HARVESTING OF AGE STRUCTURED FISH POPULATIONS

Doctoral Dissertation

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To my parents, my wife and my children.
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Osnabrück, Germany  Mostafa Kamel Saber Mohamed
2005
Synoptic view of the study

(Abstract)

The aim of this thesis is to define and study harvesting models of fish populations. These models are applied to particular fish species e.g., haddock and cod. The thesis is divided into five chapters:-

The first chapter is considered as an introductory one. In it, basics of fish biology and the recruitment process are defined. Two simple recruitment models known by the names Ricker and Beverton-Holt are used.

In the second chapter the generalized Leslie model or Usher model is introduced. In section 2.2, some matrix theory is presented. For this matrix model, the net reproductive number is defined and studied in section 2.3. It turns out to be more useful than the spectral radius. In section 2.4, this study is extended to nonlinear matrix models. The nonlinearity, however, is defined only by the recruitment process. This allows to determine the equilibrium components.

Finally section 2.5, the local stability of nonlinear matrix models is analyzed.

Harvesting of such general matrix model is defined in chapter 3. We distinguish three different harvesting models (selective, net and semicontinuous harvesting models).
In chapter 4, these harvesting models are then applied to concrete fish populations and analyzed with respect to its various parameters.

In chapter 5, the stability is studied again along the lines of the paper of Levin, Goodyear [18].

The key results in this study are:-
1) The maximum sustainable yields for selective harvesting and net harvesting are rather close.
2) Semicontinuous harvesting is more realistic harvesting models.
3) From a quantitative point of view, the choice of the recruitment function is important.
4) Harvesting process increases mortality and stability when we used Ricker recruitment model.
5) Stability of populations always holds if we use Beverton-Holt recruitment model.
Chapter 1

Mathematical Models for fishery

In this chapter we collect some important materials in biology of fish and harvesting of fish.

§ 1.1 Introduction

More than two thirds of the surface of the earth are covered by oceans or seas. As a result, fish and other marine products form an important source of food, in particular protein, for mankind. This role of marine products is still rising, because land for agriculture has been overexploited to a large extent and no new areas for agriculture can be found, because of a limitation of water.

Fishing technology has developed from small boats to swimming fishing factories with sophisticated equipment for detecting, catching and processing fish. This development was pressured and directed by an ever increasing population with a high demand for food in particular protein rich food. Thus many areas, in particular the traditional fishing areas e.g. the Northern sea, the Baltic sea or North Atlantic are overfished and a number of species of fish are near extinct e.g. herring or canadian cod. In fact in the fall of 2002 the EU proposed a complete ban on the fishing of cod because of an almost complete lack of juvenile fish. As a result of this overfishing the catch has been reduced from 270.000 ton in 1970 to 40.000 in 2000. Similarly Canada closed the cod fishery in the canadian great banks in 1992. But the cod stocks still do not show any sign of recovery with serious consequences for the canadian fishing industry. Nations with a large commercial fishing industry are particularly reluctant to agree on impose limitations for fishing. In many cases, countries have unilaterally declared fishing zones near their coasts.
Thus competition and political conflicts between fishing nations arose. This uncontrolled overexploitation of the seas has shown the need to control fishery on an international scale. On the other hand, an effective control is difficult to implement even with modern technology like planes, radar, or satellites, because of the vastness of the sea.

Effective controls are also difficult to implement politically as can be seen with the example of whaling with Japan, Russia and Norway. Thus violations of regulations are common in this domain. Yet fishery offers a large potential for the increase of food production if appropriate measures of control are introduced.

By now fishing in the North sea or North Atlantic is largely regulated. These regulation specify size of catch, the width of meshes of fishing nets, the form of fishing and species caught. So far this control is far from optimal, because of a lack of reliable data, a lack of effective control and a tendency to violate the rules.

Politically effective control measures are difficult to implement, because in many cases the fishing industry makes up an important part of the economy of a country. Thus efficient and optimal controls and regulations are watered down by politicians pursuing unilaterally their or their countries interests. In many cases they take advantage of the fact that data are not precise and scientists are overcautious in their interpretation of results.

Thus now, as many conservation biologists argue, we are but a few decades away from a worldwide collapse of fishery [Nature 419 662-665, 2002]. Even though many environmental biologists now criticise the use of individual species models and demand whole ecosystem approaches we will develop here single species optimal fishing models, because these would be part of an overall systems model anyway.
A draw back of the single species models so far is a lack of understanding of depensation, i.e the ability or inability of recovery from low or very low stock levels. At present there is no direct proof for depensation and possible effects causing it are not well understood. Decreased predation and other multispecies effect may be responsible for this. Altogether one needs robust models which operate almost optimally even on fuzzy knowledge. A serious problem in this context is the by-catch which in many cases makes up to one quarter of the intended catch. The FAO estimates that $8 \times 10^7$ ton of fish lead to about $25 \times 10^6$ tons by-catch which is returned to the sea, mostly dead. The by-catch will quite often consist of juveniles of protected fish. Thus it may also be responsible for depensation.

