---|---|---|---|
| Identity | $ABCD$ | $BC^2DEF^2$ | $AB^2D^2EF^2$ | $AC^2E^2F$ |
| Alias | $AB^2C^2D^2$ | $ABC^2DEF^2$ | $ABDE^2F$ | $ACEF^2$ |
| Identity Squared | $A^2B^2C^2D^2$ | $B^2CD^2E^2F$ | $A^2BDE^2F$ | $A^2CEF^2$ |
| Alias | $BCD$ | $AB^2CD^2E^2F$ | $BDE^2F$ | $CEF^2$ |

The next difficulty is in talking about the effect of a parameter, how should an effect be defined? Effects shall be considered in more than one way. The simplest way is analogous to the situation where there are two levels, the effect of changing from one level to another. Hence three sets of effects can be found for each parameter; the effect of changing from low to medium level, medium to high level and from low to high level. In the case of the third comparison this is assuming that there is a linear growth from low to high level (Grove and Davis 1992). We shall also consider the grand average effect as in Hoggett-Jones (2001) which is an average of the effects between different levels.

Using this method we will examine the life history parameters to see which parameters have the most effect on the fitness, and hence equilibrium adult biomass of the population.

### 7.1.3 Taguchi's Design Method

The next issue will be to observe which elements of the fishing mortality curve have the most influence on the population. Three aspects were examined, the age at which fish are first caught, the length at which the peak in fishing mortality occurs and finally the level of mortality for all lengths which are caught. As mentioned in the introduction, these three aspects of the population can be controlled by changing the mix of gear used in the fishery, setting mesh sizes, and setting quotas or restricting areas from fishing.

This problem is examined by realizing that model parameters divide into two distinct groups. The life history parameters over which we have no control and the fishing parameters which can, at least theoretically, be completely controlled. This suggests that a Taguchi design can be used, as in Gardiner and Gettinby (1998), to examine the importance of fishing parameters.

Genichi Taguchi was a Japanese engineer who was interested in quality control in manufacturing. His use of experimental design and analysis revolutionized Japanese industry and has played a large part in its continued success. His methods are beginning to become commonplace with Western industry as well, and have become well known in the industrial world (Gardiner and Gettinby

1998). The benefits of running small designs, in terms of the savings in defective production and avoidance of costly experimentation are enormous. Taguchi methods have, however, been criticized for ignoring interaction effects as many designs advocated by Taguchi confound main effects with two way interactions.

Taguchi suggested that performance variation in industry came from two key sources, design parameter variables and noise variables. This first group contains all parameters which are controlled by the operator of the system, for instance in manufacturing such things as temperature or length of a process. The second group contains all parameters which are beyond the control of the operator. This idea can be used to build an experimental design using a control matrix for the design parameters and a noise matrix for the uncontrollable parameters. In the full design each set of values in the control matrix is tested at all levels of the noise matrix.

Thus, in our model as fishing mortality is set by humans, these parameters shall form the control matrix, while the life history parameters shall be used for the noise matrix, as these are uncontrollable. We shall compare effects of the different levels of the fishing parameters using the same methods as used for the life history parameters. However as well as observing the effect changing parameters has on equilibrium adult biomass, the effect on yield will be considered.

### 7.1.4 Examination of Sensitivity Method

The idea of using this form of sensitivity analysis is due in a large part to the thesis of my colleague Dr. Hoggett-Jones (2001). In his thesis he examines reprocessing techniques for nuclear fuel. He examines the impact of different elements of his model on different recycling options using the same methods as I have used to examine the impact of life history parameters.

It has been difficult to find papers which use the same type of sensitivity analysis in the biological arena. Two fisheries papers use a somewhat similar method, Finn, Idoine, and Gislason (1991) and Sampson and Yin (1998) although neither matches exactly the method implemented in this thesis. For both, factorial design plays a large part in the sensitivity analysis, although different methods have been used to create the designs, and sensitivities have been measured differently.

Finn et al. (1991) look at multispecies assessment and examine its sensitivities for 33 parameters in the MSVPA model (see chapter 2) and 29 parameters in the MSFOR[1] model. They use a 2 factor factorial design, $2^{62-55}$ determined by the fold-over method of Box and Draper (1987), as well as a central run with all parameters set to their average values. Axial or star[2] points are also added in order to look at two-way interactions. Sensitivities were calculated as the percentage change in the response variable cause by a 10% change in the parameter. Their results found that there was not great sensitivity of the MSVPA model to any of the MSVPA parameters used, while the predictive model could be very sensitive to fishing mortality rates, recruitment levels and fleet effort. In all they conclude that the MSVPA model is very robust.

Tsou and Collie (2001) use the same type of sensitivity analysis to test the MSVPA model they use to estimate predation mortality on the Georges Bank. They find that although the MSVPA outputs varied with small perturbations in input parameters, the variation was within 10% of the base run values.

Finally Swartzman and Kaluzny (1987) include an example of this method of sensitivity analysis in their book. They apply it to a phytoplankton model, using a half fraction of a two level design. Thus they run only sixteen runs of the full design's thirty-two. They use several different outcomes of the model to look at sensitivity, and find that the zooplankton grazing rate, prey half saturation, and their interaction are the most sensitive parameters.

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[1] MSFOR being the predictive counterpart of MSVPA

[2] Star runs have each parameter of $\pm\alpha = 128^{0.25}$ while every other parameter is set to the nominal value

## 7.2 How Do Life History Parameters Affect Population Fitness?

The work in this section is performed for seven different life history parameters as established in chapter 4. These are the weight growth parameters, $b, g_2, w_\infty$, and $g_1$, proportion mature parameters, $p_x$ and $p_y$, and the fertility parameter $\beta$.

For each design the fitness, or equilibrium adult biomass, is calculated for every included set of parameters levels. The results are then combined as in section 7.1.2 to find the effects. These effects are then shown in a graph which shows the difference in level between high and low levels, high and medium levels and medium and low levels. The grand average effects for each parameter are also examined.

The parameter levels used for the sensitivity analysis were felt to be sensible end points for possible parameter values and are given in table 7.6. The medium level values are rounded versions of the parameters fit in chapter 4. The extreme values were chosen using an 'ad hoc' method. Parameter values were checked to ensure they gave a positive equilibrium adult biomass when all other parameters were at their nominal values. The graphs of the life history functions were also checked to ensure that changes in the growth curves were not too extreme. Once the values had been chosen, tests were run to make sure that all models still

Table 7.6: Chosen Parameter Values for Sensitivity Analysis

| Parameter | Low | Medium | High |
|---|---|---|---|
| $b$ | 1 | 1.1 | 1.17 |
| $g_2$ | 0.24 | 0.26 | 0.28 |
| $w_\infty$ | 15.5 | 18 | 20 |
| $g_1$ | 0.6 | 0.73 | 0.85 |
| $\beta$ | 14.5 | 15.9 | 17.5 |
| $p_x$ | 0.0028 | 0.0036 | 0.005 |
| $p_y$ | 3.8 | 4 | 4.2 |

included two growth curves, and that these curves intersected.

Table 7.7: Grand Average Effects: *This table presents the average biomass (thousand tonnes) at the high, medium, and low levels. It also presents the effect of changing between levels, and the average over the three effects.*

| | $b$ | $g_2$ | $w_\infty$ | $\beta$ | $p_y$ | $p_x$ | $g_1$ |
|---|---|---|---|---|---|---|---|
| Average (-1) level | 494 | 141 | 152 | 218 | 201 | 184 | 291 |
| Average (0) level | 236 | 276 | 293 | 285 | 287 | 273 | 273 |
| Average (+1) level | 136 | 449 | 421 | 363 | 378 | 410 | 303 |
| Effect (-1) to (0) | -258 | 135 | 14 | 67 | 87 | 89 | -18 |
| Effect (0) to (+) | -100 | 172 | 128 | 78 | 91 | 137 | 30 |
| Effect (-1) to (+) | -358 | 307 | 268 | 145 | 179 | 226 | 12 |
| Grand Average Effect | -239 | 205 | 179 | 97 | 119 | 151 | 8 |

We will first look at the full design, which with seven parameters at three factor levels has 2187 runs. The equilibrium adult biomass was calculated for each run with the package Maple (Waterloo Maple Inc ), and when negative values were found these were set to zero in order to be realistic (as real populations cannot have negative numbers of fish).

We begin by looking at the grand average effect in table 7.7. Only the $b$ parameter has a constant negative effect (i.e. fitness increases with a decrease of the value of $b$), although the $g_1$ parameter does have a negative effect for the low to medium level. This can also be seen from Figure 7.1 which plots the mean adult biomass at the different levels for the different parameters. It is clear that the weight growth parameters for the older fish have the most impact on the fitness of the stock, with the population being fittest for minimal values of $b$, a fast rate of growth $g_2$ and a large maximum size.

In figure 7.2 the effects between levels are plotted. Notice that the order of parameters is the same as for the grand average effects. Once again it is clear that the parameter $g_1$ has a non monotonic effect on fitness, as the sign of the effect changes for the medium to low effect and high to medium effect. This

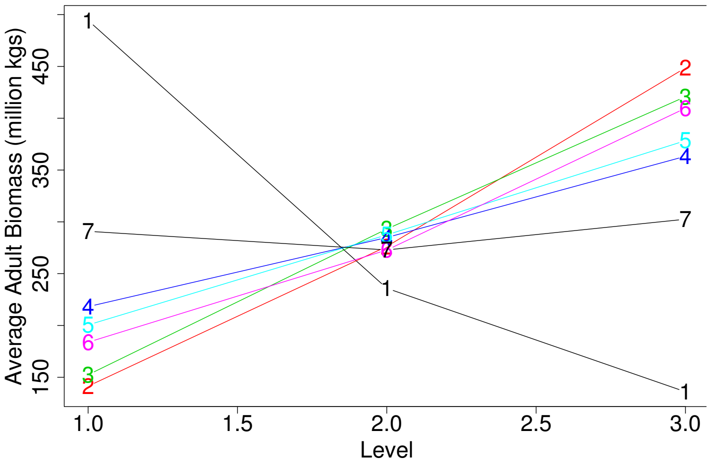
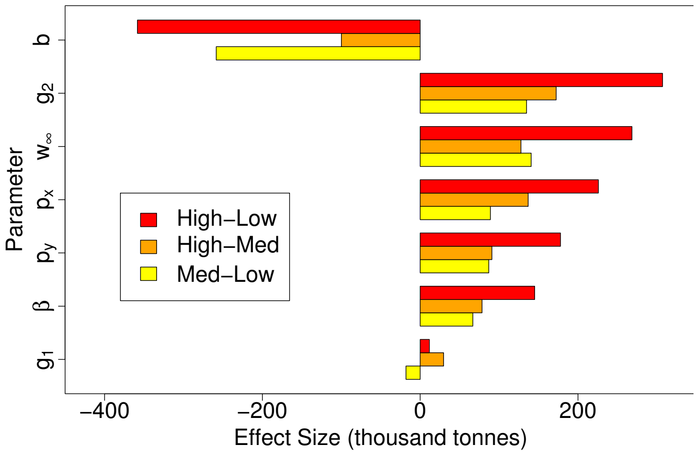


Figure 7.1: Average Responses at Parameter Levels. *Parameters are 1-*$b$ *(older weight parameter) 2-*$g_2$ *(older weight growth rate) 3-*$w_\infty$ *(maximum weight) 4-*$\beta$ *(fertility parameter) 5-*$p_y$ *(maturation parameter) 6-*$p_x$ *(maturation parameter) 7-*$g_1$ *(linear growth term for young cod)*

Figure 7.2: Effect plot: *Parameters are listed in the order of the size of the effect from High to Low level. We see that the three parameters for the growth of older fish are the most important.*



means that any change of sufficient size in the value of the linear growth rate for young fish will improve the fitness of the stock.

Examining the table and figure we note that the population increases its equilibrium adult biomass if its growth rate as an adult increases, it matures more quickly or if its juvenile growth rate either decreases or increases. The population also increases its fitness when fertility is increased.

These figures and tables suggest strongly that the weight parameters for older growth are most influential in the determination of fitness of the population. Therefore one would expect that an evolutionary path leading to increased growth rate would be beneficial for the population. However Oosthuizen and Daan (1974) suggest that North Sea cod may have already reached a maximal growth rate as they are the fastest growing cod in the Atlantic. Daan (1978) and Hempel (1978) agree with this view stating that there has been no significant change in growth rate of cod in the last 80 years though Thompson and Stokes (1996) states that there has been an increase in growth rate. There is also some evidence that populations are reducing their age at maturity (Jennings, Greenstreet, and Reynolds 1999).

### 7.2.1 Comparison of Full and Fractional Designs

We shall now compare two fractional designs with the full design of the previous section. The first of these is a $27^{th}$ design, and thus has only 81 runs, as opposed to the 2187 of the previous design. The second is known as the $L_{27}(3^{13})$ Taguchi design and has only 27 runs.

The first design is taken from Connor and Zelen (1959). We assign letters to factors as follows; A is $b$, B is $g_2$, C is $w_\infty$, D is $\beta$, E is $p_y$, F is $p_x$ and G is $g_1$. The design is built using the interactions

$$I = ABCDEF^2G = BC^2EF^2G = ABCEG^2$$

and aliases can be found by multiplying factors or effects by these three interactions and their multiples. This design has the advantage that all individual parameters are measurable (i.e. not aliased with a two way interaction) as are

Table 7.8: $L_{27}(3^{13})$ Aliases with Two Way Interactions: *The labels used in the design for parameters are given in brackets. We see that the three older weight growth parameters are aliased with 2 two-way interactions, while the other four parameters have 3 two-way interaction aliases*

| Effect | Alias | Alias | Alias |
|---|---|---|---|
| $b(A)$ | $p_x g_1^2(FG^2)$ | $\beta p_y(DE)$ | |
| $g_2(B)$ | $\beta p_x^2(DF^2)$ | $p_y g_1^2(EG^2)$ | |
| $w_\infty(C)$ | $p_y p_x(EF)$ | $\beta g_1(DG)$ | |
| $g_1$(G) | $bp_x(AF)$ | $g_2 p_y(BE)$ | $w_\infty\beta(CD)$ |
| $\beta(D)$ | $bp_y(AE)$ | $g_2 p_x(BF^2)$ | $w_\infty g_1(CG)$ |
| $p_x$(F) | $g_2\beta(BD)$ | $w_\infty p_y(CE)$ | $bp_x^2(AG^2)$ |
| $p_y$(E) | $b\beta(AD)$ | $w_\infty p_x(CF)$ | $g_2 g_1(BG^2)$ |

the following list of two way interactions $AB, AC, AE, AG^2, BC^2, BD$, $BE^2$, $BF^2, BG^2, CD, CE$,$CF, CG$, $DE^2$, $DG, EF^2$, $EG$, and $FG^2$.

The second design is taken from Gardiner and Gettinby (1998) and is essentially a $81^{st}$ fractional design. It can be generated with the identity

$$I = BCDE = CD^2E^2F^2G^2 = ACD^2E^2G = ABCE^2F^2G.$$

Of course, with increased fractionization of design, more interactions must be aliased and in this design some two way interactions are aliased with one way interactions. In table 7.8 all two way interactions which are aliased with main effects are listed. As mentioned before, this is a failing of Taguchi design as if interactions are important, confounding them with main effects will change the results.

Before running this design we look at the interaction effects from the full design. In figures C.1 and C.2 in Appendix C we see interaction plots for all 7 parameters. In figure 7.3 we reproduce the graphs which include the parameter $g_1$. This is the only parameter which shows evidence of notable two way interactions. When the two-way interaction effects for $g_1$ were found all were small

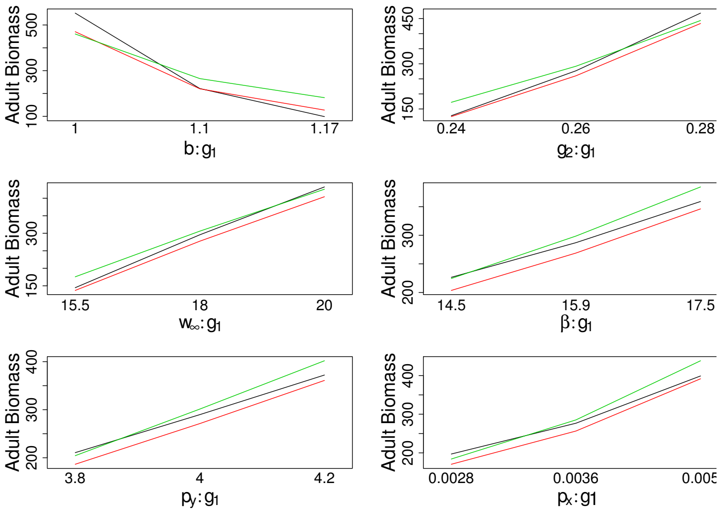


Figure 7.3: Interaction Plots. *The black line is the low level, red the medium level and green the high level of the parameter $g_1$. Adult Biomass is given in thousands of tonnes.*

with comparison to the effects found for other main effects, although all were close in value to the $g_1$ effect. However none of these effects is aliased with the $g_1$ effect in the $L_{27}(3^{13})$ design, and it would be expected that they would have little impact on the effect sizes found with this design.

We now examine the grand average effects found in the fractional designs in table 7.9. The three most important parameters have all stayed in the same order of importance, while the young growth parameter has remained the least important in all cases. The relative order of the fertility and proportion mature parameters has changed for the smallest design.

Table 7.9: Grand Average Effects for Fractional Designs

| | $b$ | $g2$ | $w_\infty$ | $\beta$ | $p_y$ | $p_x$ | $g_1$ |
|---|---|---|---|---|---|---|---|
| Full Design | -239 | 220.6 | 205 | 97 | 119 | 151 | 8 |
| $\frac{1}{27}$ design | -249 | 213 | 177 | 101 | 121 | 146.0 | 9 |
| $L_{27}(3^{13})$ | -260 | 205 | 180 | 97 | 141 | 96 | 4.5 |

Looking at the plots of effects between levels (figure 7.4 ), we observe that the order of high to medium effect and grand average effects remains the same for each separate design, thus the results of the grand average effects are replicated.

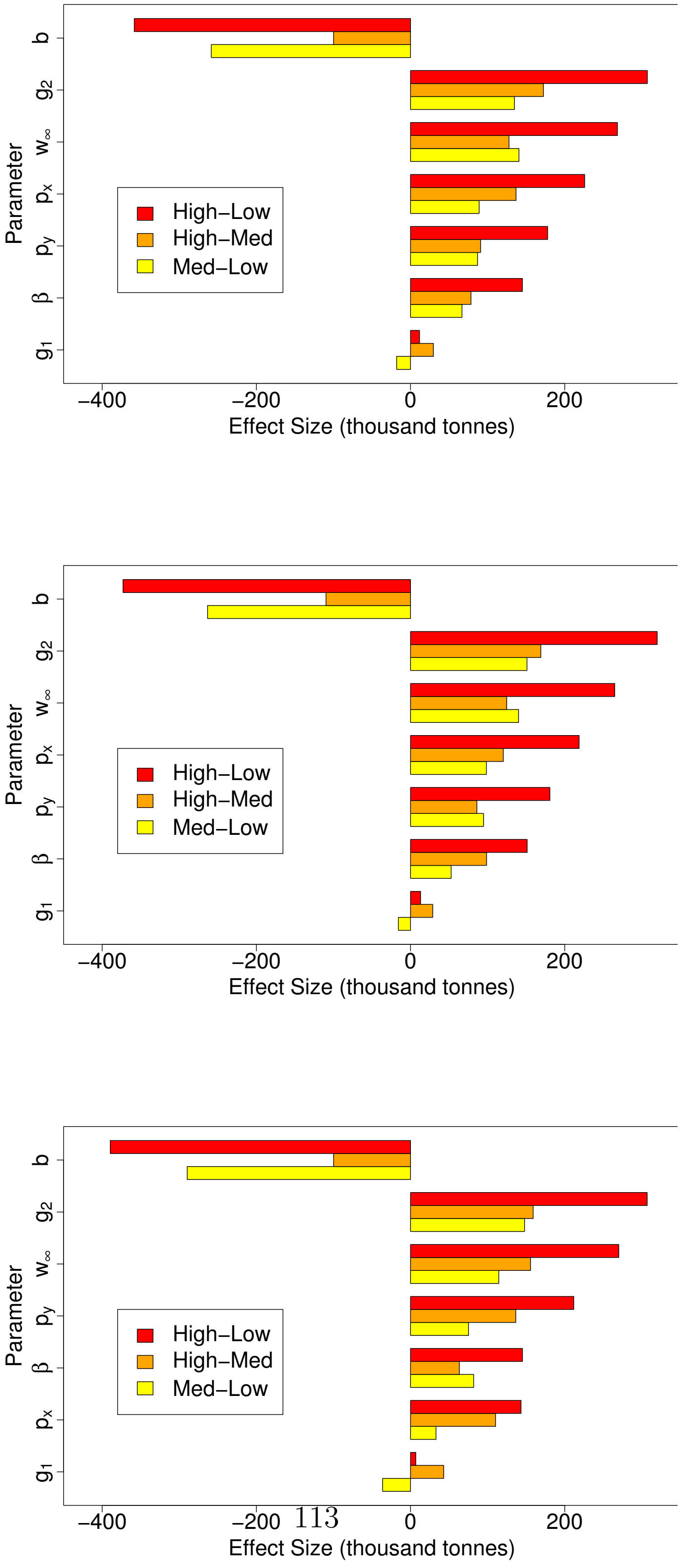
The first fractional design represents a great saving in time and effort to achieve virtually the same estimates of effect size and relative importance of factors. If the aim of the analysis is to find the most important factor (or factors) the smaller design ($\frac{1}{27}$) could be useful as it provides even larger savings in time (and possibly cost) and is fairly accurate for the larger effects. The $L_{27}(3^{13})$ design should, however, be used with care. As shown earlier, this design confounds two-way interactions with main effects, and thus there is great potential for misleading results if sufficient care is not taken in the assignment of factors in the design. Therefore, using this design, unless there is already some knowledge of what the importance of two-way interactions is, can be deceptive.

The one remaining question is what the sensitivity means in terms of the population. Simulations were run to give an approximate idea of the importance of parameters in terms of how long it takes a fitter population to dominate the community. For example, when the $b$ parameter is changed from 1.1034 to 1, a change of approximately 9.3%, an invading population starting from a 5 year introduction of age 6 month fish at a constant rate, causes the resident population to become extinct in just 360 years. Whereas when the $w_\infty$ parameter is changed by almost 13% it takes 400 years for the invading population to overtake the resident population in adult biomass. Hence, the larger the effect on fitness, the quicker a population with such a parameter change will dominate the community.

### 7.2.2 Implications for the North Sea Cod

This section has shown that the population is not at a maximal fitness level, in that relatively small changes in several life history parameters could have a beneficial effect on the population. If a mutant were to evolve with favorable parameters, this population could completely dominate the population within a relatively short period of time. For instance a population where all parameters

Figure 7.4: Equilibrium plots: *The top graph shows the effects for the full design, the middle graph is the* $\frac{1}{27}^{th}$ *design, while the third graph shows the effects for the* $L_{27}(3^{13})$ *graph.*

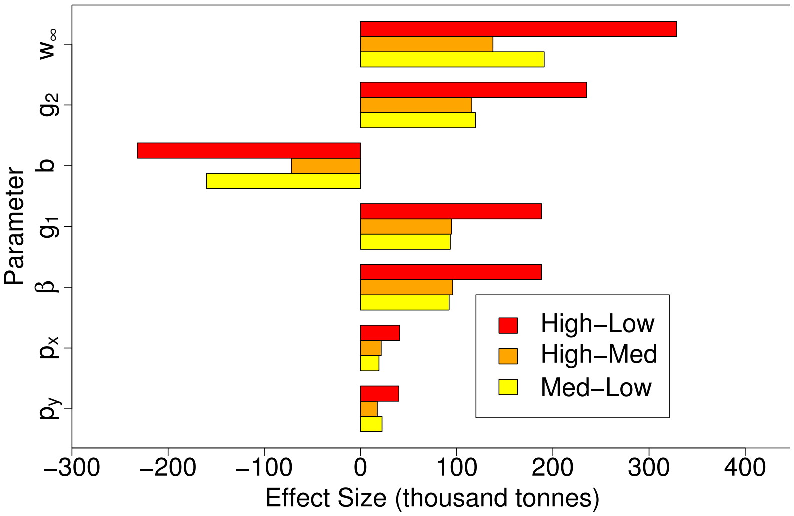


had improved slightly managed to completely extinguish the resident population in 415 years, and be the dominant population in just 260 years. Other mutants, with less favorable parameter changes, invading the region could lead to long periods of polymorphism due to the slow rate of increase of the mutant population. This means it is possible to have situations where many populations with different characteristics can coexist for long periods of time, even for thousands of years. Although, as seen with the first example where $b$ changed, life history parameters may change enough that the possibility of parameter change should be considered in management decisions, and that data on growth and maturation should be regularly updated.

I have shown that the adult growth parameters have the most effect on adult biomass, and hence the fitness of the population. As such we would expect that the most favourable evolutionary path for the population to follow would be for the population to increase its growth rate for adults. The $b$ parameter seems to be the most beneficial of these three parameters as it has a comparatively larger effect on the youngest adult fish than the other weight parameters. It is these younger mature fish which are most important to the population when there are high levels of mortality, such as those inflicted by the North Sea fishery (O'Brien, Fox, Planque, and Casey 2000). The young growth parameter has a non monotonic effect, suggesting that growing either more slowly or more quickly at this stage of life is beneficial, in one case delaying the onset of high fishing mortality until some fish have matured, and in the other helping to minimize the time spent enduring the highest fishing mortality.

The two proportion mature parameters follow the older growth parameters in importance. The exponential term ($p_y$) is found to be the less important of the two, perhaps because it has a mixed effect. It lowers the percentage mature below the age of one, while increasing the percentage mature above this age, while the multiplicative parameter ($p_x$) increases maturity over all ages.

Figure 7.5: Effect Plot for Model with No Fishing: *The four growth parameters are now the most important factors. Notice that the young growth parameter* $g_1$ *now has a positive effect for the medium-low effect*



## An Unfished Population

As a comparison, the sensitivity of the model without fishing is studied, to illustrate the impact of fishing on the model.

The four weight parameters are the most important factors, with the older growth parameters being more important than the young growth. The order of importance of the older growth parameters has changed with the maximum weight being the most important factor in a fish's life. As fish now are able to live much longer lives this is to be expected, as heavier fish produce far more eggs, and the longer life span allows fish to achieve these heavier weights. The young growth parameter has increased in importance and now has only a positive effect. This is as there is no longer an advantage to growing slowly as a juvenile because natural mortality rates decrease with size.

The fertility function is almost as important as the young growth parameter and has a larger effect on the population than under the fishing model. The proportion mature parameters are now the least important, having very little effect. As the lifespan of the fish under the unfished model is much longer, under all values of these parameters a sizeable number of fish will reach maturity, hence removing the impact of changing the rate of maturation.

This shows that although the fishery does have an effect on the order of importance of parameters, there is only one case in which there is a change in how a parameter will benefit a population, namely the $g_1$ parameter. Fishing also produces more pressure on the population. An unfished population with all parameters set at slightly more advantageous levels takes roughly 1000 years to have a larger population than the resident population and approximately 2000 to completely dominate, around five times longer than in the model where the population is fished. Thus we should not be complacent in our examination of the impact of world fisheries, as our actions do have a great impact even if the results are not immediately evident.

## 7.3 Robustness of Sensitivity Results

I proceed to observe what happens if the alternate models for growth and maturity mentioned in chapter 4 are used. By examining the results for these models it is possible to judge if the sensitivity of parameters is dependent on the model choices made. Thus to see whether the different aspects of life history have the same importance no matter how individual life history functions are modelled.

### 7.3.1 Alternate Functions for Proportion Mature

I begin with the four alternate functions for proportion mature. Only one of them, the first cumulative gamma distribution, involved two parameters for its function for proportion mature. The parameter values used for the analysis are the same as for the main model, except for those given in table 7.10. For values in this table, the medium values are again rounded values of the parameters fit in chapter 4 with extreme values being chosen on an ‘ad hoc’ basis. The only

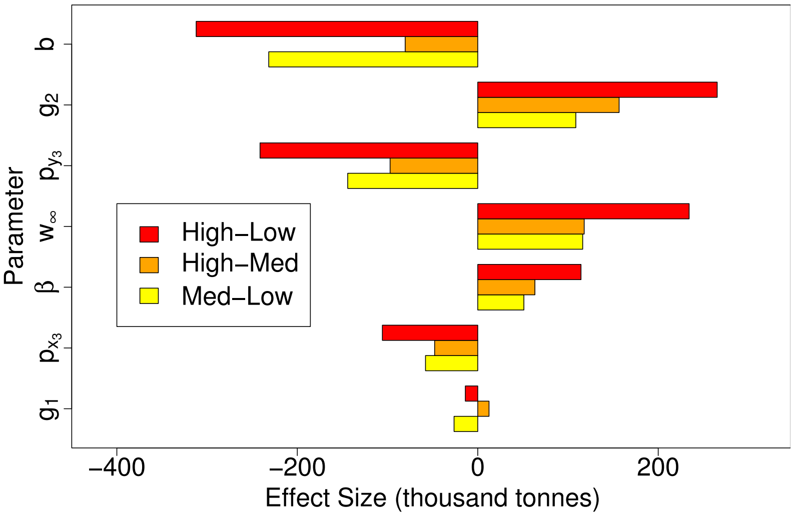
Table 7.10: Parameter values for Alternate Proportion Mature Models: *For each model the parameters for proportion mature needed to be changed. Also in one case the fertility parameter $\beta$ had to be changed in order to examine a parameter region where the population was viable*

| Parameter | Low | Medium | High |
|---|---|---|---|
| Concurrent Maturation | | | |
| $p_{x_1}$ | 3.5 | 3.75 | 4 |
| $\beta$ | 18 | 19.5 | 21 |
| Exponential maturation | | | |
| $p_{x_2}$ | 0.22 | 0.25 | 0.28 |
| Gamma(3) maturation | | | |
| $p_{x_3}$ | 0.55 | 0.61 | 0.67 |
| $p_{y_3}$ | 1.7 | 2 | 2.3 |
| Gamma(4) maturation | | | |
| $p_{x_4}$ | 0.9 | 0.95 | 1 |

exception being the $\beta$ parameter for the concurrent maturation model where values were chosen to have the same range as for the other models, only at high enough values to ensure that a sufficiently high number of parameter level combinations gave a viable population.

For this function the effects are plotted in figure 7.6 and very similar results are obtained as in figure 7.2. The parameters are not in the same order, the maximum weight parameter is now the fourth most important parameter, however the initial growth parameter is still the least important of the parameters. Note that the proportion mature parameter $p_{y_3}$ and the two growth parameters $g_2$ and $w_\infty$ are almost equally important. The probable reason for the increase in importance of the proportion mature parameters is that unlike the Weibull distribution, this distribution has no fish maturing before the age of $p_{y_3}$. This shows that, as before, a population is favored if it begins to mature at an earlier age, as then fish have more chances to reproduce.

Figure 7.6: Effect Plot for Gamma(3) Maturation

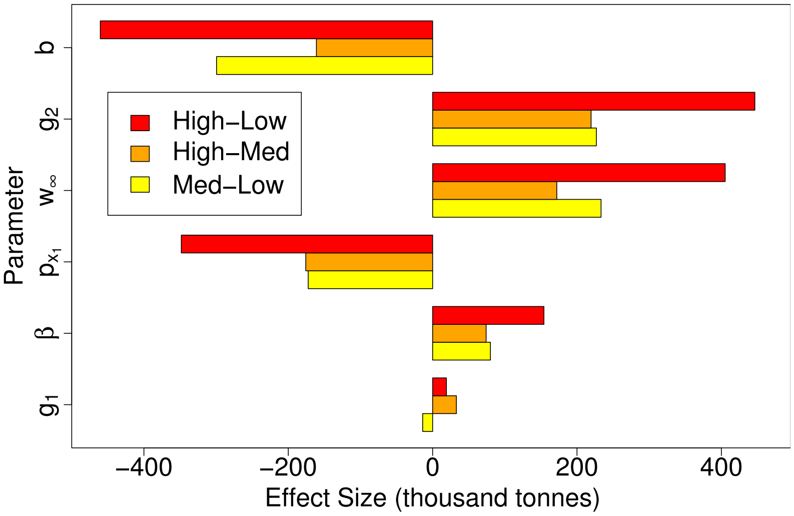


In Appendix C the fractional design plots for this model (figure C.3) are included. There is a change in order in that for both fractional graphs the maximum size parameter is once again the third most important. However this is not a significant change as the effect sizes for $w_\infty$ and $p_{y_3}$ are very similar. The fertility parameter and the other proportion mature parameter also change order. More seriously the $g_1$ parameter has changed the sign of its effects for the $L_{27}(3^{13})$ graph, suggesting that the two way interactions aliased with $g_1$ are non-negligible. It should be noted that for this model, $g_1$,$p_{x_3}$, and $p_{y_3}$ are the E,F,G factors respectively when interactions are considered.

The other three models for proportion mature have one less parameter, thus the full design has only 729 runs and different fractional designs are used. In table 7.10 we give the values used for any parameters which are different from the main model.

For the first function for proportion mature (figure 7.7), where all fish mature at the same age, the parameter effects are much the same as for the main model, with once again the parameter for proportion mature being almost as important

Figure 7.7: Effect Plot for when all fish mature concurrently: *The results are very similar to those found for the main model*



as the growth parameters $w_\infty$ and $g_2$. It should be noted that the values of $\beta$ used for this model were higher, as the minimum value of the fertility parameter needed for a viable population has increased. For the exponential function and the cumulative gamma(4) distribution models (figures 7.8 and 7.9) results are similar to that of the main model only the fertility parameter is relatively more important. For the exponential function fertility is the third most important parameter, although it must be noted that $\beta$, $w_\infty$, and $p_{x_2}$ give almost the same effect size. Notice that for this maturation function, fish begin to mature earlier, explaining the increased importance of this parameter. For the cumulative gamma(4) distribution the change is less dramatic, as the three older growth parameters are still clearly the most important, while $\beta$ is found to be slightly more important than $p_{x_4}$. It should also be noticed that for these two models, although young growth is still the least important parameter, it always has a positive as opposed to a negative effect. Thus there is no longer any advantage to growing slowly as a juvenile.

Figure 7.8: Effect Plot for Second Alternate for Proportion Mature

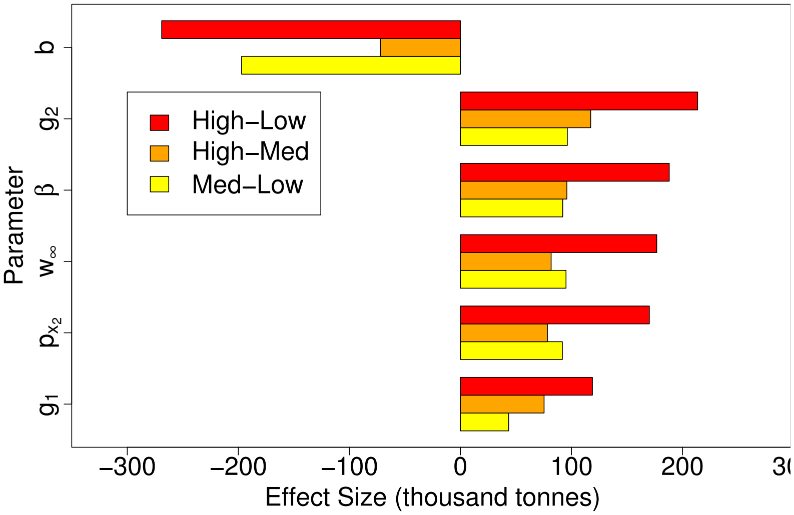
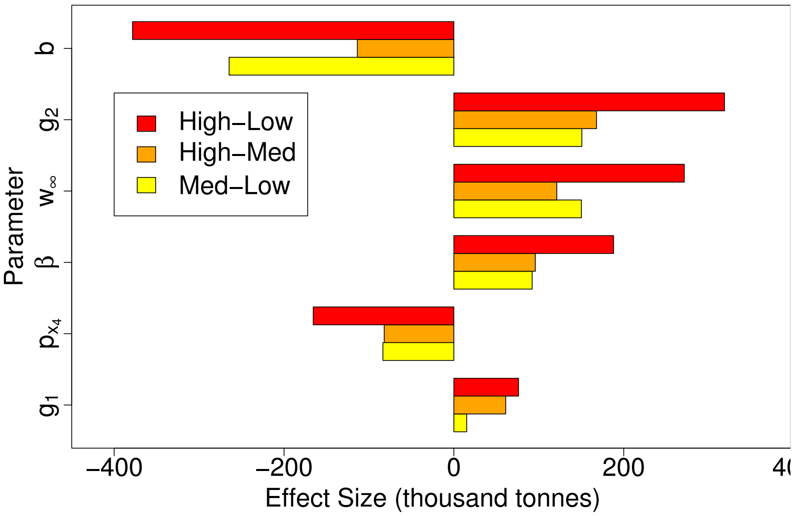


Figure 7.9: Effect plot for Gamma(4) Maturation



In Appendix C the effect plots for the fractional designs are given for these three models (figures C.4, C.5, and C.6). We note that in this case a ninth design from Connor and Zelen (1959) generated by the identity

$$I = ACDE = BC^2DE^2F$$

and a $27^{th}$ design generated by

$$I = ABD = ACE = CDF.$$

are used as the fractional designs. The ninth design predicts the effects extremely well and is never more than 2% out on the true value of the effect. It is often as little as a tenth of a percent out. A larger difference is seen with the $27^{th}$ fractional design, due to the increased confounding of main effects with interaction effects (in particular all main effects are now aliased with two-way interactions). When fish mature with an exponential distribution, this design sees the proportion mature and maximum weight parameter switch order of importance. However, for the case where all fish mature at the same age or via a cumulative gamma(4) distribution this design gives the same order of importance as the full design.