The control and optimization of yield will require a series of political and technological steps like binding international agreements on size and structure of catch, verification of size and structure of fish stocks or limits to equipment and modification of equipment. Based on reliable data, it should be possible to give detailed recommendation for the fishing industry so that in the long run, the catch can be optimized.

This is the problem of maximum sustainable yield (MSY). For such recommendations mathematical models, as they are used for whaling and some fish species now, are important. A serious problem for modeling is a lack of reliable data, because these are mostly inferred from actual catches and a few isolated studies. Unreported catches and unreliable reporting of catches may lead to serious errors in the data. Even though fresh water fishery and fish farming are increasingly important, we shall concentrate here on marine fishery, because it yields between 60% to 80% of all fish caught.

\[1 \text{ Fishery experts agree that with proper technology and strategy the overall catch could be doubled.}\]
Table 1.1: list of important food fish and its description

<table>
<thead>
<tr>
<th>fish</th>
<th>habitat</th>
<th>description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Herring</td>
<td>Northern; inshore; pelagic; schooling; plankton feeders</td>
<td>20 to 40 cm.; silvery, rather deep-bodied; sawlike scales on belly</td>
</tr>
<tr>
<td>Pilchard and sardine</td>
<td>Temperate; inshore; pelagic; schooling; plankton feeders</td>
<td>15 to 20 cm.; silvery, with row of dark spots on side behind head; cylindrical</td>
</tr>
<tr>
<td>Tuna</td>
<td>tropical; offshore; pelagic; schooling; fish eaters</td>
<td>61 to 305 cm.; darkish above; row of finlets on back and belly</td>
</tr>
<tr>
<td>Anchovies</td>
<td>tropical; inshore; pelagic; schooling; plankton feeders</td>
<td>to 16 cm.; usually cylindrical; piglike overhanging snout</td>
</tr>
<tr>
<td>Atlantic salmon</td>
<td>north temperate; anadromous; loose schooling; fish eaters</td>
<td>61 cm. or more; silvery or brown, with many spots on sides; adipose fin on back</td>
</tr>
<tr>
<td>Pacific salmon</td>
<td>north temperate; anadromous; loose schooling; fish eaters</td>
<td>45 cm. or more; silvery or brown, with many spots on sides; adipose fin on back</td>
</tr>
<tr>
<td>Cod</td>
<td>northern; bottom; mollusk eaters</td>
<td>61 to 110 cm.; greenish or reddish; cylindrical; three dorsal and two anal fins</td>
</tr>
<tr>
<td>Haddock</td>
<td>northern; bottom; mollusk eaters</td>
<td>25 to 47 cm.; grayish with dark spot on shoulder; cylindrical; three dorsal and two anal fins</td>
</tr>
<tr>
<td>Hake</td>
<td>temperate; inshore; loose schooling; fish eaters</td>
<td>25 to 79 cm.; grayish cylindrical; two dorsal and one anal fin</td>
</tr>
</tbody>
</table>
Among the marine fishes, one distinguishes demersal fish, living at or near the bottom and pelagic fish living in the ocean. Demersal fish are cod, haddock, hake, pollock and various forms of flatfishes. Herring, tuna and their relatives are pelagic. Fishing methods and gear are of course adapted to the type and habitat of fish. An international classification of fishing methods recently adopted includes 16 types:

1. Fishing without gear.
2. Grappling and wounding gear.
4. Line fishing.
5. Trapping.
6. Trapping in the air.
7. Fishing with bag nets.
8. Dredging and trawling.
10. Fishing with surrounding nets.
11. Driving fish into nets.
12. Fishing with lift nets.
13. Fishing with falling gear.
15. Fishing with entangling nets, and

Of these only net fishing of pelagic fish and dredging and trawling of demersal fish are commercially important. The most important here is the surrounding nets used on pelagic fish shoals like tuna, herring, sardines and mackerels. Gill nets and long lines are also used. Modeling the harvesting of fish and optimizing the catch requires a good knowledge of their biology and physiology.
§ 1.2 The Biology of Fish

Fishes have been living on this earth for almost 500 million years. Thus they occupy all possible niches of the seas and vary greatly in their structure and habitat. Here we will concentrate essentially on the commercially valuable marine fish. All life in the sea is eventually based on small plants in the top 50 m of the sea, the photic layer. These plants, algae mostly, are eaten by small copepods and crustaceas of 0.3 – 3 mm in length. These two classes thus form the two lowest levels of aquatic food webs. These animals in turn are eaten by smaller fish and those again by bigger fish, which make up the higher layers of aquatic food webs.