This model, in terms of sensitivity of parameters, is fairly robust to assumptions made about how the population matures. All of these models could be expected to follow similar evolutionary strategies and could be managed by a fisheries manager with the same guiding ideas. It should be noted that the current level of fishing would have to be lowered if it was believed that all fish matured concurrently, as under this model the population is in a non-viable state (see table 5.3). This model is not realistic, however, and has been included only as it is a common assumption in many models that fish mature concurrently.

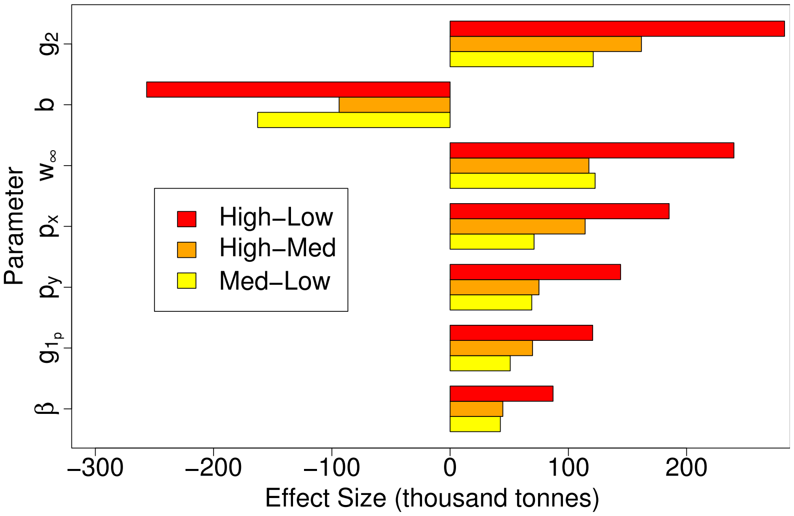
### 7.3.2 Alternate models for Growth

Next the different growth models will be considered. The sensitivities were found using seven factors in all cases even though with power growth model there are two parameters for young growth rather than one, giving a total of eight factors.

Table 7.11: Chosen Parameter Values for Alternate Growth Models

| Parameter | Low | Medium | High |
|---|---|---|---|
| Power Model | | | |
| $b$ | 1.03 | 1.1 | 1.17 |
| $\beta$ | 20.5 | 22 | 23.5 |
| $g_{1_p}$ | 0.78 | 0.86 | 0.94 |
| Logistic Model | | | |
| $w_{0_L}$ | 0.25 | 0.27 | 0.31 |
| $g_2$ | 0.55 | 0.6 | 0.666 |
| $w_{\infty_L}$ | 11 | 12.5 | 14.4 |
| $\beta$ | 20 | 22 | 24 |
| $g_1$ | 0.73 | 0.85 | 0.95 |
| Gompertz Model | | | |
| $G$ | 4.9 | 5 | 5.13 |
| $g_G$ | 0.36 | 0.38 | 0.407 |
| $w_{0_G}$ | 0.083 | 0.097 | 0.092 |
| $\beta$ | 20 | 22 | 24 |
| $g_1$ | 0.73 | 0.85 | 0.95 |

Figure 7.10: Effect Plot for Power Growth



In this case we used the multiplicative term of the young growth function for the sensitivity analysis. The levels for parameters which were different from those used for the main model are given in table 7.11.

We begin by looking at the effects found for the parameters as in figures 7.10, 7.11, and 7.12. These once again are for the full design. For the power model (figure 7.10) the only changes in parameters are for $\beta$ as this model requires a higher fertility level to be viable, while the parameter for young growth varies from 0.78 to 0.86 to 0.94. Once again the medium level is the value fit in chapter 4 while the exterior levels were chosen on an ‘ad hoc’ basis. The low value for the $b$ parameter was increased in order to obtain more viable combinations of parameters. The results of the sensitivity analysis are similar to the main model in that the three most important parameters are the older growth parameters. The $b$ parameter has decreased in importance and the effect size is just smaller than the $g_2$ effect size. The proportion mature parameters have the next largest effect. The fertility parameter now has the least effect, while the young growth parameter for this model has significantly more effect than it did when linear

Figure 7.11: Effect Plot for Logistic Growth

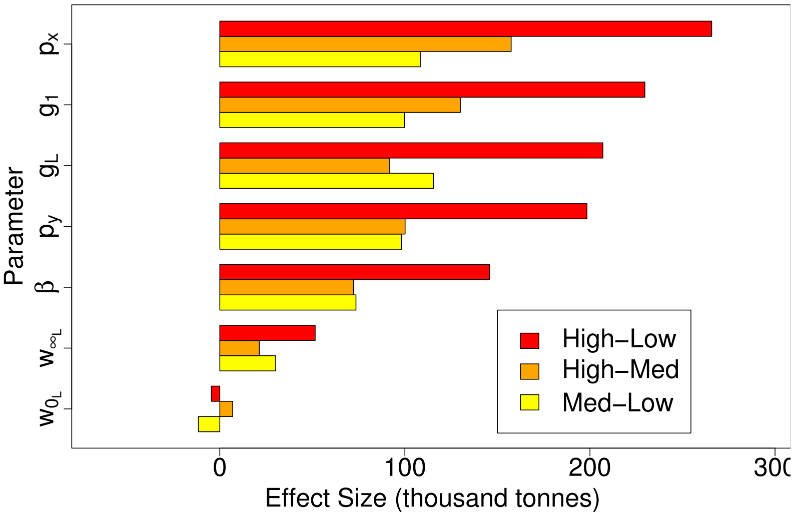
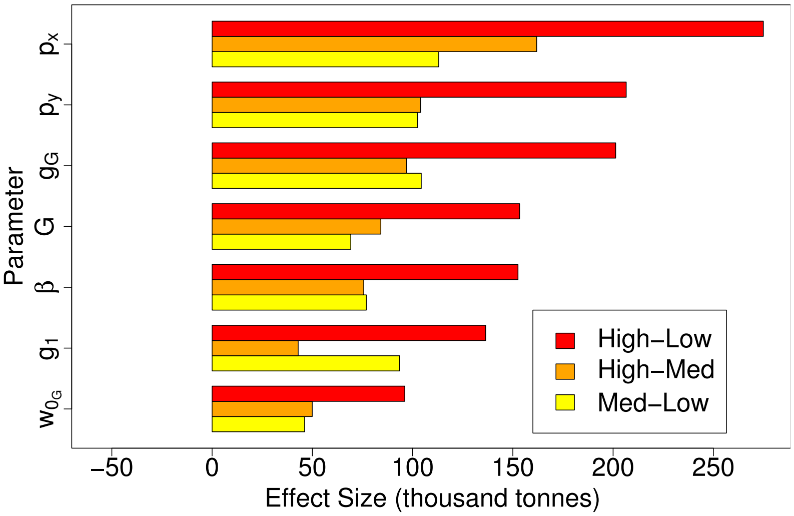


Figure 7.12: Effect Plot for Gompertz Growth



growth was considered. Note also that under this model there are only positive effects for this parameter, i.e. there appears to be no advantage in growing slowly, unlike the case for the main model.

For the Logistic growth model (figure 7.11) the growth parameters which were fit for older cod in chapter 4 have been used as the high levels of the growth parameters, rather than the medium levels as in the other designs. This is so that the two growth curve model could be kept, otherwise certain parameter level combinations required having only one growth curve over the lifetime of the fish. The fit for $g_1$ from chapter 4 provides a minimum level for this parameter for the same reason. The fertility parameter, $\beta$, had to be increased so that viable populations existed at all parameter levels. The results are quite different for this model, with the order of importance of parameters being the reverse of that for the main model. The proportion mature and young growth parameter are the most important, while two of the three older growth parameters are relatively unimportant. Notice that the young growth parameter now only has a positive effect as we do not include a value low enough to be beneficial to the population. The parameter $w_{o_L}$ now has a change in sign of effect, showing that the medium value is the least fit of the three end values tried.

The Gompertz growth model (figure 7.12) also differs substantially from the main model. The parameters chosen for this model were chosen in the same way as for the Logistic model. The two most important parameters are the proportion mature parameters followed by two of the growth parameters. The fertility parameter $\beta$ is almost as important as the second of these, $G$. The young growth parameter is no longer least important, and has quite a large effect size, with no negative effect being seen. The least important parameter is the $w_{0_G}$ parameter which is purely multiplicative in this model. It should be noted that there are significant interactions between parameters taking place. This can be seen in figure C.9, where the smallest fractional design gives very different results for the effects in comparison to the full design.

This shows that the model is not robust, in terms of life history sensitivities, with respect to the growth curve chosen for older fish. This sensitivity analysis was also tried for the Logistic and Gompertz models with the young growth being refitted when these older growth curves were fit. The ensuing sensitivity analysis, however, found the same results. The power growth model made far less of a change to the importance of various parameters, with the most important part of life history being how weight is added for older fish. One would, however, expect to observe quite different evolutionary paths being favourable for the two models where older growth has changed. It is noted once again that if growth in the North Sea is at a maximum, then all models would suggest that there would be a change in maturation, towards fish maturing at an earlier age. This is true for the Logistic and Gompertz growth models, even if the population is not at a maximal growth rate. This all suggests that how the population grows as older fish has a key effect on model outcome, and thus it is important this this growth function is modelled correctly.

### 7.3.3 Comparison with Results from Similar Work

Other papers have looked at the same problem for cod, using different methods (as mentioned in chapter 6). Thompson and Stokes (1996) who used a similar model only with a genetic component had very similar results, finding that fast growing fish were favored, unless a very large initial capture size was used or if mortality rates were extremely high (higher than those used in their study). This was also true for an unfished model. Similarly Blythe and Stokes (1990) found that harvesting promotes increased body size although their later paper, Stokes and Blythe (1991), did find a downward pressure on size at age. Whether body size is increasing for the population is debatable. As previously mentioned Oosthuizen and Daan (1974) speculated that North Sea cod may have reached a maximum growth rate, citing that no change has been seen in growth rate for the last 80 years (Daan 1978; Hempel 1978). However both Jennings et al. (1999) and Thompson and Stokes (1996) suggest that there is evidence that the growth rate for cod has increased, and Jennings et al. (1999) state that this is a general phenomenon for fishes of the North Sea.

There is also agreement with the seminal papers of Law and Grey (1989) and Stokes and Blythe (1991) that it should be expected that populations will mature earlier. This has already been observed for several different cod populations including Scotian shelf (Beacham 1983) and the North Sea populations (Jennings, Greenstreet, and Reynolds 1999; Rowell 1991; Oosthuizen and Daan 1974).

## 7.4 Reducing Fishing for Maximum Results

### 7.4.1 Construction of Design

The next concern is fishing mortality and how it effects the population. I used the Taguchi method of section 7.1.3 to search for this effect, by creating a noise design and a control design and then proceeding to test each run of the control design on every run of the noise design. The outcome variables were fitness, in the form of equilibrium Adult Biomass, and equilibrium yield from the population. Equilibrium yield is simply calculated by using the integral of the mortality at age times the equilibrium biomass at age over all ages included in the model.

The noise matrix consists of values of the parameters which are not controlled, namely the life history parameters. The smallest fractional design from the previous section is used, the $L_{27}(3^{13})$ design, which has 27 runs. Thus each set of control levels is studied for 27 underlying situations. The parameter levels used in the noise matrices are the same as those for the previous section.

The control matrix has three factors, the initial length at entry to the fishery, a term which increases or decreases fishing mortality over the fished age classes, and a term for the length of peak fishing mortality. A full design has been used for this matrix, with three levels, thus we have a $3^3$ or 27 run design. Therefore the analysis consists of 729 simulation runs. The parameter levels used are given in table 7.12. The fishing mortality curve for the population is altered using these different levels for the three parameters. This is done in the same way that the values in table 4.2 were used to fit the fishing mortality for the standard population.

When initial length of entry to the fishery is changed from 25 centimeters to

Table 7.12: Chosen Parameter Values for Sensitivity Analysis of Fishing Parameters

| Parameter | Low | Medium | High |
|---|---|---|---|
| Initial length | 22 | 25 | 35 |
| Length at peak | 42 | 47 | 70 |
| Level of Fishing | -0.1 | 0 | 0.1 |

either 22 or 35 centimeters, the fishing curve is refit (and in the later case the total fishing mortality at 32 is set to 0 prior to this refitting). These values were chosen as end points as the length weight relationship is believed only to be valid for fish of 22 centimeters and above (Daan 1974), and 35cm is the legal catch size of cod (Alverson et al. 1994). Hence, the latter case ensures that no undersized cod are caught, and that most fish will be caught at a size much larger than minimum capture size. Such a large size could be achieved by increasing mesh size of nets, although it is unlikely that the EU would agree to setting such a large mesh size, as it would have a large impact on the whiting fishery (Alverson et al. (1994), Oliver (2001)).

When the peak length of fishing mortality is changed, the value in table 4.2 of 47 is changed to either 42 or 70 centimeters, and the fishing curve is refit. This is in many ways unrealistic, as if the peak length for fishing mortality were changed it is likely that fishing mortality for all lengths would change. This does, however, give an idea of what would happen if small changes were made to the shape of the fishing mortality curve. Values of this parameter were chosen to remain between 40 and 98 centimeters, which are the surrounding lengths used to help define the fishing mortality curve (see table 4.2).

Finally the level of fishing was changed by increasing or decreasing by 0.1 over the fishing mortality curve. This was done by changing the second column of table 4.2 accordingly and refitting the fishing curve. Note that as there cannot be negative fishing mortality, that fishing mortality will be increased or decreased on a sliding scale between 0 and 0.1 between the initial length of entry to the fishery and second level defining the fishing mortality (either 32 or 40 cm, depending on which run is used). This parameter is completely controllable in terms of effort and quotas set for the North Sea. It should be mentioned that estimating the mortality inflicted in a year is quite difficult and often not completely determined till later years when all cohorts alive that year have died (See chapter 2).

### 7.4.2 Results

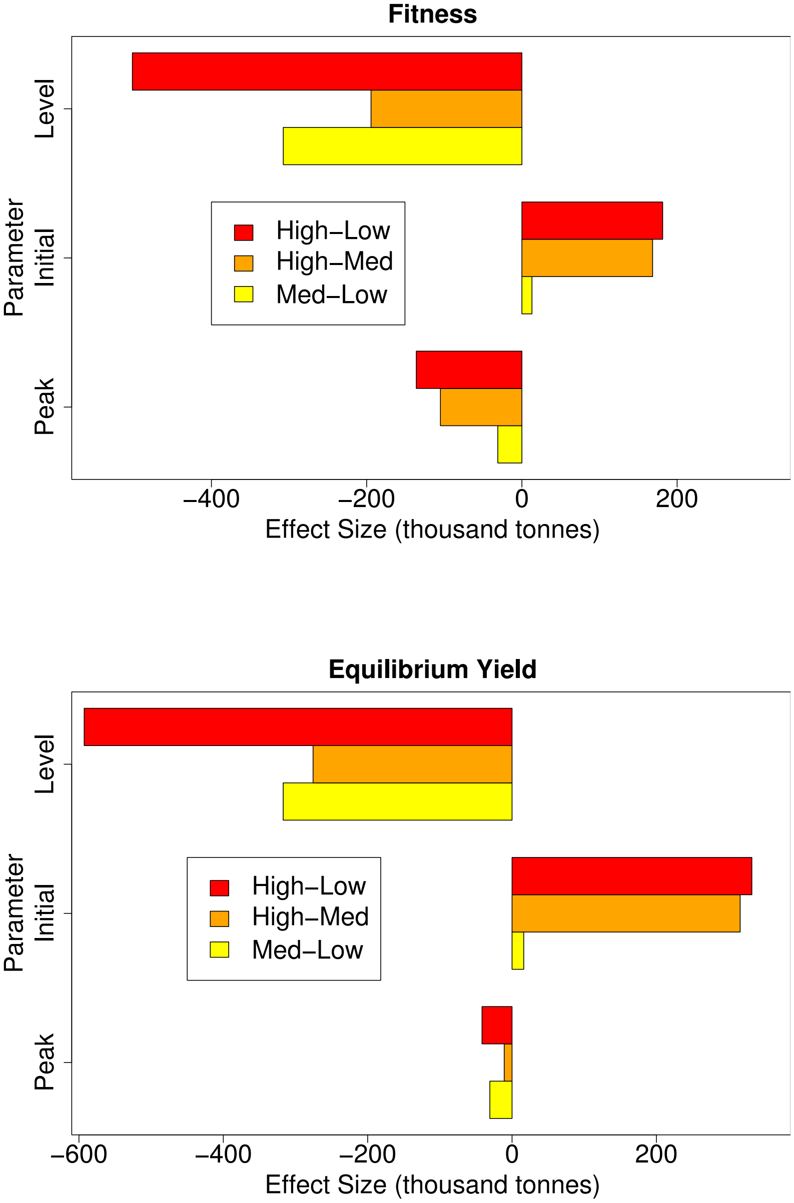
When studying the table of grand average effects (see table 7.13) it is clear the total level of fishing has most impact on the fitness and yield of the stock, with the initial length of fishing being second in importance. Notice that the population is fitter and equilibrium yield increases if the level of fishing mortality is decreased and if the initial length of capture is increased. A population is also fitter if its peak mortality occurs at an early age, this is as mortality tails off for longer fish. Thus moving forward the peak decreases the region of high mortality, enabling more fish to survive to older age and hence to reproduce more often and more successfully.