Eggs and larvae

One of the most remarkable characteristics of fishes is their high fecundity. A herring for example will lay about $5 \times 10^4$ eggs in each spawning. A cod up to $10^7$. Correspondingly the eggs are rather small about 1-2 mm diameter. Exceptions are salmon, halibut, the eggs of which are 4-5 mm diameter. Eggs have an extremely high mortality of up to 7% per day for cod. A 7% mortality per day means that the survivability for 200 days for example is $0.93^{200} \approx 4.97 \times 10^{-7}$.

Some species put the eggs directly into the sea – pelagic eggs. Others e.g. herring put them on the sea bed or sheltered places for better protection. The pacific salmon for example spawns on the gravel redds in rivers during the autumn and winter. Their eggs take about a week to hatch. Because the eggs and young fish larvae require moderate temperature and particular external conditions and more protection, many marine fish travel to particular spawning grounds. This happens usually in a yearly cycle, which is tied to the cycles of plankton growth, because fish larvae live on this plankton.
The abundance of plankton depends on various external factors like sunlight, salinity and temperature of the water. In recent years pollution has an increasingly negative effect on plankton growth. These external factors have an immediate influence on the growth of fish larvae and thus an indirect influence on the recruitment of fish. Thus, the fish stocks exhibits large fluctuations. Larval growth depends critically on the abundance of food since the larvae grow from 1 mm egg to 20-30 mm in the first year. So at young age they will consume food at a daily rate which is higher than their body weight. Thus recruitment is closely determined by the availability of plankton. An increase from a 1 mm egg to a 1 gm recruit however will take about 120 days.

Larval fish die almost as quickly as they grow, e.g. plaice at 5 % per day, haddock at 10 % per day, cod at 10 % per day and herring at 4 % per day. The death rate of either eggs or larvae depends upon their numbers (density-dependent mortality). The main reasons of mortality are lack of food and predators. During its life a large cod may grow by seven orders of magnitude from an egg weighing 1 mg to an adult of 10 kg.
Since the growth of plankton depends strongly on external conditions (temperature, sunlight, weather, salinity of the water), recruitment should be considered as a stochastic process, which proceed in the following stages

\[
\text{Egg} \rightarrow 1 \text{ month larvae} \rightarrow \ldots \rightarrow 1 \text{ year fish}
\]

Recruitment

Figure 1.1. Diagrammatic recruitment for fish.

i.e. recruitment will lead to a stochastic input into the dynamical equations. Recruitment is thus not only density dependent, but also varies strongly with external conditions. As yet recruitment is poorly understood and it is difficult to determine statistically the influence of various factors. For fish in lakes, density dependent recruitment has been established. For marine fish however, whose density may be three orders of magnitude lower, this is not so. Indirect evidence for this would be the synchronization of spawning with the plankton cycles. Here, an extension of the spawning period would make fish larvae less sensitive to the plankton cycle, while exposing larvae more to predators. The match-mismatch hypothesis of Cushing [5] explains the fluctuation due to recruitment by a lack of matching between spawning and plankton cycle. Thus fish with a longer spawning period should be less sensitive to plankton cycle variations. One could consider recruitment as a series of stages, where the transition to the next stage is successful only, if sufficient food is available.

Thus the variability of year classes of fish is high. This becomes apparent when one considers actual catch data in various years.
Spawning grounds are mostly in more shallow and temperate water zones to which the mature fish migrate once a year. When the eggs hatch the larvae are ready to settle on a nursery ground (larval drift which means the migration from spawning ground to nursery). The motion to the nursery ground is aided and depends on the current system. The larvae live off the plankton and small copepods. As they grow, they move from their shallower nursing grounds to deeper water. The commercially used species are abundant and during their adult lives they migrate periodically from their feeding ground to spawning ground.

The spawning season may last from 10 days as for herring to 3 months as for cod, but its main part is usually concentrated to a short time interval.

With some tuna, however this spawning season is spread over the whole year. Most fish are spawning in spring or autumn, depending on the onset of planktonic growth. The term of recruitment is not well defined. Some scientists use it to describe the recruitment to the adult class or the class which is commercially exploited. Others describe it as the recruitment to the class of fertile adults.
**Adult fish, growth and mortality**

As fish get older, they join the adult groups, most of which move in large shoals through the open sea and migrate with a yearly cycle from feeding ground to spawning ground.

![Diagrammatic migration circuit used by fish](image)

*Figure 1.2. Diagrammatic migration circuit used by fish*

For majority of fish, the growth is isometrically which biologically means growth occurs without changing either its shape or its density.

Mathematically, the growth of adult fish is generally described by von Bertalanffy growth equation

\[ L(t) = L_\infty (1 - e^{-k(t-t_0)}) \]

where \( L(t) \) is length.

By scaling this gives for the weight

\[ W(t) = W_\infty (1 - e^{-k(t-t_0)})^3 \]

where \( K \) is von Bertalanffy growth parameter which biologically measures the rate of growth Beverton and Holt [2].
The growth rate of individuals depends upon the mortality rate of the population. Adult fish grow relatively little and relative weight increments in juvenile fish generally exceed those of adult fish. During the immature phase of the life history, the average growth rate of the fish population is density dependent. This phenomenon has been widely observed in Atlantic cod, haddock, Atlantic herring and Pacific sardine.

Mortality is the ratio of individuals of a population dying in a given period. The fishing mortality, caused by catches, is often greater than the natural mortality which is caused by many natural factors such as predation or starvation. The fishing mortality may exceed the natural mortality by a factor of two or three. Some species die at once after the first spawning as some Gobiidae or salmons. Mortality of eggs and young larvae is extremely high. During the life cycle, mortality decreases with age in the juvenile stage and after middle age, mortality increases exponentially with age amongst older adult stage [Gompertz domain]. If the total exploited area can be taken as constant in size and if fishing is distributed either uniformly over it or in a constant way relative to the fish concentrations, then fishing mortality will be proportional to the fishing effort. This latter term is usually measured in fishing days.
**Fecundity**

Fecundity is the total amount of eggs produced by a female during a single reproductive cycle. Fish are very fecund and lay as may as $10^4$ to $10^7$ eggs in each spawning per female. In fish population, an estimate of the number of eggs laid by an age group is obtained by multiplying the number of breeding females by their average fecundity Pitcher, MacDonald [26]. Fish populations are more fecund in lower latitudes and species in the Pacific are more fecund than similar ones in the Atlantic. These difference are due to the pressure of predators. Fecundity is usually proportional to the weight i.e., if the eggs are of the same size, bigger fish are more fecund than smaller ones. In the literature, fecundity is sometimes related to the biomass. Here, however we shall usually relate it to individual fish.
§1.3 Specific Fish Species

**Herring**

The herring is found in different forms in both the North Pacific and North Atlantic Oceans. These have been grouped together as a single species. Both types of herring have similar feeding habits, produce demersal eggs and have pelagic larvae. Atlantic herring spawns at various times throughout the year and does so at depths of 40-200 m. They spawn on shingle or gravel beds which may sometimes be far from the shore or oceanic rises. Pacific herrings spawn in the spring with the heaviest concentrations in March. They spawn in shallow coastal water and deposit their eggs on various seaweeds as well as on different abiotic substrates. Spawning period of herring lasts 2 or 3 weeks. Herring display seasonal migrations that cover a relatively large area. They also perform a daily vertical migrations over short distances. Atlantic herring stocks inhabit deep water during the daytime and migrate vertically to the surface at sunset. The fish move close to the coast near the spawning grounds about five to six weeks before spawning. In late Autumn and winter, Pacific herrings move into inshore water in their pre-spawning migration.

Young herrings spend their first year of life in inshore waters and their second in an offshore nursery ground. In the third year of life individuals larger than 19.5 cm in length become mature and recruit to the adult classes. If, however, an individual does not reach to 19.5 cm by its third year, it does not become mature and does not recruit to the adult class until its fourth year. Similar statements hold for other fish species.
In the southern North sea, herring eggs take three weeks to hatch. Spawning occurs between February and April after which the herring appear to move north, northwest and west. They move north with the current during spring and summer at a time when populations of copepods are increasing. The maximum age of herring is 20-25 years with a maximal weight of 1000 gm and a length of about 40 cm.

Maturity begins with 3-7 years with a weight of about 125 gm. Mortality of herring is about 0.1-0.2. Maximum fertility of herring is between 20,000 to 50,000 eggs/year.

**Cod**

Cod species have a wide distribution over the North Atlantic Ocean, ranging from the middle United States to Baffin Island on the west. Cod usually spawn from February to June in cold water near the bottom or further up in the water column. The spawning period of cod lasts 2 or 3 months. Fertilized eggs are distributed in the upper 100 m of the ocean and hatch in approximately two weeks.

The Arcto-Norwegian cod spawn in March-May in patchy areas off northern and mid-Norway, with spawning taking place mainly in the Lofoten region. Spawning occurs at the same sites each year, but the spawning depth varies considerably. Cod may possibly migrate to shallow inshore waters during the summer and return to deeper waters in the winter much in the same way as do young herring. As the cod grow they change their diet to small pelagic fish and some crustaceans. Depending on the race of cod, spawning begins at age 5, but it may be delayed for another 10 years.
There are spawning populations of cod on both the west and east sides of Greenland as well as near southern Iceland.

Cod that spawn along the Norwegian coast migrate north in April and spend the summer in the north and east parts of the Barents Sea. In the fall these fish move south and west to winter off the coast of Norway and eventually spawn near the coast in early spring. The young of these fish drift to the nursery areas which are in the northern part of the Barents Sea. The recorded returns to the feeding area in the Barents Sea are poor. However, this may be a reflection of the large size of the area.