We next look at the effects of changing between levels in figure 7.13. The order of importance of effects is the same as for the table of grand average effects. Notice that there is a significantly more important effect for changing the level of mortality when changing from the low to medium level than from medium to high level. This suggests that there is an increasing return as this parameter

Table 7.13: Grand Average Effects for Fishing Parameters: *Observe that the level of mortality is the key component of the fishing curve, with fitness increasing as it decreases. Initial length is the next important factor, only as initial length increases so do fitness and yield.*

| Parameter | Initial Length | Peak Length | Level of Mortality |
|---|---:|---:|---:|
| Fitness | 121 | -91 | -335 |
| Yield | 221 | -28 | -395 |

Figure 7.13: Fishing Effect Plot: *The level of fishing mortality is clearly the most important factor. Notice that for this factor there is a larger effect from changing from the medium to low level than medium to high although the parameter value has been changed by the same amount*



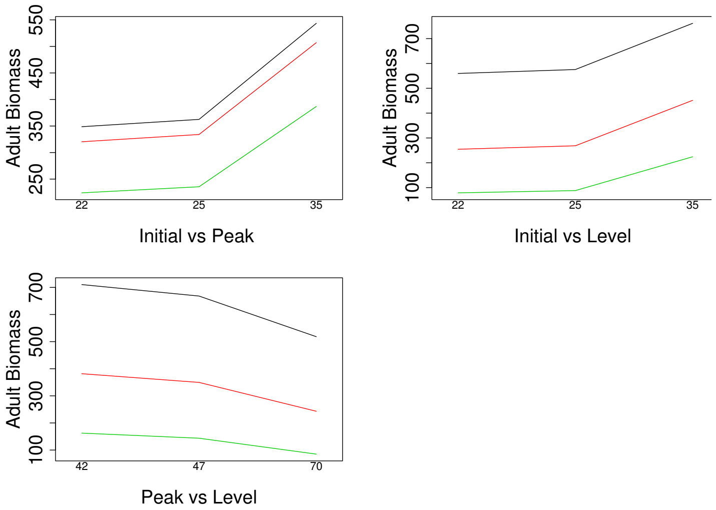


Figure 7.14: Interaction Plots. *The black line is the low level, red the medium level and green the high level. As in all three graphs the lines are virtually parallel, we do not expect there to be significant two-way interactions*

is lowered. Obviously at some point lowering the mortality level will begin to decrease the yield, however for the values of the parameter chosen this effect is not evident. Notice also that changing the peak of mortality has very little effect on yield, and in terms of economics it would certainly make little sense to try and change this facet of the mortality.

Interaction plots, figure 7.14, have been made for the three parameters with respect to fitness. It is clear that any interaction effects are relatively unimportant, as the lines in the plot are virtually parallel in all cases.

### 7.4.3 Implications for the Fishery

There is one clear implication of the grand average effects and the level effect plot. If it is desired to increase the equilibrium adult biomass and hence resilience of the population to environmental effects and occasions of over fishing, the key is to decrease the level of fishing. Although increasing the initial length at entry to the fishery will have an impact, it is less pronounced than the effect of reducing fishing mortality as a whole. Decreasing the level of fishing should also increase yield in the long term, making this a very sensible action. However changing the initial length by as much as 10 centimeters has a small effect on yield in comparison. Thus it is suggested that it should be a priority to lower the general level of mortality experienced by cod, rather than concentrating on mesh sizes.

It must be stated however, that this work has been done with a deterministic model. In the real world, recruitment to the fishery has very high variability, therefore in the real world situation increasing mesh size may have more impact than in this model. If very low recruitment years are completely fished out before they can reproduce, this could have an extreme effect on the population. Whereas in this model, recruitment does not have the extreme behaviour exhibited by real world populations (see figure 1.3) and there is no danger of having comparatively weak years in the population.

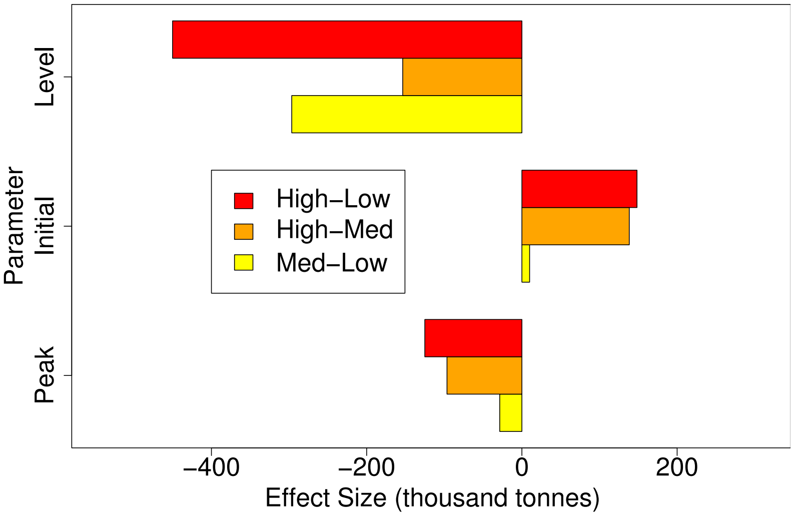
### 7.4.4 Alternate maturation models

Next consider the effect of fishing parameters on the alternate models for proportion mature. Only the results for the equilibrium adult biomass are discussed, as results for yield are very similar. We first consider the third alternate model, which has a gamma(3) distribution for maturation.

On comparison with the graph for the main model (see figures 7.13 7.15) we observe that these are virtually identical results, and suggest that the two models can be considered in the same way from the view of a fisheries manager.

To examine the fishing parameters for these three alternate models for proportion mature the $27^{th}$ design mentioned in section 7.3.1 was used. We include the plots of effects in Appendix C in figure C.10. These match the results for the main model and for when the gamma(3) function for maturation is used. Note that the initial length of capture is proportionally more important for all three models especially that with exponential maturation, although it still comes second in importance to the level of fishing. For the exponential model this is due to the relatively large number of fish that start reproduction before reaching the initial length of 35 centimeters.

Figure 7.15: Plot of Effects of Fishing Parameters on Fitness in Model with Gamma(3) Maturation



**Fishing Parameters for Alternate Growth Models**

For all three models the overall level of fishing has clearly the most impact on the population (see figures 7.16, 7.17, and 7.18), while the initial length is second in importance. Observe that for all three models the length at peak fishing mortality is almost as important as the initial length when the effect from high to low level is considered. In summary, the results are a close match with those of the main model, with the same being true for yield from the three models.

## 7.5 Conclusions

Thus one main conclusion can be drawn from the work in this section. Namely, that in order to increase equilibrium levels of adult biomass, and also increase yield, the most important change which can be made to the fishery is to decrease the level of fishing. This conclusion resulted, no matter what assumptions were

Figure 7.16: Plot of Effects on Fitness for Power Growth Model

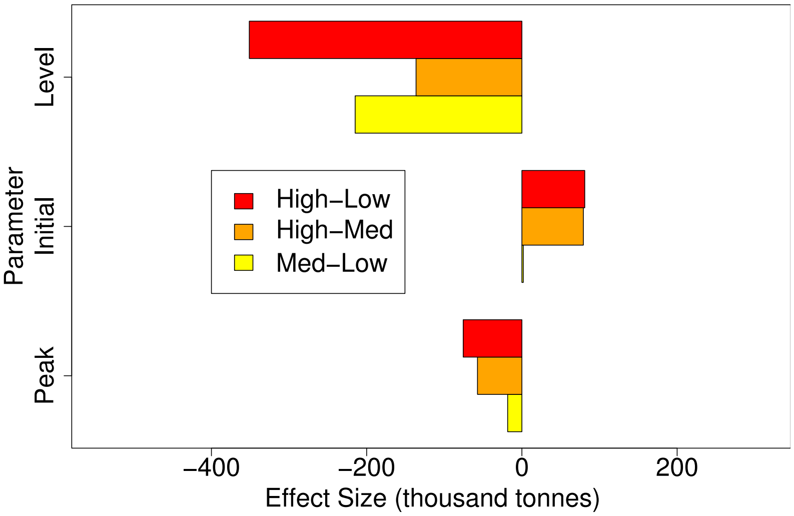


Figure 7.17: Plot of Effects on Fitness for Gompertz Growth Model

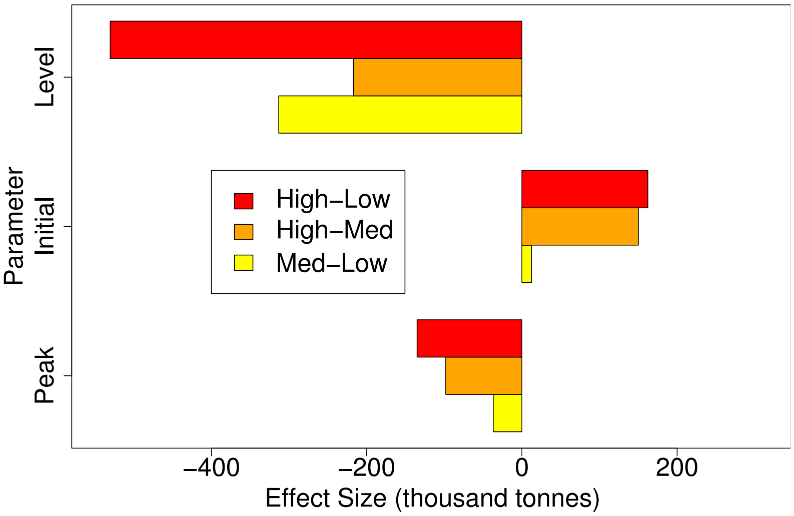
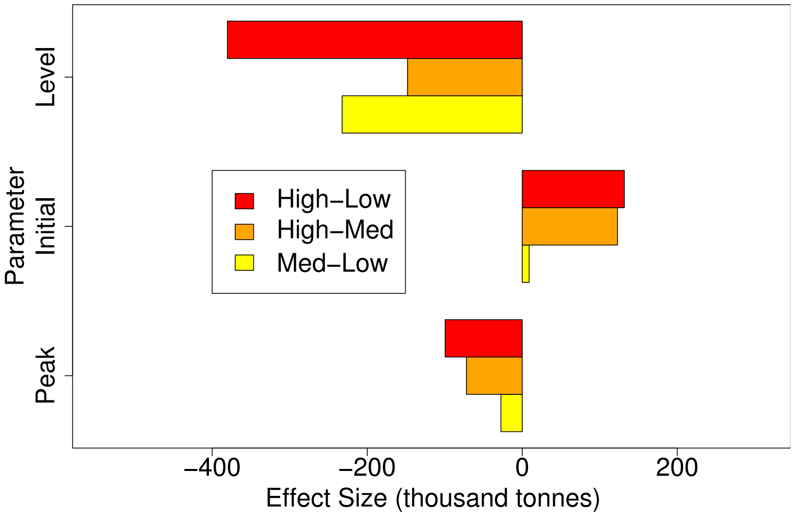


Figure 7.18: Plot of Effects on Fitness for Logistic Growth Model



made about how fish grew or how they matured. Increasing initial length of entry to the fishery also seems a sensible step, even if it does not have as large an impact as decreasing the fishing mortality. As stated earlier, this model does not consider the high variability of recruitment, and as such in the real world initial length on entry to the fishery may have a far more emphatic effect on population fitness.

This agrees with the work of Stokes and Blythe (1991) who found that decreasing the harvest rate would increase equilibrium yield but that raising the size at first capture would have little effect on yield. Similarly Brown and Parman (1991) find that a manager who considers evolutionary effects will select a lower harvest rate than one who is concerned only with current effects on the population.

# Chapter 8

# Seasonal and Spatial Considerations

In this chapter, seasonal and spatial considerations will be examined as final additions to the model. Both will be explored with very simple model additions. Seasonality shall be included by making the fertility function a simple step function, where fish reproduce for a quarter of the year (between February and April). When considering the spatial additions, the model will be divided into two regions, and I will look briefly at some of the changes that this can bring in terms of the ability of populations to invade.

## 8.1 The Effect of Seasonal Reproduction

Cod do not spawn year round, instead for the North Sea there is a peak in their spawning from February to April (Anonymous 1981). As such, a model which includes a reproductive term all year round has the potential to be misleading. Thus the model will now be changed such that

$$f(0.5,t) = R(t) = \int_{0.5}^{\infty} B(a,t-0.5)f(a,t-0.5)da \tag{8.1}$$

where if t is such that the day of the year is between approximately the 26th and 117th of the year then $B = \beta$ and otherwise $B = 0$ and hence $R(t)$ is zero. Therefore, spawning will take place during February through April. Although this introduces seasonality in a simple way, this is still a gross generalization as spawning is not uniform through the spawning season. This is due to temperature dependence for egg production (Fox, O'Brien, Dickey-Collas, and Nash 2000) and females spawning batches of eggs (ten to twenty batches per season) which differ in quality and quantity of eggs (MacKenzie, Tomkiewicz, Köster, and Nissling 1998). This lack of uniformity, however, will be ignored in the interests of simplicity.

### 8.1.1 Transfer Functions

A common way to examine seasonal additions to a model is to use transfer functions. These functions are used as they give a relationship between input and output functions. Thus if the fertility term is thought of as the input function, the transfer function will give information on how the output function, in this case the adult biomass, will react.

These functions are frequently defined using Laplace transforms but in this case they will be defined using Fourier transforms. The transfer function is the ratio of the Fourier transform of the output function, Adult Biomass, to the Fourier transform of the input function, Fertility. Therefore if the Fourier transform of the input is multiplied by the transfer function the result is the Fourier transform of the output function. Thus the transfer function shows which frequencies in the input function will most affect the output function.

Two equations can now be written for the number of 6 month old fish,

$$R = \beta e^{\frac{-A}{K}} A, \tag{8.2}$$

and the change in Adult Biomass,

$$\begin{aligned} \frac{dA}{dt} &= \int \frac{dp(a)}{da} p(a)w(a)S(a)R(t-a)da + \int \frac{dw(a)}{da} p(a)w(a)S(a)R(t-a)da \\ &\quad - \int \delta(a)p(a)w(a)S(a)R(t-a)da. \end{aligned} \tag{8.3}$$

The notation in these equations is the same as in chapter 4 with: $p(a)$ the proportion mature, $w(a)$ the weight at age, $S(a)$ the survival to age, $\beta$ the production parameter, $K$ the competition parameter and $\delta(a)$ the mortality.

The differential equation for adult biomass gives the change in adult biomass with respect to time as each age class increases weight and proportion mature and suffers mortality.

The system is then linearized by letting

$$\begin{aligned} A &= A^* + \theta(t) && (8.4)\\ R &= R^* + \rho(t) && (8.5)\\ \beta &= \beta^* + \gamma(t) && (8.6) \end{aligned}$$

where $\theta(t), \rho(t), \gamma(t)$ are all assumed to be small.

On substitution of these linearizations into 8.2

$$\begin{aligned} R^* + \rho(t) &= (\beta^* + \gamma(t))e^{-\frac{A^*+\theta(t)}{K}}(A^* + \theta(t)) && (8.7)\\ &= (\beta^* + \gamma(t))e^{\frac{-A^*}{K}}(1 - \theta(t)/K)(A^* + \theta(t)) && (8.8)\\ \rho(t) &= \beta e^{\frac{A^*}{K}}(1 - \frac{A^*}{K})\theta(t) + \gamma(t)e^{\frac{A^*}{K}}A^* && (8.9) \end{aligned}$$

This can then be substituted into the differential equation 8.4. The following substitutions are made for ease of reading. Let

$$\begin{aligned} Q &= \beta e^{\frac{A^*}{K}}(1 - \frac{A^*}{K}) && (8.10)\\ P &= e^{\frac{A^*}{K}}A^* && (8.11)\\ u_1(a) &= \frac{dp(a)}{da}p(a)w(a)S(a) && (8.12)\\ u_2(a) &= \frac{dw(a)}{da}p(a)w(a)S(a) && (8.13)\\ u_3(a) &= \mu(a)p(a)w(a)S(a). && (8.14) \end{aligned}$$

Hence,

$$\rho(t) = Q\theta(t) + P\gamma(t).$$

Now as $dA/dt = d\theta/dt$ we can write

$$\begin{aligned} \frac{d\theta}{dt} &= \int u_1(a)(Q\theta(t-a) + P\gamma(t-a))da + \\ &\quad \int u_2(a)(Q\theta(t-a) + P\gamma(t-a))da - \\ &\quad \int u_3(a)(Q\theta(t-a) + P\gamma(t-a))da. \end{aligned}$$

Applying Fourier transforms to both sides, such that $\tilde{\theta}$ is the transform of $\theta$ we obtain

$$i\omega\tilde{\theta} = P\tilde{\gamma}(\tilde{u_1} + \tilde{u_2} - \tilde{u_3}) + Q\tilde{\theta}(\tilde{u_1} + \tilde{u_2} - \tilde{u_3}). \tag{8.15}$$

The transfer function can now be written simply as $T(\omega) = \tilde{\theta}/\tilde{\gamma}$ or

$$T(\omega) = \frac{P(\tilde{u_1} + \tilde{u_2} - \tilde{u_3})}{i\omega - Q(\tilde{u_1} + \tilde{u_2} - \tilde{u_3})}.$$

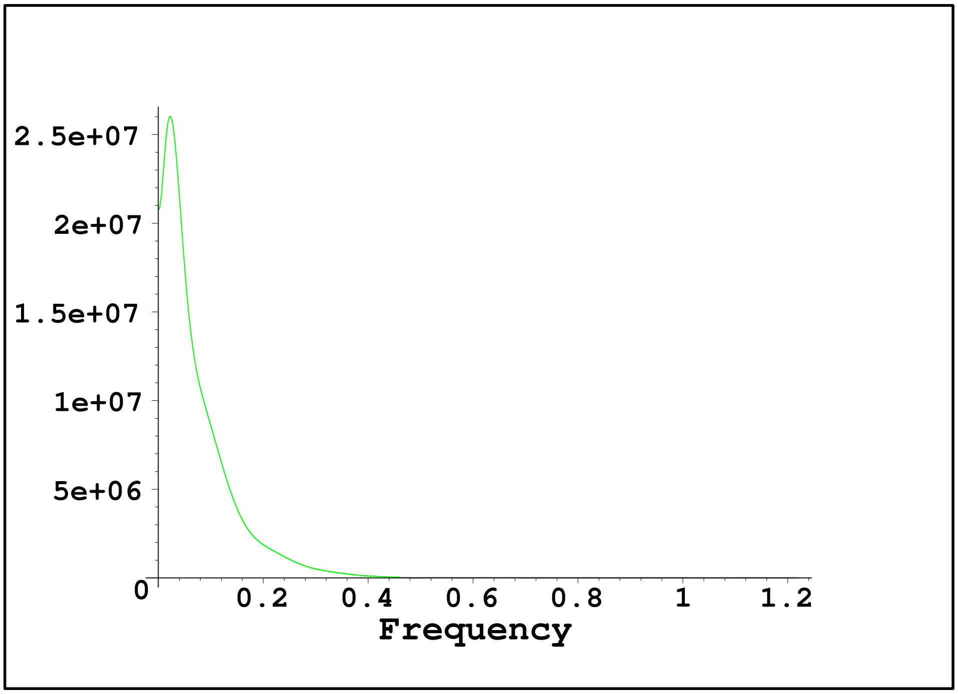
This transfer function is not only correct for the fished model, but also for the alternate models with exponential and cumulative gamma functions for the proportion mature, as well as the alternate growth models. A small change is made when considering the transfer function for the model where all fish mature concurrently, as with all fish maturing at a single age, $p(a)$ is not a continuous function.

Unfortunately, due to the intractability of the fishing function, I am unable to calculate the transfer function using Fourier transforms for any of the models. However, FFTs can be used to estimate the value of the transfer function. The plots of the transfer functions for the unfished and fished models are given in figure 8.1. In the unfished case a period of approximately 44.5 years in the fertility function will have the maximum effect on adult biomass. The period is simply the inverse of the frequency. In the fished case periods of 19 and 6 years have the most impact on adult biomass.

The period of the function used for the fertility function is one year. From examining the graphs it is clear that there is no large effect on the adult biomass when the fertility function has frequency one. Thus we would not expect that there would be a large change in the resultant behaviour of the population with the change in fertility function. If there were, however, some systematic change in fertility corresponding to either the 6 or 19 year period, we would expect a more dramatic effect to be noticeable.

### 8.1.2 Simulation results

Simulation results are given as a comparison. Although certain periodicities of seasonal behaviour may have a great impact on the model behaviour, these



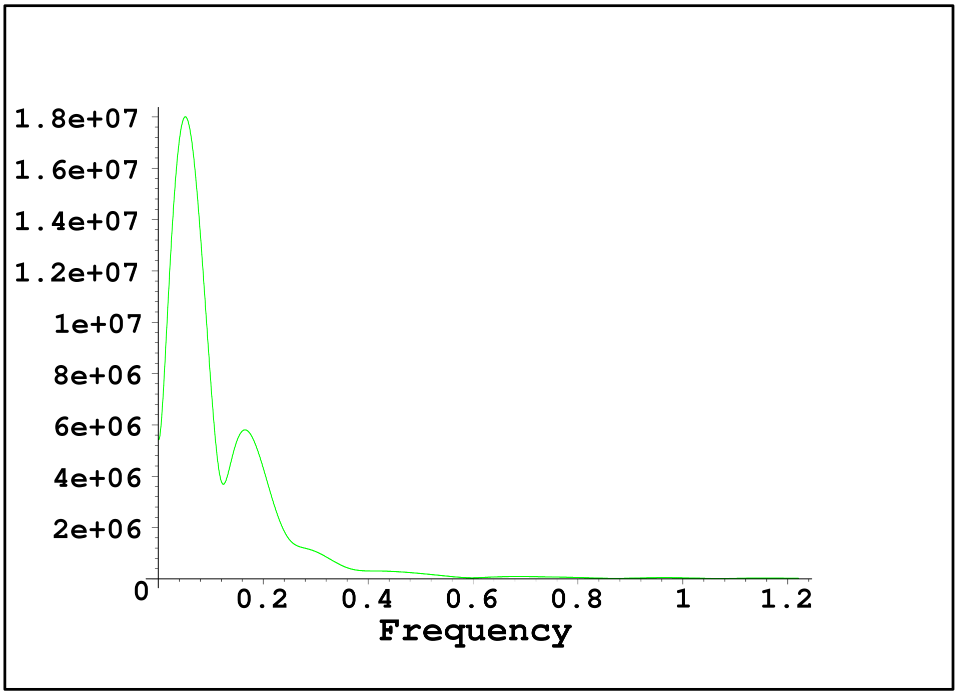


Figure 8.1: Transfer Functions for the Population. *We see that there will be an*

Table 8.1: Behaviour of the Seasonal Model For Different Levels of Fertility

| Boundary of large scale behaviour | Estimate of $\beta$ value |
|---|---|
| Viability | 52-53 |
| Oscillatory convergence | 175-180 |
| Oscillatory Divergence | 980-985 |

simulations are for the seasonal behaviour of interest which has a period of a single year. Thus, the fertility and hence reproduction of the population behave as a step function which is zero apart from short period in the spring of each year.

In figure 8.2 simulation results for different values of $\beta$ are shown. As now the population only reproduces for a quarter of a year, we expect that the values of $\beta$ needed to see each type of behaviour will be roughly four times as large. Note that in all simulations, even if it appears as though the population has settled to equilibrium, there remains a small variation in this value due to the seasonal behaviour of the model. However in terms of larger scale behaviour, the results can be compared to the model without seasonality. In table 8.1 rough suggestions of where limits between different types of behaviour lie are given. A comparable value for equilibrium biomass, as for the normal model with $\beta = 15.9$, is found for $\beta = 61.3$ where the biomass cycles in a small region surrounding 155 thousand tonnes. In general a rough estimate is obtained by multiplying the value found for the boundary of the nonseasonal model by four.

In the figure 8.2 the behaviour of the seasonal model for different values of $\beta$ is presented. Again, it is emphasized, that although the population may appear to have achieved equilibrium, there are constant small oscillations in the value to which the population settles. This is due to the time dependency in the model which only disappears if the population becomes extinct.

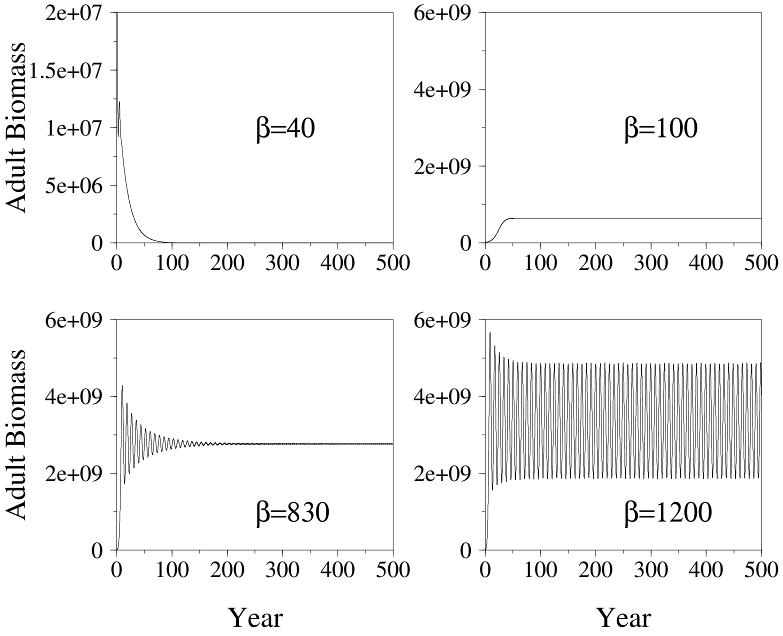


Figure 8.2: Plots of Behaviour for Various Values of $\beta$

## 8.2 The Effect of Migration

Until now one main feature of the North Sea has been ignored, that it has size, i.e. that there is a distinct possibility that fish are not equally dispersed through the sea. An approximate regional grouping has been arrived at for the North Sea with six regions (Brander (1994) quoting the ICES North Sea Roundfish Working Group from 1970 and 1971). These six regions are the Norwegian side of the Skagerrak; the Danish side of the Skagerrak; one or possibly several coastal regions from Flaborough to the Scottish east and north coasts; the central North Sea; the Southern Bight, from the Straits of Dover to latitude 54°N; the English Channel, south and west of the Straits of Dover (Brander 1994). Although these suspected regions exist for stocks there is no clear basis for the distinction on a genetic basis (Brander 1994).

Rather than consider separate regions which do not intermix, two regions which experience two way migration will be used in the new spatial model although their exact location is not identified. This can be thought of as the two final locations in the migratory route of a regional stock. In the North Sea, this migration is on a small scale varying from 20 to 120 miles between spawning feeding grounds (Brander 1994). This is not typical as other stocks such as the Newfoundland and North-East Arctic stocks can travel 500 km (approximately 300 miles) or more (Rose, deYoung, and Colbourne 1995)

The two regions will have different main purposes, the first being a spawning ground and the second a feeding ground. The stocks will spawn for a quarter of a year, with migration towards the spawning ground beginning approximately a month and a half before spawning and continuing through spawning. Migration occurs towards the feeding grounds during the rest of the year. A model where spawning happens throughout the year is also examined.

### 8.2.1 Introduction to Spatial model

The general spatial model is written in terms of differential equations. The number of fish entering the population must be calculated for both regions, and

6 month old fish are assumed to join the population in the region in which they were spawned. Remember

$$A = \int_{0.5}^{25} p(a)w(a)S(a)R(t-a)da.$$

Thus the change in adult biomass is the sum of the change in maturity and the change in weight, minus the change due to mortality, plus the change due to migration. Here the migration term is written as two directional terms where $\nu_1$ is migration from region one to region two and $\nu_2$ is migration from region two to region one.

$$\begin{aligned}
R_1 &= \beta * exp(-A_1(t-0.5)/K_1)A_1(t-0.5) \\
R_2 &= \beta * exp(-A_2(t-0.5)/K_2)A_2(t-0.5) \\
\frac{dA_1}{dt} &= \int_{0.5}^{50} \frac{dp(a)}{da} A_1 da + \int_{0.5}^{50} \frac{dw(a)}{da} A_1 da - \int_{50}^{50} \delta_1(a) A_1 da - \nu_1 A_1 + \nu A_2 \\
\frac{dA_2}{dt} &= \int_{0.5}^{50} \frac{dp(a)}{da} A_2 da + \int_{0.5}^{50} \frac{dw(a)}{da} A_2 da - \int_{50}^{50} \delta_2(a) A_1 da + \nu_1 A_1 - \nu_2 A_2
\end{aligned}$$

Thus the spatial model can be represented by a set of four equations, two of which are differential equations for adult biomass.

### 8.2.2 Examination of Results of Simulations

Having derived the spatial model a Solver program was created to run simulations. The program is similar to that in Appendix B, except now four populations are considered as there are resident and invader populations for both regions. The invading population was set to have exactly the same parameters as the resident population, apart from the maximum weight ($w_\infty$) which was slightly higher. This provides a competing population which is only slightly more competitive in the single region case, allowing any change in which population is favoured to be more obvious. The programs ran for 200 years with only the resident population in order for it to achieve equilibrium, and then 5 years worth of age 6 month fish of the invader stock were added before allowing the program to run as normal. The simulations were left to run for 1000 years total (hence 800 years with both populations) to observe whether the invader population would die out or establish itself. In the latter case it was also of interest how well established it was able to become in the time frame. Several different scenarios were run including both seasonal and non-seasonal reproduction to see if the migration by itself would have an effect or if seasonality of reproduction was essential. In the case of seasonal reproduction, migration starts approximately a month before spawning. I also studied three different fishing regimes: fishing both regions, only the spawning region or only the feeding region. In each case the fishing mortality function from chapter 4 was used for each fished region.

This gave six scenarios. For each situation a series of 336 simulations were run to create a graph. This graph compares populations at the end of 1000 years under different levels of migration and with different time lags in spawning and migration between the resident and invader populations. The lag in each graph is how many weeks before the invading population, the resident population began migration and spawning. At high levels of migration, all spawning in the seasonal model takes place in the spawning region, while under low levels of migration and nonseasonal spawning, spawning takes place in both regions.

For each plot the lag in weeks between the resident population and invader population spawning is plotted on the horizontal whilst the vertical axis gives the percentage migrating between the regions per week. The colours code the proportion of residents to invaders for the population in region one, the spawning region. This is calculated by dividing for the first region the adult biomass of residents by that of invaders and then taking the log base ten. If there are no residents in the population this was coded to be $-10$ and if there were no invaders left in the population this was coded as 10 (these values were well beyond the limits of the other values found). Results were very similar when this proportion was calculated using the second region or the whole population.

In the graphs the parameter region where the invaders have died out are white. The blue regions are where the invaders have almost equaled or just exceeded the resident population levels, and correspond to a scaling close to zero

(zero being when the populations are equal in biomass). The lighter colors show parameter regions where the invader population is growing, however this growth is quite slow and at the end of 800 years co-existence the resident population is still the larger of the two populations.

In figure 8.3 we study the case where both the feeding and spawning regions are fished. In the first graph reproduction is seasonal while in the second there is no reproductive seasonal behaviour. We observe that there is an effect due to the spatial component, even when reproduction is nonseasonal. Examining the graph for the nonseasonal behaviour, it is clear that increased migration and an increased lag in spawning allow the invading population to dominate the population more quickly. When seasonal reproduction is added this picture changes, as now the fastest domination by the invader population is for a mid-value of percentage migrating, and for a lag of spawning of about seven weeks. For all combinations of parameters, under both types of reproduction, the invading population is successful but the invasion rate is slow.

In figure 8.4 only region one, the spawning region, is fished. This has a very dramatic effect on the population. There is now a very clear difference between the seasonal and nonseasonal case. The non-seasonal case is similar to that where both regions were fished, only there is now an increase in the speed with which the invading population dominates the population for high migration and large lags in spawning time. There are also regions at relatively smaller lags and lower migration rates, where there is a decrease in the rate of domination of the resident population in comparison with the case where both regions were fished.

A completely different picture emerges for the seasonal case. There is now a large region where the invader population becomes extinct (the area coloured white in the graph) and migration rates must be either very large or very small to avoid this region if the lag in spawning is larger than two weeks. This suggests creating a reservoir which included the feeding grounds could have substantially detrimental effects for the population, with smaller fish being favoured by selection. Also notice that if the migration levels are high, selection for larger fish (the invaders) does increase, unlike the situation where both regions were fished.

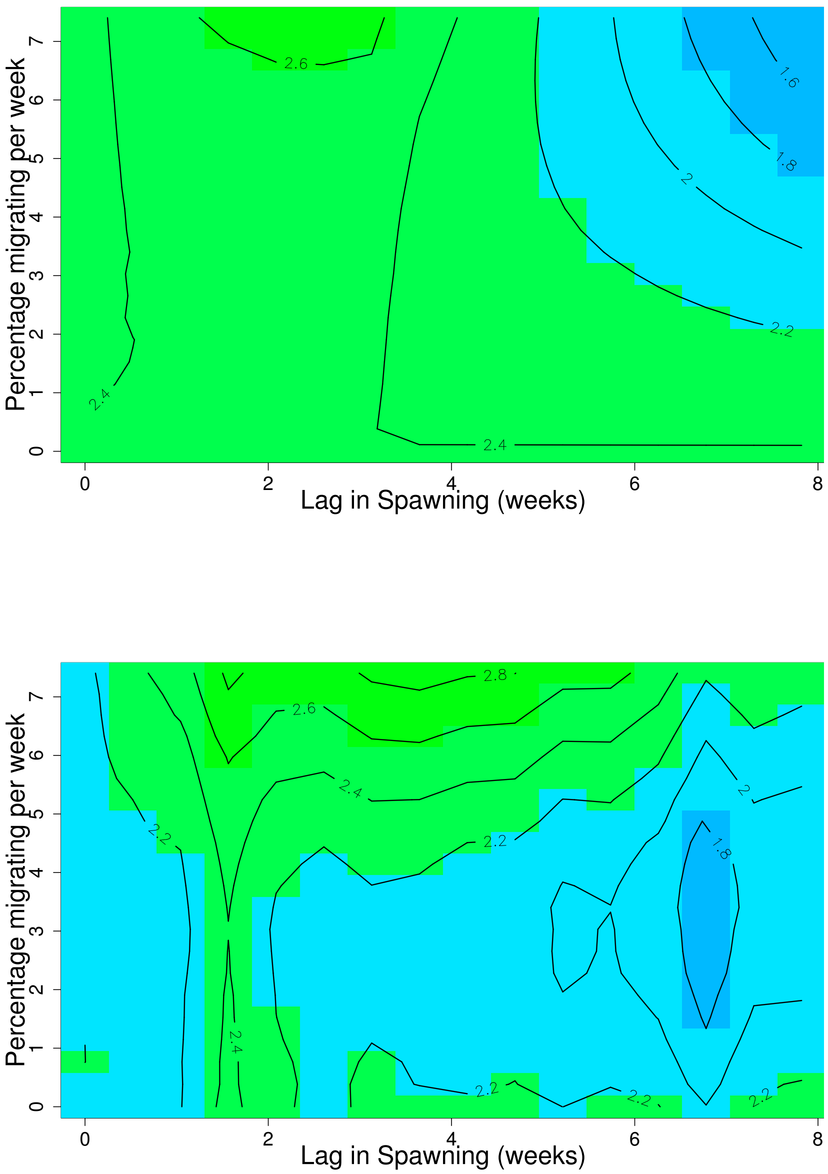


Figure 8.3: Spatial Behaviour: *These graphs are for the situation where both regions are fished. The top graph shows the results for year round reproduction while the other graph shows seasonal reproduction. The colour in the graph becomes darker as the proportion of invaders in the population increases. In the non seasonal case invaders dominate more quickly with increasing migration, and lag in spawning. For the seasonal case a peak is reached with a lag of seven weeks and a medium level of migration.*

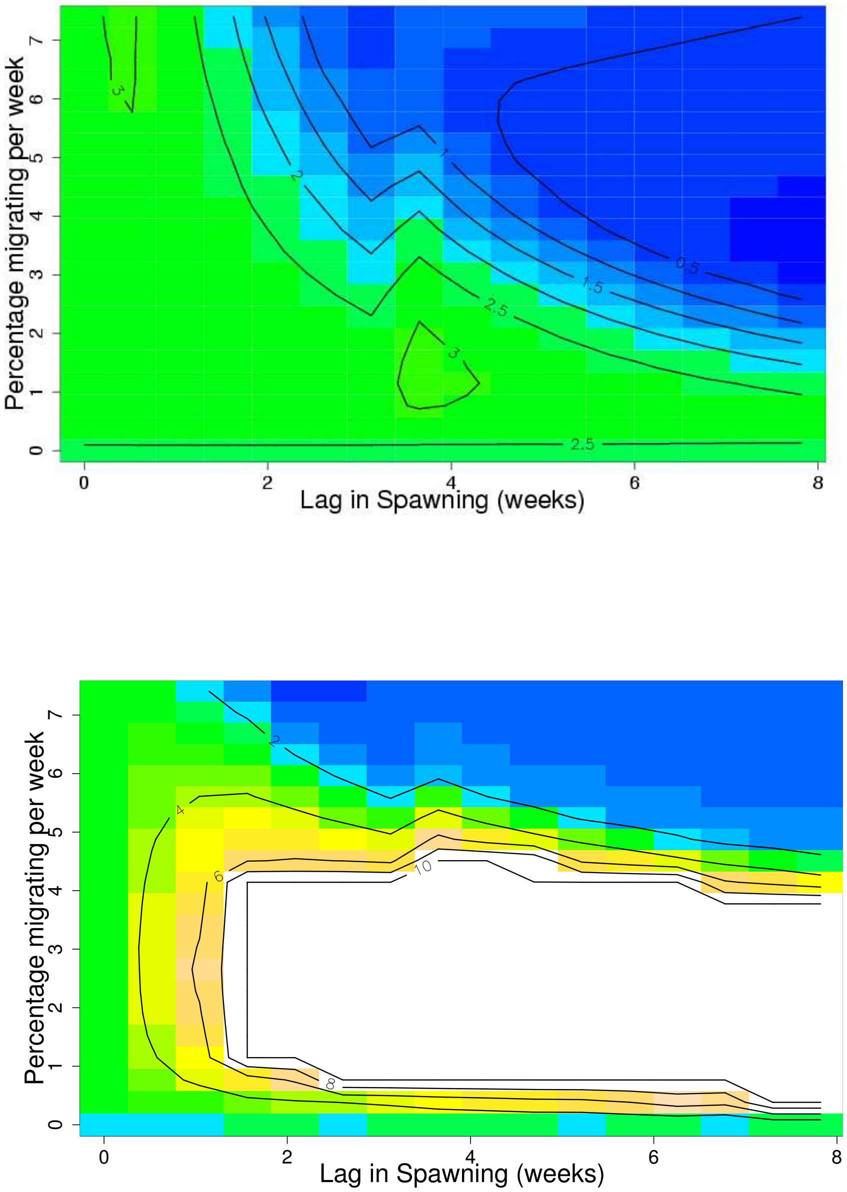


Figure 8.4: Spatial Behaviour: *These graphs are for the situation where the spawning region is fished. The top graph shows the results for year round reproduction while the other graph shows seasonal reproduction. The colour in the graph becomes darker as the proportion of invaders in the population increases. Thus in the seasonal case the white area represents a parameter region where the invading population becomes extinct. Otherwise in both graphs, the larger fish are increasingly favored as lag in spawning increases and migration increases.*