There may be movement between isolated races within the general area. When the young cod start to feed on pelagic fish, they follow their food source and migrate principally with the current. When cod migrate to the spawning ground they are generally in deeper water, whereas the spent fish seem to migrate in shallower water with surface currents. The return spawning migrations may thus be in deeper counter-current systems. The maximum age of cod is 30 years with a maximal weight of 17 kg and length 1.1 m. Maturity begins with 8-12 years with a weight of 3-8 kg. Natural mortality of cod is rather close to 0.18 per year. Maximum fertility of cod is between 500,000 to 5,000,000 eggs/year.

**Plaice**

The plaice is found as far north as Iceland and the Faeroes and south along the coasts of France, Spain and Portugal with specimens being recorded in the Mediterranean Sea. They are found in the Irish Sea in the west and extend east to the North Sea, Baltic Sea and as far as the White Sea off the northwest coast of USSR.
The eggs and larvae of plaice are pelagic and thus are carried by currents from the spawning grounds to nursery areas. Plaice have completed metamorphosis by about eight weeks of their life when they descend to the bottom to feed mainly on benthic invertebrates. During the first few years of life the plaice are found in relatively shallow water (up to 20 m) and as growth continuous these older fish frequent deeper water.

At sexual maturity which takes place at age 3-4 years the plaice appears to return to its natal area. North sea plaice growth virtually ceases during the winter months.

Following the breeding season from January to March, first time spawners do not return to the deep water nursery areas from whence they came but disperse over larger feeding areas that overlap with those of other North Sea plaice races. Maximum age of plaice is 30 years with a maximum weight of 2.867 kg and length 51.25 cm. Maturity begins around 4-5 years with a weight of 210 gm. Mortality of plaice is about 0.18 for males and 0.13 per year for females. Maximum fertility of plaice is 180,000 eggs/year.

The biological difference between plaice and herring is that, the plaice grows twenty times in weight during its life in the fishery, whereas the herring only grows about one and one-half times. For plaice, the gain in numbers is greater than the loss in weight as fishing intensity increases. In other words, the little fish are caught before they have a chance to grow.
**Anchovy**

Anchovy is a small and short-lived pelagic species with maximum age of 5 years. The maximum weight of Anchovy is 35 gm and length 16 cm. Females begin to spawn at the age of 12 months. There are two spawning periods each year. In September it produces about 75 percent of the eggs for the year. A smaller one in January produces the remainder. A single anchovy produces between 13,000 and 20,000 eggs and there is a direct relationship between fecundity and size. Only adult anchovies are harvested because those younger than 12 months are too small to be caught in the nets. The average female anchovy weight is 16 gm. Mortality of Anchovy is about 0.2 per year.

**Haddock**

Maturity of male haddock begins approximately at an age of 5 years, for the females, only about 25% are mature when they are 4 years old, but more than 90% are mature by the age of 5. The 50% maturity size was found to be 41 cm for males and 46 cm for females. In January and February, Haddock species are approaching the spawning stage. In March the presence of some ripe and spent females in the catch indicates that spawning had begun. The maximum age of haddock is 20 years with a maximum weight of 1.34 kg and length 47 cm. Mortality of haddock is about 0.2 per year. Maximum fertility of haddock is 580,000 eggs/year.
Table 1.2: Biological parameters for some fish species

<table>
<thead>
<tr>
<th>Species</th>
<th>K “von Bertalanffy parameter”</th>
<th>Max age (m)</th>
<th>Max weight</th>
<th>Max length</th>
<th>Onset of fertility</th>
<th>Weight at begin of fertility</th>
<th>Mortality per year</th>
<th>Max Fertility Eggs/year</th>
</tr>
</thead>
<tbody>
<tr>
<td>Herring</td>
<td>0.35</td>
<td>20-25 years</td>
<td>1000 gm</td>
<td>40 cm</td>
<td>3-7 years</td>
<td>125 gm</td>
<td>0.1-0.2</td>
<td>20.000-50.000</td>
</tr>
<tr>
<td>Cod</td>
<td>0.12</td>
<td>30 years</td>
<td>17 kg</td>
<td>1.1 m</td>
<td>8-12 years</td>
<td>3-8 kg</td>
<td>0.2-0.3</td>
<td>500.000-5.000.000</td>
</tr>
<tr>
<td>Plaice</td>
<td>0.19</td>
<td>30 years</td>
<td>2.867 kg</td>
<td>51.25 cm</td>
<td>4-5 years</td>
<td>210 gm</td>
<td>0.13-0.18</td>
<td>180.000</td>
</tr>
<tr>
<td>Haddock</td>
<td>0.26</td>
<td>20 years</td>
<td>1.34 kg</td>
<td>47 cm</td>
<td>2 years</td>
<td>89 gm</td>
<td>0.2</td>
<td>580.000</td>
</tr>
<tr>
<td>Hake</td>
<td>0.8</td>
<td>15 years</td>
<td>3.8 kg</td>
<td>79 cm</td>
<td>3 years</td>
<td>0.3 kg</td>
<td>0.2</td>
<td>140.000</td>
</tr>
<tr>
<td>Anchovy</td>
<td>0.43</td>
<td>5 years</td>
<td>35 gm</td>
<td>16 cm</td>
<td>2 years</td>
<td>24.2 gm</td>
<td>0.2</td>
<td>13.000-20.000</td>
</tr>
</tbody>
</table>

Fig. 1.3. The relation between Von-Bertalanffy growth parameter $K$ and maximum age $m$. 
From fig. (1.3), the Von-Bertalanffy growth parameter $K$ is approximately linearly dependent on the maximum age $m$.