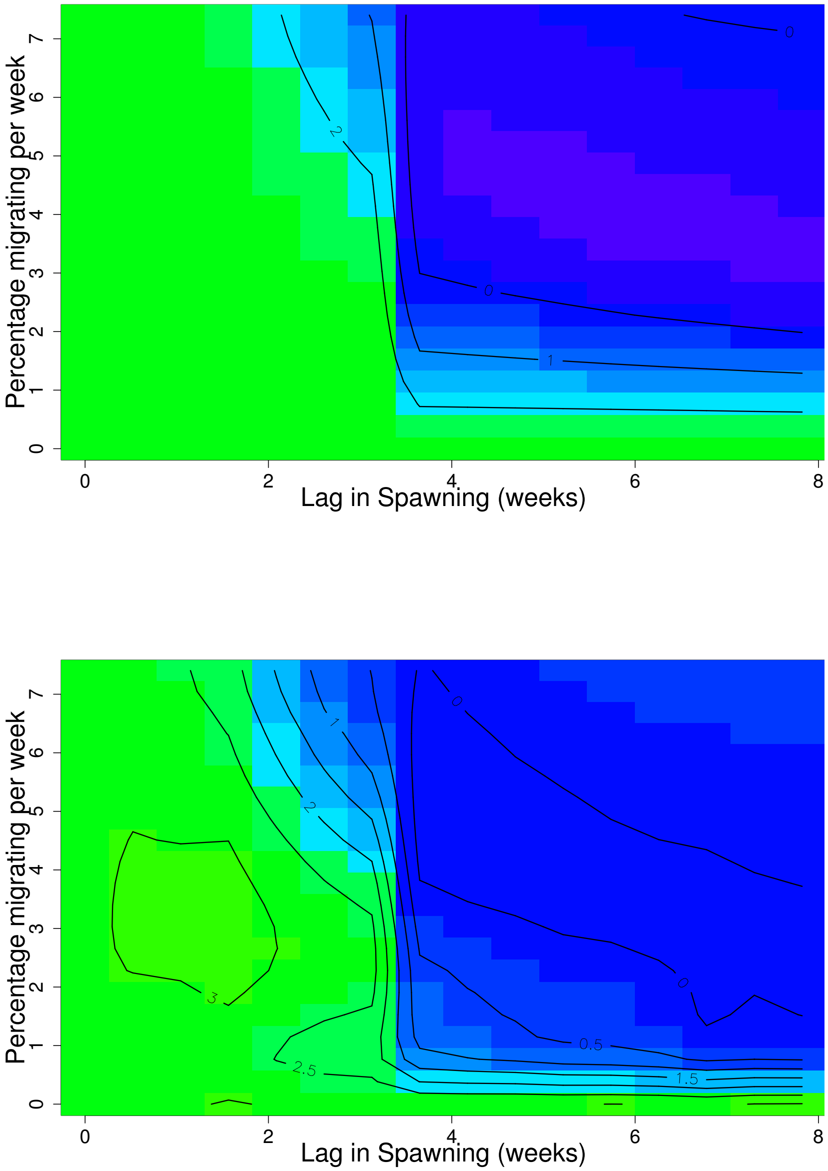


Figure 8.5: Spatial Behaviour: *These graphs are for the situation where the feeding region is fished. The top graph shows the results for year round reproduction while the other graph shows seasonal reproduction. The colour in the graph becomes darker as the proportion of invaders in the population increases. The seasonal and non-seasonal cases are very similar with increased migration and lag in spawning favouring increased selection of the invading population*

The final situation is when the feeding region is fished, as shown in figure 8.5. There is very little difference between the seasonal and nonseasonal situation in this case. In both cases the invading population dominates more quickly if the percentage migrating and lag in spawning increases. Hence there is a large difference in result if the feeding ground as opposed to the spawning ground is fished.

Therefore even with a very simple spatial model, it is evident that spatial considerations are important. Using seasonal terms in the model can have a greater effect, especially in conjunction with migration. Furthermore we see that a lag in the spawning term has little effect in a non migratory model (this can be seen by examining the contour graphs for 0% migration), but can have a noticeable impact when migration (and hence a degree of spatial modelling) is included in the model. Similar results are obtained using invader populations with different parameter changes.

This shows further that the pattern of fishing in a spatial context can have a great impact on the population, possibly changing how fish will grow and mature. It certainly also suggests that any marine reserves which are created, should be well thought out, as if such reserves have the effect of favouring smaller fish, they could be damaging to the population from an economical sense.

## 8.3 Discussion

The results for the spatial form of the model, show that there is much room for future work on this aspect. If introducing a simple two region dynamic can have such an effect on model results, then considering a more accurate depiction of the ocean including dispersion effects and different migration routes, may have an even more interesting effect on results. We do note that these spatial results appear contrary to those found by Law and Grey (1989) who found that greatest yields from the fishery would be obtained when fishing was centered on spawners. The results in this chapter show that although larger fish are favoured by high migration rates and large lags in spawning, there are levels of migration which favour smaller fish. One difference in the two models is that, in the paper by Law and Grey (1989), immature fish are not caught in the spawner fishery, as young fish do not migrate to the spawning grounds in their model. Hence, their model provides a method of restricting fishing to older fish (or raising the initial length at capture), which from the previous chapter would be beneficial both to fitness and yield. Thus essentially there is an agreement between the models on the effect of capturing small fish.

# Part IV

# Discussion and Conclusions

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# Appendix A

# Downhill Simplex Method

As non linear functions are fit to the data, the standard method of least squares taught in beginner's statistics classes is not a useful method. I decided to use the Downhill simplex method introduced by Nelder and Mead in 1965, which has the advantages that derivative calculations are not performed and the program used (an adaptation of that in Press et al. 1989) is fairly concise.

I solve by minimizing the sum of squares. The method works by creating a N+1 dimensional shape (simplex) on N unknown parameters. This simplex is created using initial guesses at parameters and the step size. Once given an initial simplex a series of reflections, expansions and contractions are used to move the simplex downhill towards a maximization of the sum of squares. Most steps taken are reflections, reflecting the corner of the simplex with largest error value through the opposite face of the simplex to a point with a lower error calculation. When it is possible, the method can then expand the simplex to find areas with lower error calculations, and when such an area is found contracts to find the lowest point, eventually contracting in all directions. When all movements of corners are below a specified tolerance, the algorithm is then stopped and a minimum has been found.

At this stage it should be mentioned that if the error structure is complicated, it is possible that the minimum found is only a local minimum, and the algorithm should be restarted in order to check that the global minimum has not been missed.

# Appendix B

# Solver Programs

Solver (Gurney, Tobia, Watt, and Dobby 1998a) is a package for solving systems of differential equations. It requires two programs to be input, a constants (.con) and a definitions (.def) file. The constants file lists any constants that shall remain fixed for the duration of the program and also gives the number of state variables, constants, output variables, plotting variables and variables for which historical data is needed.

The definition file, has four key programs which are used by solver. These are called Get_History, Get_Initial_State, Get_Gradient, and Get_Memo. Each of these is designed to give Solver a specific piece of information. The Get_History program, sets historical values for any parameters which are needed at times prior to the start of the simulation. The program Get_Initial_State sets initial values for state parameters. If not all state parameters are initialized in this program then Solver will ask the user to supply these values. The Get_Gradient program feeds solver the differential equations which must be solved. Finally the Get_Memo program has the principal function of outputting the data, although in my program it also recycles cohorts and finds the number of fish which will join the population in six months.

In the next two sections the two basic programs are included, from which all simulations in this thesis have been run. The alternate proportion mature and growth models have slight changes to individual programs to give the correct functions but are otherwise identical. For the spatial simulations four populations must be tracked as opposed to one. This is as there are resident and invader populations in both regions. For these simulations the functions dealing with seasonal reproduction and migration have been called in the body of the main program.

## B.1 Constants Program

```
{*******************************************************}
{**                                                   **}
{****                EBTsingle.CON                  ****}
{**                                                   **}
{*******************************************************}


CONST  Cohorts      =250;  {*The maximum number and age *}
       MaxAge       =25;   {* of age groups considered  *}

       IstateVars   = 3;   {*Types of state variables   *}
       AuxVars      = 0;

       NoofStaVar   = IstateVars*Cohorts+AuxVars+1;
       NoofHisVar   = 1;
       NoofOptVar   = 5;   {*These lines set up the State*}
       NoofPltVar   = 2;   {*Historical, Output, Plotting*}
       NoofCoeffs   = 1;   {*and Constant variables      *}
       RingBufLen   = 500001;

       Clock=NoofStaVar;
       ClockThreshold=0.99999999;
       CohortWidth=MaxAge/Cohorts;

        wr=0.01;                  {*Recruitment weight*}
        b=1.1034208;              {*Growth constants  *}
        myswitch=2.66;
        g2=0.26033235;
        g1=0.7326;
        wf=17.7252186;

        bl=3;                     {*Length conversion *}
        al=0.0104;

        deltao = 0.2;           {*Natural Mortality Rates*}
        delta1 =0.8;
        delta2 =0.35;
        delta3 =0.25;

        lenone=25;          {*Fishing Mortality Parameters*}
        lentwo=32;
        lenthree=40;
        lenfour=47;
        lenfive=98;
```

```
fish1=0;
fish2a=0.0642857;
fish3a= 0.0725;
fish3b=0.45;
fish4a=0.0028571428;
fish4b=1.03;
fish5a=-0.0058823529;
fish5b=1.05;
fish6a= 0.75;

py= 3.983855;             {*Maturation Parameters*}
px=0.003581546;

rstar =7000000;           {*Initial value*}

myk = 1000000000;         {*Competition coefficient*}
```

## B.2 Definition Program

```
{*************************************************************}
{**                                                         **}
{**                      EBTsingle.DEF                      **}
{**                                                         **}
{*************************************************************}
Type

shortarray= array[1..Cohorts] of double;

VAR ClockGrad,beta:DOUBLE;  CurRecCo:INTEGER;  leninf:double;


function myexp(x:double):double;
{*Exponentiation Function*}
var z:DOUBLE;
BEGIN
  IF x<-50  THEN  z:=0
    ELSE z:=exp(x);
  myexp:=z;
end;

function power1(x:double;y:double):double;
{*A power function which assumes x is non-negative*}
var z:DOUBLE;
BEGIN
  IF x>0.0 THEN  z:=myexp(y*ln(x))
    ELSE IF y=0 THEN z:=1 Else z:=0;
  power1:=z;
end;

function findadwt( add:integer;S:SVEC; p:shortarray):double;
var z,x,y:double; i,num,age,wt:integer;
{*This function finds adultweight, where p is an array of*}
{*proportion mature and S is the vector with age,numbers *}
{*and weights                                            *}
begin
  z:=0;
  For i:=1 to cohorts
  Do Begin
    num:=i+add*cohorts; age:=num+cohorts; wt:=age+cohorts;
    z:=z+p[i]*S[wt]
  END;
  findadwt:=z;
end;
```

```
procedure findavage( S:SVEC;add:integer;var A:shortarray );
var  i, age,wt,num:integer;
{*This function finds the average age for each cohort *}
{* and stores them in an array                        *}
begin
  For i:=1 to cohorts
  Do Begin
    num:=i+add*cohorts; age:=num+cohorts; wt:=age+cohorts;
    IF S[num]=0 THEN A[i]:=0.0 ELSE A[i]:=S[age]/S[num];
  END;
END;

procedure findpmat(A:shortarray;mat1:double; mat2:double;
                         var P:shortarray);
var i:integer;
{*This function finds the proportion mature for each *}
{*cohort and puts it in an array                     *}
begin
  For i:=1 to cohorts
  Do Begin
    IF A[i]>30.0 THEN P[i]:=1.0
    Else IF A[i]>0.1 THEN
      P[i]:=1.0-myexp(-mat2*power1(A[i],mat1))
    Else P[i]:=0.0;
  END;
END;

function findrec(add:integer;S:SVEC;b,Adult:double;
                         p:shortarray):double;
 var z,x,y,myexpadult:double; i,num,age,wt:integer;
{*This program finds the recruitment where p is the array of*}
{*proportion mature Adult is the Adult weight, b is the beta*}
{*parameter and S contains age,weight and numbers. add shows*}
{*where in the vector S the values should be placed.       *}
begin
  z:=0;
  myadult:=myexp(-Adult/myk);
  For i:=1 to cohorts
  Do Begin
    num:=i+add*cohorts; age:=num+cohorts; wt:=age+cohorts;
    z:=z+ p[i]*b*S[wt]*myexpadult;
  END;
  findrec:=z;
```

```
end;

procedure getavwt(S:Svec;add:integer;  var wtarray:shortarray);
var i,num,wt,age:integer;
{This procedure finds the Average weight for each cohort}
begin
  for i:=1 to cohorts
  Do Begin
    num:=i+add*cohorts; age:=num+cohorts; wt:=age+cohorts;
    IF S[num]=0 THEN wtarray[i]:=0.0 ELSE wtarray[i]:=S[wt]/S[num];
  end;
end;

procedure getmortality (B:Shortarray;al,wr:double;fish:
                           integer; var mort:shortarray);
var i:integer; f,m,lenconst:double;
{*This function finds the mortality term for each cohort*}
{*and places it in an array                             *}
Begin
  lenconst:=power1(1000/al,1/3);
  For i:=1 to cohorts
  Do Begin
    IF B[i]>4.033365399 THEN m:=deltao
      ELSE IF B[i]>2.14580119 THEN m:=delta3
      ELSE IF B[i]>1.00900 THEN m:=delta2
      ELSE m:=delta1;
    IF fish=1 THEN
    Begin
      IF B[i]>power1(98,3)*al/1000 Then f:=fish6a
      ELSE IF B[i]>power1(47,3)*al/1000 THEN
         f:=fish5a*(lenconst*power1(B[i],1/3)-lenfour)+fish5b
      ELSE IF B[i]>power1(40,3)*al/1000 THEN
         f:=fish4a*(lenconst*power1(B[i],1/3)-lenthree)+fish4b
      ELSE IF B[i]>power1(32,3)*al/1000 THEN
         f:=fish3a*(lenconst*power1(B[i],1/3)-lentwo)+fish3b
      ELSE IF B[i]>power1(25,3)*al/1000 THEN
         f:=fish2a*(lenconst*power1(B[i],1/3)-lenone)
      Else f:=fish1;
    end
    ELSE f:=0;
      mort[i]:=m+f;
   End;
END;

procedure getcog(A:Shortarray;m,wf,b,g2,g1:double;
                    var cg:shortarray);
```

```
var i:integer;
{*This procedure finds the rate of growth for each cohort*}
Begin
  For i:=1 to cohorts
  Do Begin
    IF A[i]<m  Then cg[i]:=g1
    ELSE cg[i]:=3*wf*(b*g2*myexp(-g2*A[i]))*
            sqr(1-b*myexp(-g2*A[i]));
  end;
end;

function getnumber(A0:double;A1:double; delta:double;
                         rstar:double):double;
var z:double;
{*This function gets the initial number in each cohort*}
begin
  z:= (myexp(-delta*A0)-myexp(-delta*A1))*rstar;
  getnumber:=z;
end;

function getage(delta:double; A1:double; A0:double):double;
var z:double;
{*This function gets the initial total age in each cohort*}
begin
  z:=myexp(-delta*A1)*(A1+1/delta)-
            myexp(-delta*A0)*(A0+1/delta);
  z:=z/(myexp(-delta*A1)-myexp(-delta*A0));
  getage:=z;
end;

function getoldwt(b,g2,A0,A1,delta:double):double;
var z:double;
{*This function gets the total weight in a cohort where*}
{*the age is high enough to use the old wt function    *}
begin
  z:=(-b*sqr(b)*myexp(-(delta+3*g2)*A0)/(delta+3*g2) -
     3*b*myexp(-(delta+g2)*A0)/(delta+g2) +
     3*sqr(b)*myexp(-(delta+2*g2)*A0)/(delta+2*g2)+
         myexp(-delta*A0)/delta);
  z:=z +(b*sqr(b)*myexp(-(delta+3*g2)*A1)/(delta+3*g2) +
     3*b*myexp(-(delta+g2)*A1)/(delta+g2) -
     3*sqr(b)*myexp(-(delta+2*g2)*A1)/(delta+2*g2)-
        myexp(-delta*A1)/delta);
  getoldwt:=z;
end;
```

```
function getyoungwt(A0,A1,g1,wr,delta:double):double;
var z:double;
{*This function gets the total weight in a cohort where*}
{*the age is low enough to use the young wt function   *}
begin
  z:=myexp(-delta*A1)*(g1*(-1/delta-A1)-wr)-
     myexp(-delta*A0)*(g1*(-1/delta-A0)-wr);
  getyoungwt:=z;
end;

function getmybeta(beta,t,spawnstart:double):double;
var z:double;testtime:integer;
{*This function creates a seasonal beta value*}
begin
  testtime:=round(t*100)-100*round(t);
  IF testtime<0 THEN testtime:=100+testtime;
  IF testtime>(spawnstart+25) THEN z:=0
  ELSE IF testtime<spawnstart  THEN z:=0
  ELSE z:=3*beta;
  getmybeta:=z;
end;

function getmig1(im1,t,spstart:double):double;
var z,migstart,migend:double;testtime:integer;
{*This function is one of two controlling migration*}
begin
  testtime:=round(t*100)-100*round(t);
  migstart:=spstart-7;
  migend:=spstart+32;
  IF testtime<0 THEN testtime:=100+testtime;
  IF migstart>0 THEN BEGIN
  IF testtime>migend THEN z:=im1
    ELSE IF testtime<migstart  THEN z:=im1
    ELSE z:=0;
   end
  ELSE begin
    migstart:=100+spstart-7;
    IF testtime<migend THEN z:=0
    ELSE IF testtime<migstart THEN z:=im1
    ELSE z:=0;
  end;
  getmig1:=z;
end;

function getmig2(im2,t,spstart:double):double;
var z,migstart,migend:double;testtime:integer;
```

```
begin
{*This function is one of two controlling migration*}
  testtime:=round(t*100)-100*round(t);
  migstart:=spstart-7;
  migend:=spstart+32;
  IF testtime<0 THEN testtime:=100+testtime;
  IF migstart>0 THEN
  begin
    IF testtime>migend THEN z:=0
    ELSE IF testtime<migstart  THEN z:=0
    ELSE z:=im2;
  end
  ELSE begin
    migstart:=100+spstart-7;
    IF testtime<migend THEN z:=im2
    ELSE IF testtime<migstart THEN z:=0
    ELSE z:=im2;
  end;
  getmig2:=z;
end;


PROCEDURE Get_History( VAR History:HVEC; Coeffs:CVEC;
                      time:DOUBLE );
{*This function establishes the histories of any*}
{*variables where previous values are needed    *}
BEGIN ;
  History[1]:=rstar;
END;

PROCEDURE Get_Initial_State( VAR Init:SVEC; C:CVEC );
VAR num,age,wt,len:INTEGER; N0,A0,A1:DOUBLE;
{*This function gives initial values for the State Variables*}
BEGIN  ClockGrad:=1/CohortWidth;
  Init[Clock]:=0.0;
  beta:=C[1];
  FOR num:=1 TO Cohorts DO
  BEGIN age:=num+Cohorts; wt:=age+Cohorts;
    A0:= (Cohorts-num)*CohortWidth;
    A1:= (Cohorts+1-num)*CohortWidth;
    IF A0>=4 THEN Init[num]:=myexp(-1.4)*(5)*
                        getnumber(A0,A1,deltao,rstar)
    ELSE IF A0>=3 THEN Init[num]:=myexp(-1.2)*4*
                        getnumber(A0,A1,delta3,rstar)
    ELSE IF A0>=2 THEN Init[num]:= myexp(-0.9)*1/delta2*
                        getnumber(A0,A1,delta2,rstar)
```

```
    ELSE Init[num]:=5/4*getnumber(A0,A1,delta1,rstar);

    IF A0>=4 Then Init[age] :=getage(deltao,A1,A0)*Init[num]
    ELSE IF A0>=3 THEN Init[age]:=getage(delta3,A1,A0)*
                        Init[num]
    ELSE IF A0>=2 THEN Init[age]:=getage(delta2,A1,A0)*
                        Init[num]
    ELSE  Init[age]:=getage(delta1,A1,A0)*Init[num];

    IF A0>=4 THEN Init[wt]:=rstar*myexp(-1.4)*wf*
                           getoldwt(b,g2,A0,A1,deltao)
    ELSE  IF A0>=3 THEN Init[wt]:=rstar*myexp(-1.2)*wf*
                        getoldwt(b,g2,A0,A1,delta3)
    ELSE IF A0>=myswitch  THEN  Init[wt]:=rstar*myexp(-0.9)*
                        wf*getoldwt(b,g2,A0,A1,delta2)
    Else IF A0>2 THEN
      IF A1>myswitch THEN Init[wt]:=rstar*myexp(-0.9)*
            (wf*getoldwt(b,g2,myswitch,A1,delta2)+ 1/delta2*
    getyoungwt(A0,myswitch,g1,wr,delta2))
      ELSE Init[wt]:=rstar*myexp(-0.9)/delta2*
            getyoungwt(A0,A1,g1,wr,delta2)
    ELSE Init[wt]:=rstar/delta1*
            getyoungwt(A0,A1,g1,wr,delta1);
  END;
  CurRecCo:=1;
END;

PROCEDURE Get_Gradient( VAR G:SVEC; S:SVEC; C:CVEC;
                      t:DOUBLE );
VAR  num ,age,wt:INTEGER;
  CoR,R,AdWt,TOTWT:DOUBLE;
AVAGE, pmat,delta,CoG, AVWT:shortarray;
{*This function gives the differential equations to Solver*}
BEGIN
  findavage(S,0,Avage);
  findpmat(Avage,py,px,pmat);
  Adwt:=findadwt(0,S,pmat);
  R:=Pastvalue(1,t-0.5);
  getavwt(S,0,AVWT);
  getmortality(AVWT,al,wr,1,delta);
  getcog(Avage,myswitch,wf,b,g2,g1,CoG);
  FOR num:=1 TO Cohorts
  DO BEGIN age:=num+Cohorts; wt:=age+Cohorts;
    IF (num=CurRecCo) THEN CoR:=R ELSE CoR:=0.0;
    G[num]:=CoR - delta[num]*S[num];
    G[age]:=CoR*0.5+S[num] - delta[num]*S[age];
```

```
    G[wt]:=CoR*wR+CoG[num]*S[num]-delta[num]*S[wt];
  END;
  G[Clock]:=ClockGrad;
END;


PROCEDURE Get_Memo(VAR memo:MPAD; VAR S:SVEC; C:CVEC;t:DOUBLE);
VAR num,age,wt:INTEGER;
TotWt,AdWt,R,mybeta,Adnum:DOUBLE;
AVAGE,pmat,avwt,delta: shortarray;
{*This function writes the output, plots variables, recycles*}
{*the cohorts, and sets the historic values                 *}
BEGIN
  IF S[Clock] > ClockThreshold
  THEN BEGIN
    IF CurRecCo<Cohorts THEN CurRecCo:=CurRecCo+1
       ELSE CurRecCo:=1;
    num:=CurRecCo; age:=num+Cohorts; wt:=age+Cohorts;
    S[num]   :=0.0;
    S[age]   :=0.0;
    S[wt]    :=0.0;
    S[Clock] :=0.0;
  END;
  findavage(S,0,Avage);
  findpmat(AVAGE,py,px,pmat);
  Adwt:=findadwt(0,S,pmat);
  R:=findrec(0,S,beta,Adwt,pmat);
  WITH memo DO
  BEGIN
    opt[1]:=R;
    opt[2]:=Adwt;
    plt[1]:=R;
    plt[2]:=AdWt;
    HIS[1]:=R;
  END;
END;
```