From linear regression method Douglas C. Montgomery, Elizabeth A. Peck and G. Geoffrey Vining [8], one can get the relation between $K$ and $m$ as:

$$K(m) = 1.06 - 0.03 m$$

with correlation coefficient $r = -0.967$

Also the relation between natural mortality $\mu$ and $m$ is

$$\mu(m) = 0.67 - 0.02 m$$

with correlation coefficient $r = -0.8$
§ 1.4 Stock and Recruitment

Recruitment describes the number of fish reaching a specific size or age. This may be 1 year, or maturity or the time when they are caught by commercial fishing gear. Recruitment can be expressed in units of numbers or biomass. A fish stock will consist of a number of different age or size classes of fish. Spawning level may be measured as the number of spawners, biomass of spawners, number of eggs, or some other measure of spawning potential i.e., the process lies in the mortality from egg to recruit. Factors that result in population changes that are unrelated to population size are known as density independent factors. Examples include climatic variables such as temperature. Factors that can influence populations in relation to the size of the population, such as competition, predation or disease, are referred to as density dependent factors.

Since adult fish migrate freely in the open sea, density dependent effects due to competition or predation will be rather small. In fact, so far this has not been observed. For lake fish, density dependent effects have been observed and demonstrated. Thus they might indeed be present, but due to the much lower density at a considerable smaller scale, so that such effects are completely masked by stochastic factors. This is not so for the larval stage of fish. In [4] Cushing argues that density dependent effects for fish populations arise during the larval drift.

Density dependence can arise through cannibalism, competition for food and predation. These effects should be more pronounced for fish with pelagic eggs, because for such fish the number of eggs tend to be higher, thus leading to stronger competition and predation. In fact Cushing [4] shows that highly fecund fishes show higher density dependence.
According to Cushing [4], density dependent control is most likely not active in the egg stage but predominant during larval drift. In this case, competition for food seems to be the main cause. Results on density dependent effects are difficult to obtain, because the high variability of external conditions and influence of other external factors. The main reasons that competition for food is the dominant factor are:-

1) The spawning of fish is timed closely to the plankton production cycles Cushing [4].
2) Correlation between catches of cod and climatic changes.
3) Highly fecund fishes exhibit the most pronounced density dependent.

The total process of recruitment involves the stages

Eggs → Larvae → Juvenile → Recruits → Spawners → Eggs

For population modeling, the recruitment function $R$ expresses the number of viable 1 st (2 nd, 3 rd) year old fish as a function of the number of fecund females.

Fish stock-recruitment models are based on the assumption that some form of density dependent compensation will help maintain a stable population size despite losses of adults due to fishing. Different functional forms of the stock-recruitment relationship represent different hypotheses about the response of recruitment to changes in the density of the spawning stock. There are three basic hypothetical stock-recruitment relationships, a density independent relationship, the Beverton-Holt curve, and the Ricker curve, as described below. However, many other functional forms can easily be proposed. Important are forms, which are flexible and which can be manipulated easily mathematically.
For the simple population model we assume that a constant number of fish are recruited on the same date each year.

**Basic principle on stock-recruitment curves:-**

*Ricker* [28] discussed the properties of stock-recruitment curves and listed four basic properties which are:-

1) A stock-recruitment curve should pass the origin; when there is no parental stock there is no recruitment.

2) The curve should not fall to the abscissa at higher levels of stock, so that there is no point at which reproduction is completely eliminated at high densities.

3) The rate of recruitment (recruits-per-spawner) should decrease continuously with increases in parent stock (overcompensation principle in *Ricker* recruitment model).

4) Recruitment must exceed parent stock over some part of the range of possible parent stocks.

Property (4) is really only applicable to semelparous species (those who spawn only once) such as Pacific salmon.

There are two more general principles associated with spawner-recruit relationships. These are continuity and stationarity.

*Continuity* means that the average spawner-recruit curves shows no sharp jumps and do not change rapidly over a very small range of stock sizes.

*Stationarity*. A more important assumption is that the average stock-recruitment relationship is constant over time.
**Density Independent Model:**

The simplest assumption regarding stock and recruitment is that a certain number of eggs are produced per unit of the spawning stock, and these eggs have the same probability of surviving to the age at which recruitment is measured and where the probability of survival is independent of stock size or number of eggs produced. In the absence of any density dependent effect, it is assumed that there is a strictly linear relationship between stock and recruitment (Fig. 1.4).

![Density Independent Relationship between Spawning Stock and Recruitment](image)

Fig. 1.4: A Density Independent Relationship between Spawning Stock and Recruitment

This density independent relationship between stock and recruitment changes if recruitment is influenced by the number of spawners or eggs (i.e., if recruitment is density dependent). There are two general types of density dependent compensation modeled by stock-recruitment curves, the *Beverton-Holt* and the *Ricker* models [Harris 12].
**Beverton-Holt Model:**

The *Beverton-Holt* model depicts density dependent recruitment of a resource limited population in which resources are not shared equally. According to the *Beverton-Holt* formulation, a population consists of “winner” or “losers” – each individual receives some of the available resources, or not. This means that as resources such as spawning sites become fully utilized, further increases in population size will not result in additional recruits, and when spawner abundance is reduced, there is reduced recruitment. This is expressed in the *Beverton-Holt* formulation as:

\[
R(P) = \frac{P}{\alpha + \beta P} = \frac{\alpha P}{1 + \beta P} = \left(\frac{P}{P_0}\right) \left(\frac{P / P_0}{1 + (P / P_0)}\right)
\]

\[\therefore \beta = \frac{1}{P_0}\]

Here \(R\) stands for the recruits and \(P\) for the parent stock. \(\alpha\) and \(\beta\) are parameters which define the shape of the stock-recruitment curve. \(\beta^{-1}=P_0\) can be interpreted as the critical stock size where density dependent effects begin to be dominant. Parameter \(\alpha\) is the productivity parameter, representing the number of recruits per spawner at low densities. It also includes the probability of an egg to develop into a viable larva. The slope at the origin \(\alpha\) is considered as an indicator of the population’s maximum reproductive rate. The parameter \(\beta\) has the dimensions of \(1/P\) and may be interpreted as the “Threshold Biomass” for the model i.e., for \(P > \beta\) density dependent effect dominate [Myers and Barrowman 22]. \(\beta\) also represents compensatory mortality as a function of stock size. According to the *Beverton-Holt* model, recruitment increases in relation to stock size up to an asymptote \((\alpha / \beta)\), or maximum, at high stock abundance (Fig. 1.5).
**Ricker Model:**

The *Ricker* model shows “overcompensation” i.e., declining recruitment at high stock levels according to the equation:

$$ R(P) = \alpha P \cdot e^{-\beta P} = (\alpha P_0) \cdot \frac{P}{P_0} e^{\frac{P}{P_0}} \Rightarrow \beta = \frac{1}{P_0} $$

$\beta = P_{\text{max}}^{-1}$ is the critical stock size where density dependent effects begin to be dominant. $\alpha$ is again the productivity parameter. It represents the probability of an egg to survive to a recruit at low density. In order to determine $\alpha$; it is necessary for the units of stock and recruitment to be the same *Myers, Barrowman and Bowen* [21]. $\alpha, \beta$ are free parameters and can be estimated for concrete models *Hilborn and Walters* [13].
According to the *Ricker* model, the exponential term \((-\beta \cdot P)\) gives the
density dependent effect of parent stock on recruitment and \(\alpha\) is the slope
of the curve at the origin when \(P\) is small (Fig. 1.6).

![Fig. 1.6: The Ricker Stock-Recruitment Relationship](image)

The assumption of the Ricker model is that resources are divided equally
among individuals in a population. As the density increases all members
of the population receive an increasingly smaller amount of available
food or other resource.

These forms can be generalized to

\[
R(P) = \frac{\alpha P^\delta}{1 + \left(\frac{P}{P_0}\right)^\delta} \quad \text{or} \quad R(P) = a \cdot P^\delta \cdot e^{-\beta P^\gamma} = a \cdot P^\delta \cdot e^{-\left(P/P_0\right)^\gamma}
\]

The parameter \(\delta\) controls the degree of depensation, also known as Allee
effect *Thomson* [30]. If \(\delta = 1\), the function reduces to the Beverton-Holt
function; if \(\delta > 1\), the function displays depensation; if \(0 < \delta < 1\), the initial
increase will be greater than for the Beverton-Holt function *Myers* [23].
The parameter \(\delta\) is dimensionless and can be compared across
populations. Depensation always occurs for dioecious species at very low
population density.
More generally, a description of the recruitment should distinguish the following domains:-

I ) Small number of eggs (larvae).
II ) Intermediate.
III ) Large number of eggs.

In the domain ( I ), one expects little influence of density dependent effects and thus an almost linear increase of $R$. The effect of depensation or sublinear increase will arise from difficulties in finding fertilizing males or cannibalism and predation. Species with pronounced depensation will have difficulties in recovering from low stock levels. As yet there is no clear evidence for depensation Myers, Barrowman, Hutchings and Rosenberg [20]. For commercial fish this difficulty, was observed for Canadian Cod, though it is not clear to which extent juveniles by catches were responsible for this.