# Appendix C

# Taguchi Sensitivity

This Appendix includes graphs mentioned in Chapter 7.

Figure C.1: Interaction Plots: *The interaction plots for the full design fishing model are given. The black line is the low level, red the medium level and green the high level.*

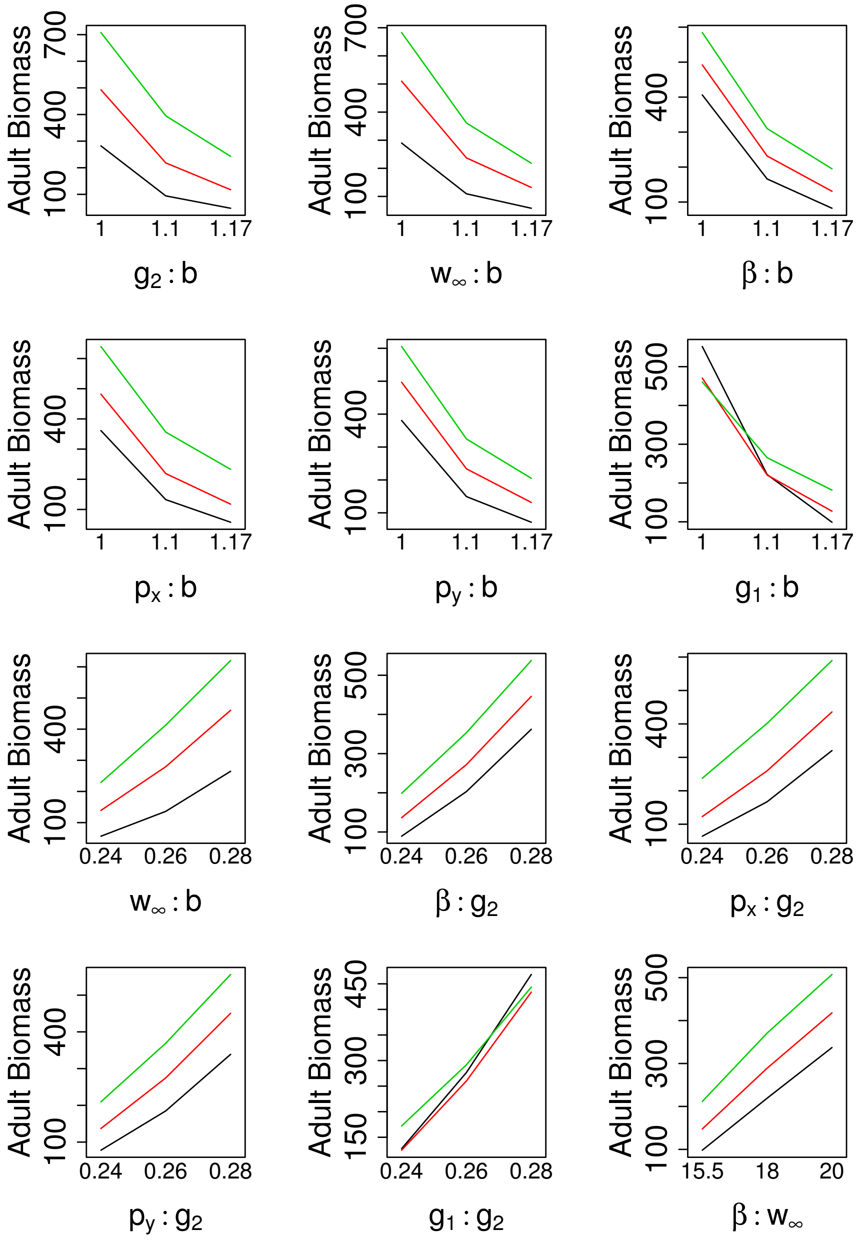


Figure C.2: Interaction Plots (Continuation). The black line is the low level, red the medium level and green the high level.

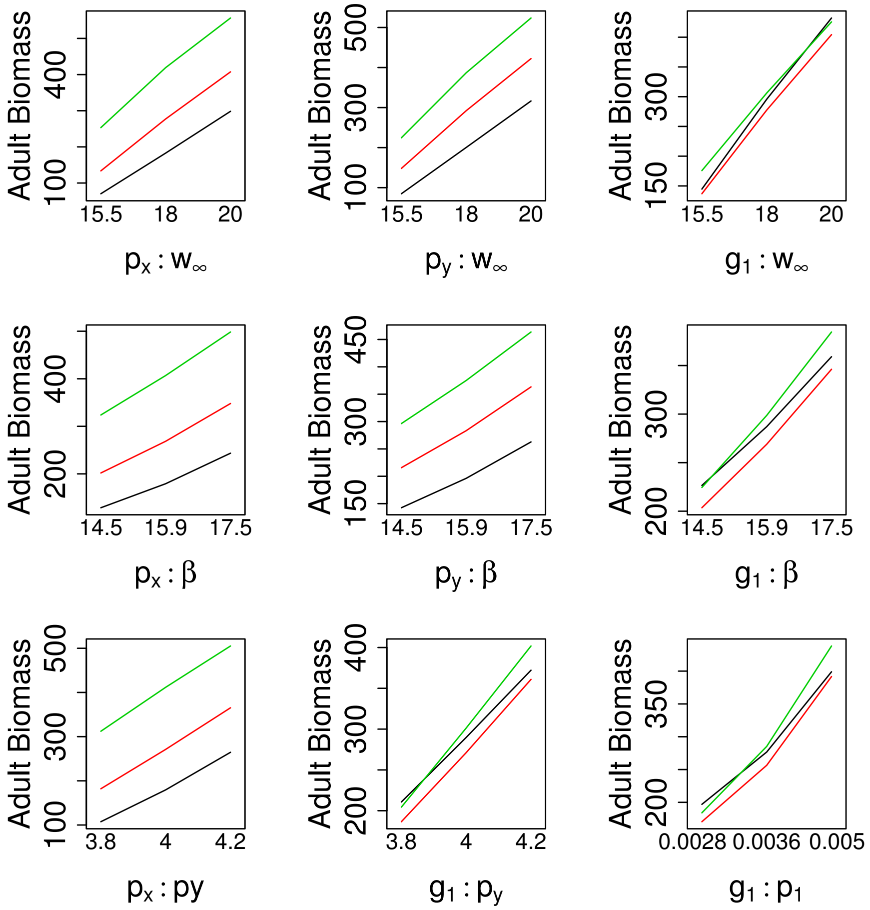


Figure C.3: Effect Plots : *The full and fractional effect plots when proportion mature is modelled with a cumulative gamma(3) distribution.*

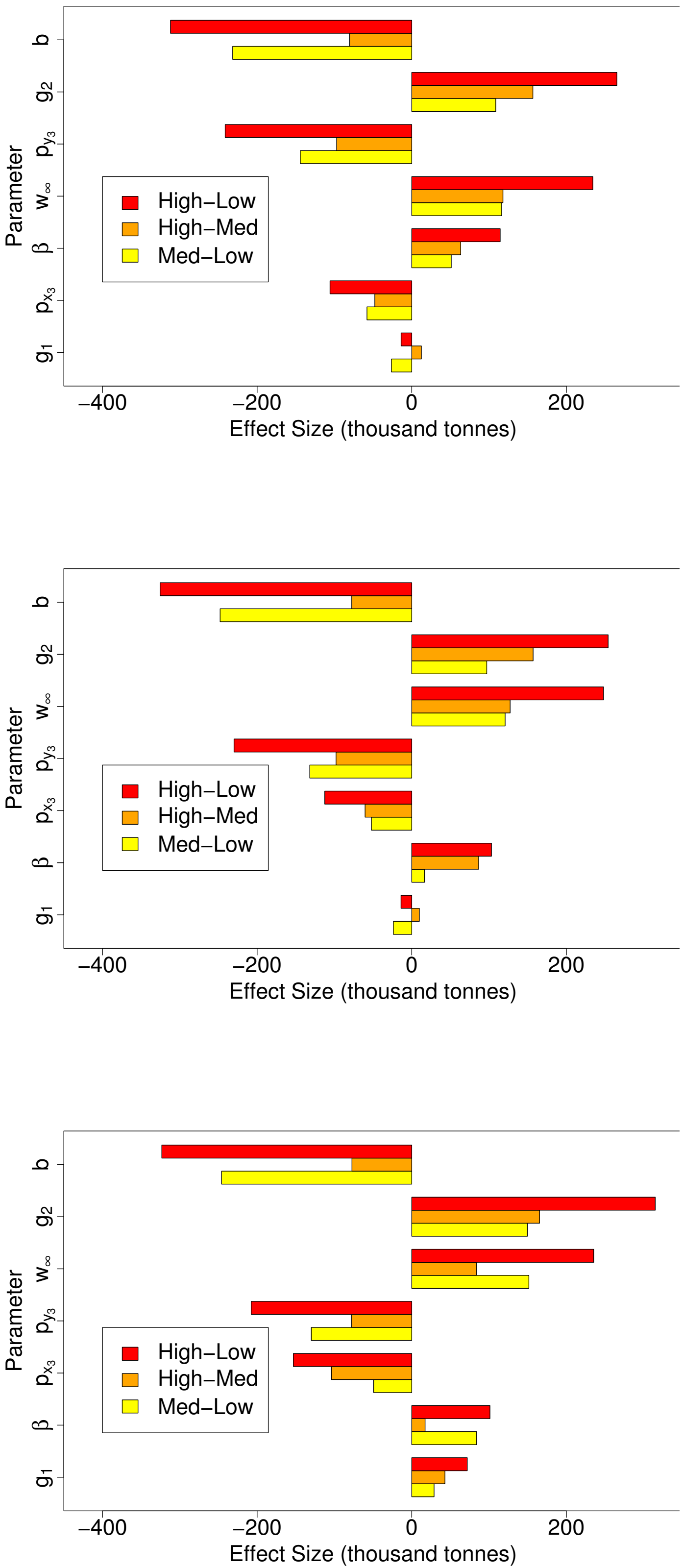


Figure C.4: Concurrent Maturation Effect Plots: *The full and fractional effect plots when proportion mature is modelled with a single maturation age*

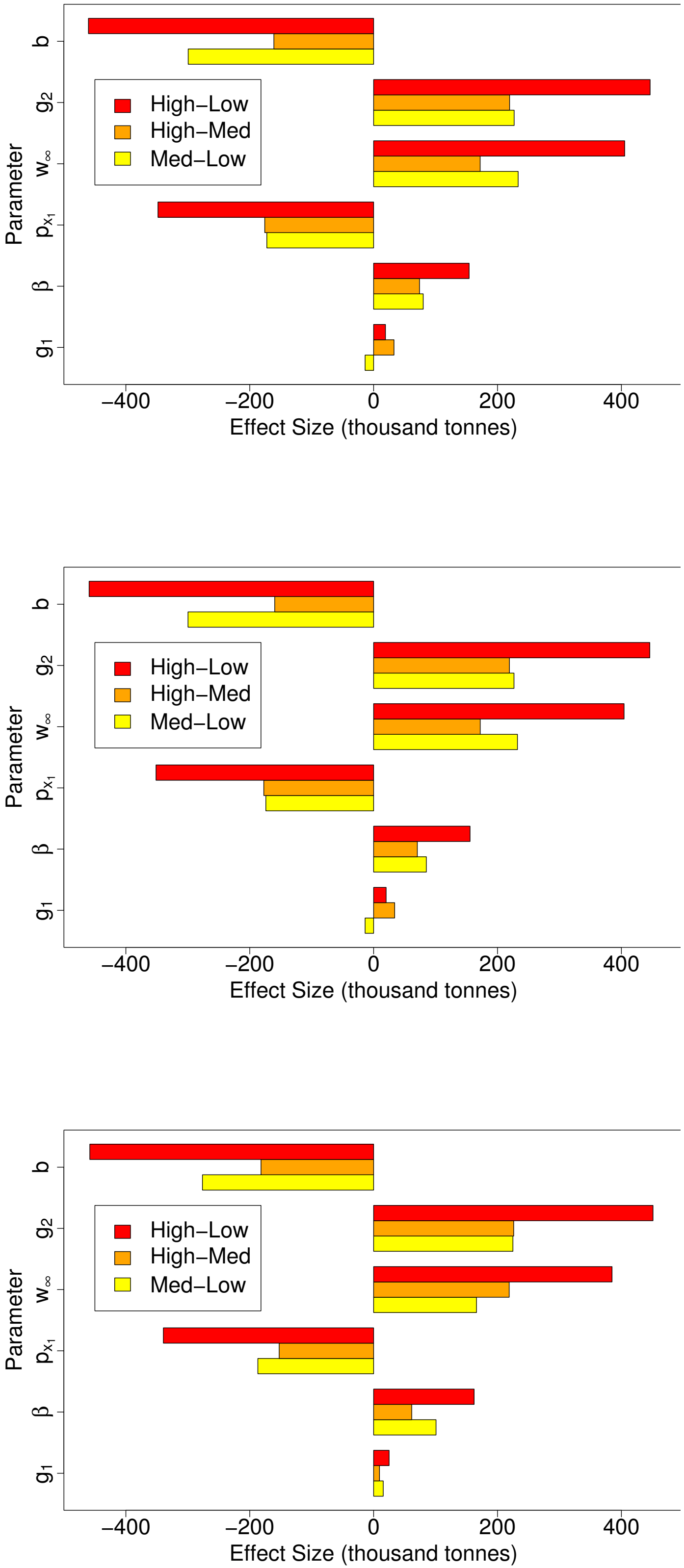


Figure C.5: Exponential Effect Plots: *The full and fractional effect plots when proportion mature is modelled with an exponential distribution.*

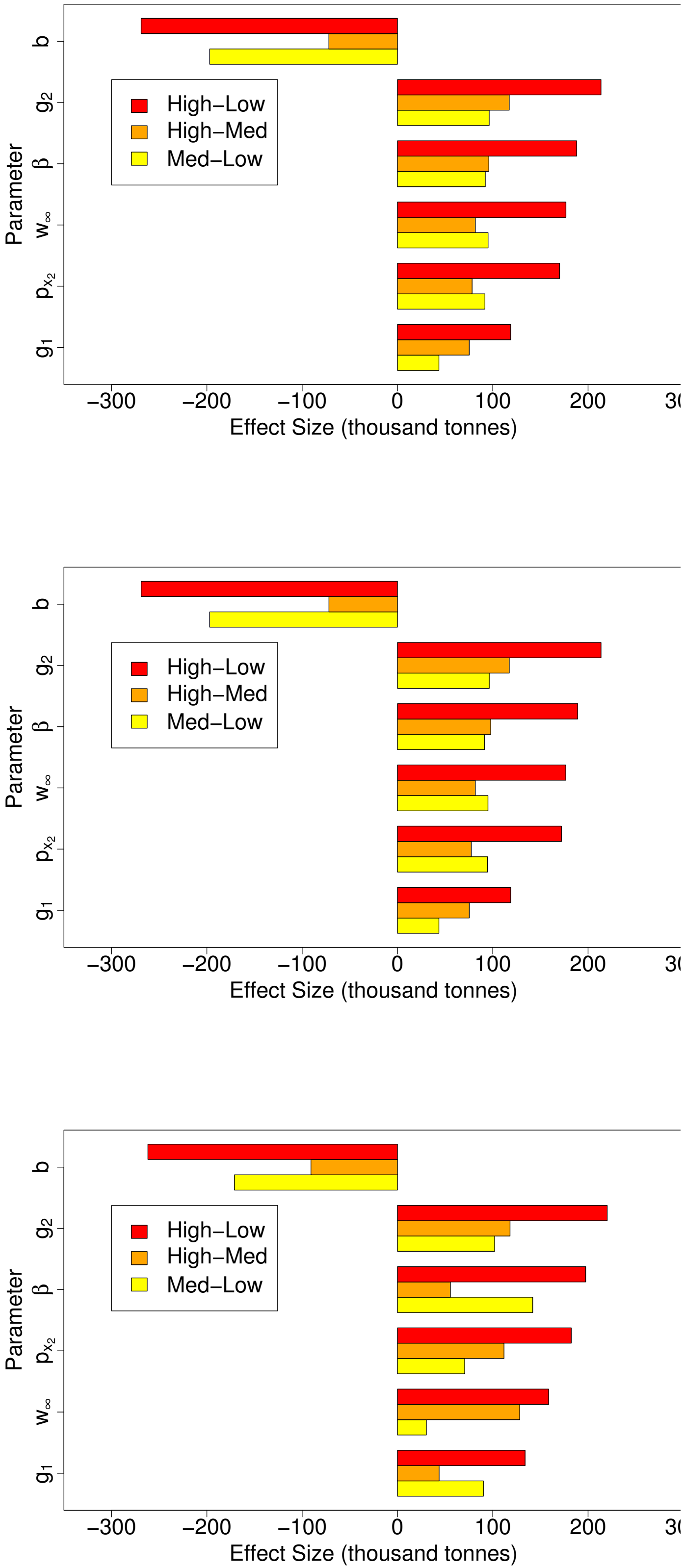


Figure C.6: Gamma(4) Effect Plots: *The full and fractional effect plots when proportion mature is modelled with a cumulative gamma(4) distribution.*

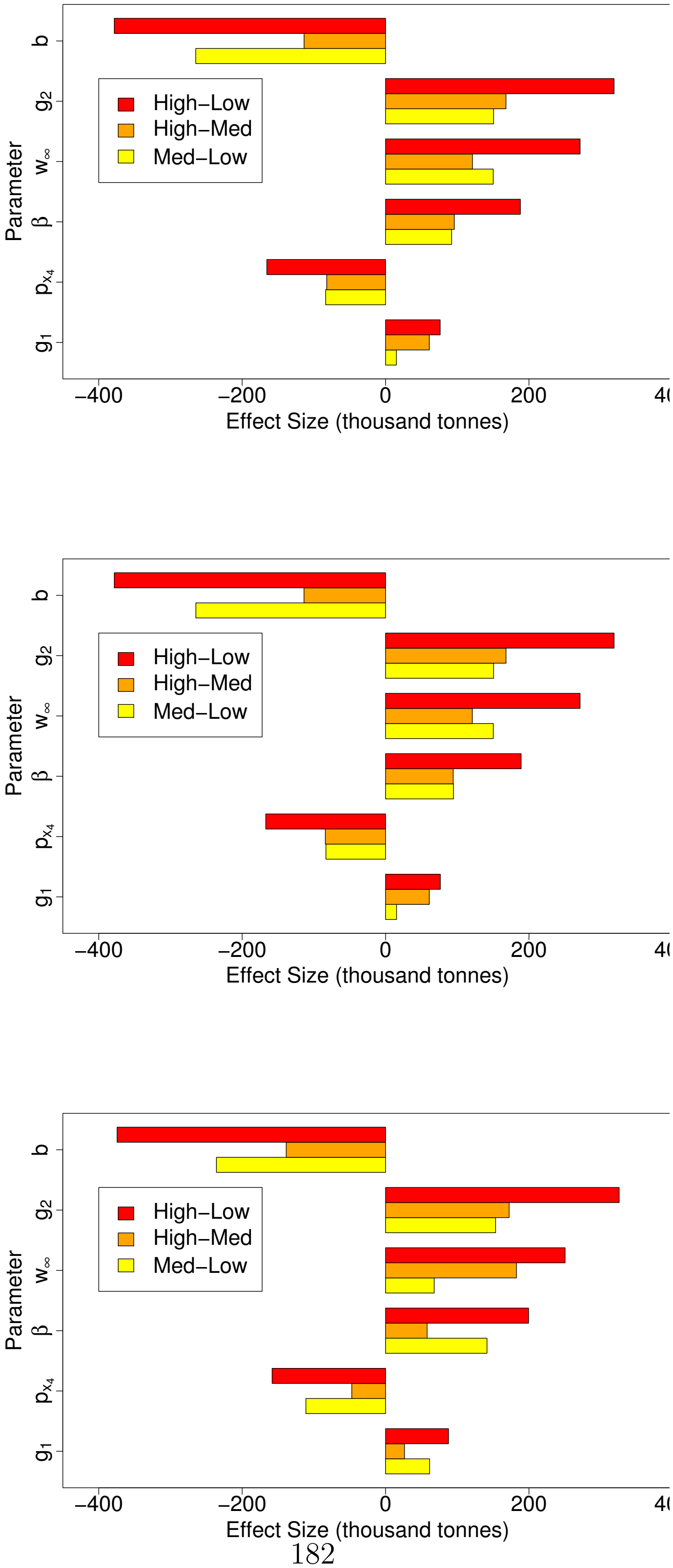
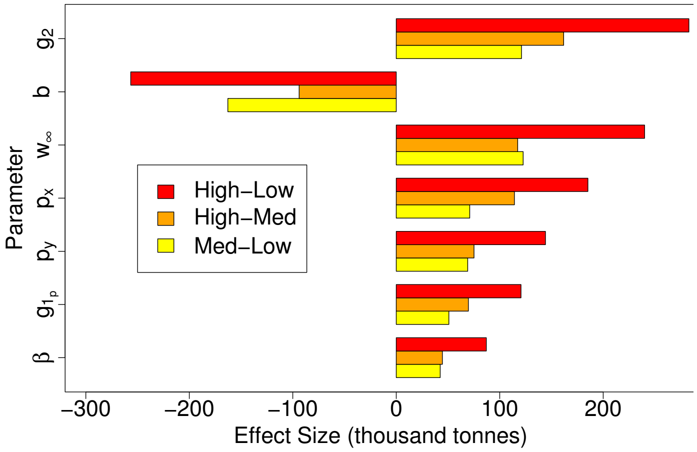
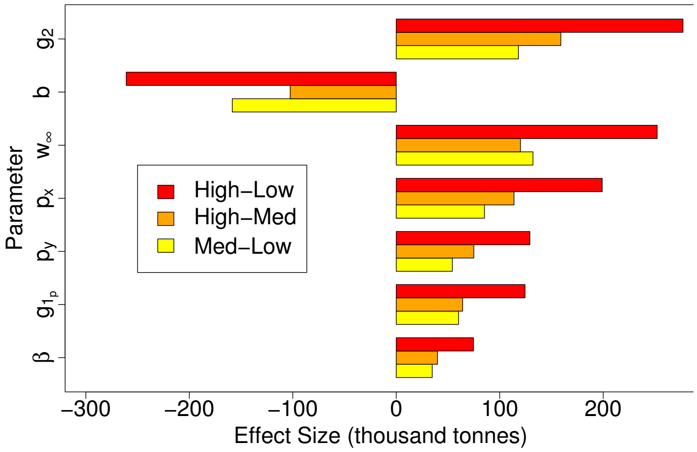


Figure C.7: The Effects of Life History Parameters: *The full and fractional effect plots when growth is modelled with a power curve.*





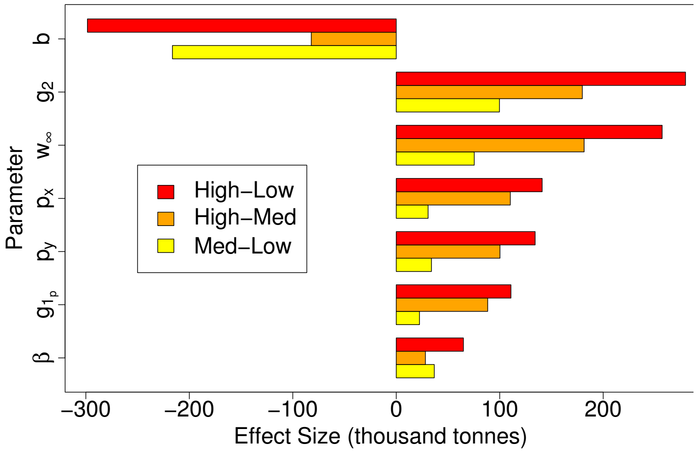


Figure C.8: The Effects of Life History Parameters: *The full and fractional effect plots when growth is modelled with a logistic curve.*

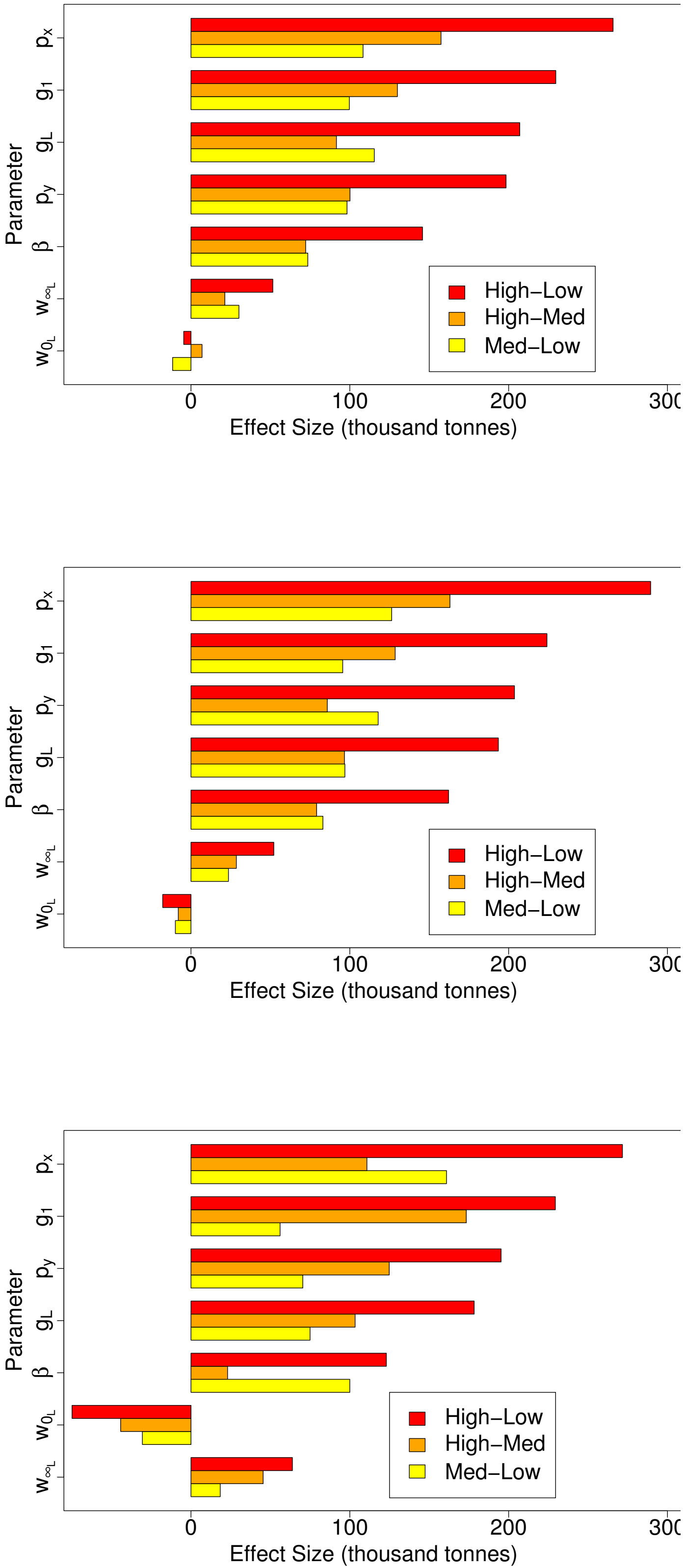


Figure C.9: The Effects of Life History Parameters: *The full and fractional effect plots when growth is modelled with a Gompertz curve.*

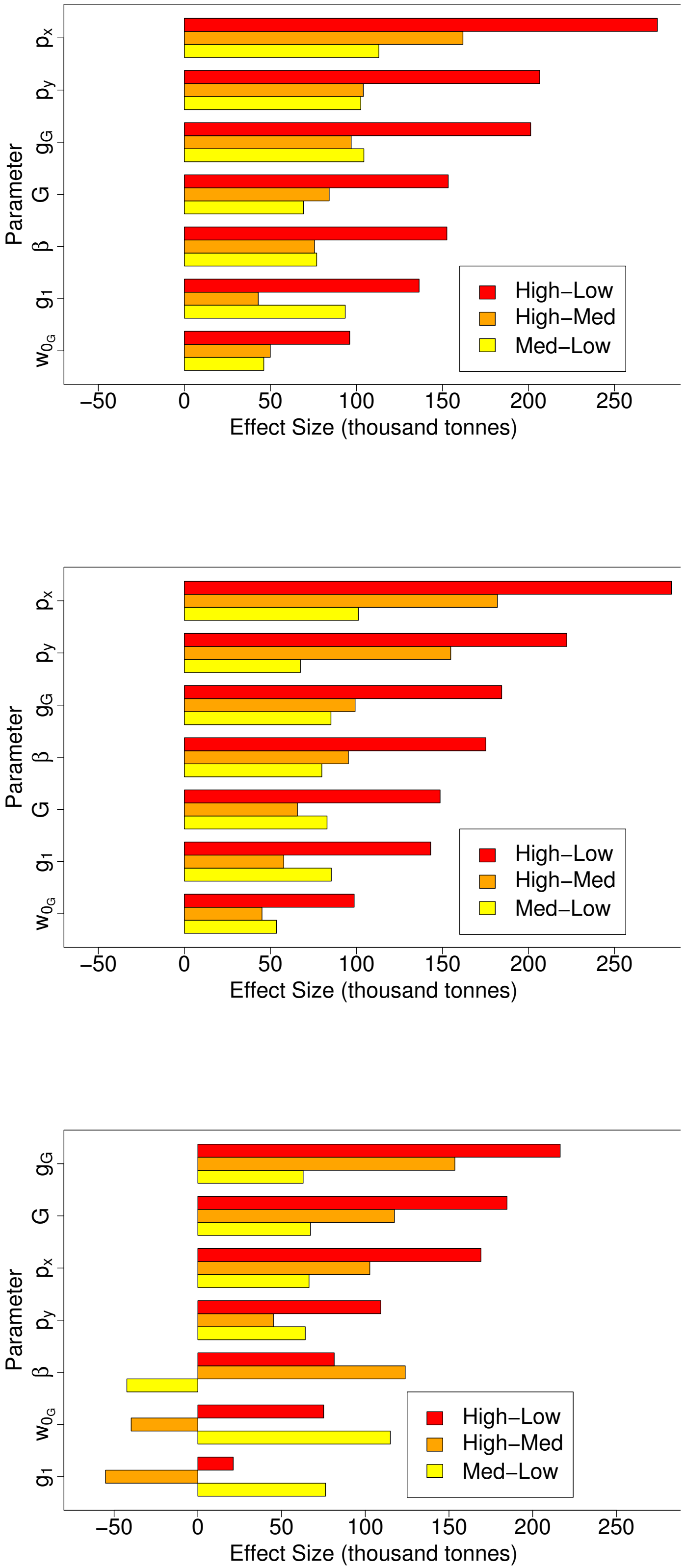


Figure C.10: The Effects of Fishing Parameters: *The effects of fishing in the models where all fish mature at the same time, fish mature exponentially, and fish mature following a gamma(4) function.*