In the intermediate domain ( II ), there is still limited competition for food and the Allee effect is hardly active. Thus we expect an almost proportional increase. As the numbers of viable eggs increase competition between larvae increases. Thus the slope of $R$ decreases. If this decrease is small, we will have recruitment with saturation (Beverton-Holt). If it is strong, $R$ will decrease again to 0 (Ricker). So for actual data from catches and recruitment give no clear cut evidence for the Beverton-Holt, Ricker or any other possible model. Similarly there are as yet few models on larval development which allow a discrimination between these models. Thus both models are still used, mainly because of their simplicity.
All of the major spawner-recruit models contain “compensatory” mortality, which is defined to be early life mortality that increases (or survival that decreases) with increasing spawner abundance.

Compensatory mortality occurs for spawning levels that satisfy the condition

\[
d\left(\frac{R}{P}\right) < 0
\]

Overcompensation refers to a decrease in recruitment with increasing spawning level; it occurs when the slope of the spawner-recruit curve is negative; hence when

\[
dR < 0
dP
\]

The opposite type of mortality is called “depensatory” mortality, where early life mortality decreases (or survival increases) with increasing spawning abundance.

It is advantageous to write

\[
R = \alpha P \cdot r(P)
\]

where:

\( \alpha \) = the slope at the origin if \( r \) is normalized, \( r(0) = 1 \).

\( r(P) \) = the relationship between survival and spawner abundance. \( r(P) \) describes the influence of density dependent effects in the recruitment process Myers and Mertz [24]. The above considerations make it very plausible that \( r(P) \) is strictly decreasing. This will be assumed in the remainder.
Chapter 2

Models for the population of marine fish

§ 2.1 Description of the model

Models for fish will be used to

1) understand the biology and development of the particular species.
2) aid the preservation of the species.
3) optimize the catching of fish.

For this reasons, the models should be general and flexible and they should be based on sound biological reasoning. Modelling will proceed in several steps.

In the first step, a very general class of models is formulated. This model is based on general biological principles and will contain a large number of parameters and functions. Concrete data and further informations will be used to reduce the number of parameters and functions and determine the range of critical parameters in a second step. In a third step, properties of this model class will be investigated and compared with observations. Though in principle all models should be stochastic, models at this level should be deterministic. An important role will be played by simplified models, which can be studied analytically or numerically.

In the fourth step, these models should allow to relate actual catch data to the state of species. For this it will be imperative to supplement the total catch data by samples regarding the age composition of the catch, because the ultimate goal of these models is to obtain precise informations about the state of the species. These informations can then be used to generate recommendations on catches, quotas and equipments.
Since most marine fish exhibit a clear yearly cycle of spawning, recruitment, migration and growth, an age structured matrix model (general Leslie model) is most appropriate for the description of population dynamics. Such models have been described in numerous books, e.g. Caswell [3], Cushing [6], Pielou [25] and paper of Leslie [16]. In such a model, time is considered a discrete variable, measured in years. It is most sensible to identify the beginning of the year with the spawning period. Even though time is discrete in this description some properties will be derived from a version with continuous time. Thus we will have to consider mortality and harvesting as a continuous process. In this case the old formulae remain valid.

Let \( x_i(t) \) be the number of fish in age class \( i \) in the year \( t \). Then

\[
\bar{x}(t+1) = A \cdot \bar{x}(t)
\]  

\( \ldots (2.1) \)

where \( \bar{x} = (x_1, x_2, \ldots, x_m) \) and

\[
A = \begin{pmatrix}
\sigma_1 & f_2 & f_3 & f_4 & f_5 & \cdots & f_m \\
\tau_1 & \sigma_2 & 0 & 0 & 0 & \cdots & 0 \\
0 & \tau_2 & \sigma_3 & 0 & 0 & \cdots & 0 \\
0 & 0 & \tau_3 & \sigma_4 & 0 & \cdots & 0 \\
0 & 0 & 0 & \tau_4 & \sigma_5 & \cdots & 0 \\
\vdots & \vdots & \vdots & \vdots & \ddots & \ddots & \vdots \\
0 & 0 & 0 & \cdots & 0 & \tau_{m-1} & \sigma_m
\end{pmatrix}
\]
The meaning of theses coefficients is as follows:  

- \( f_i \) is the average number of recruits (eggs or larvae to the first age class) produced by a member of class \( i \).  
- \( \sigma_i \) is the probability to remain in class \( i \),  
- \( \tau_i \) is the probability to move to class \( i+1 \). Then

\[
\tau_i + \sigma_i = 1 - \mu_i
\]

where \( \mu_i \) is the mortality in age class \( i \), i.e. the probability to die within the next year.  

- \( m \) is the average maximum age. If \( T_i \) is the duration length of class \( i \), we also have

\[
\tau_i = \frac{1}{T_i} (1 - \mu_i) \quad \text{and} \quad \sigma_i = \left(1 - \frac{1}{T_i}\right) \left(1 - \mu_i\right)
\]

This discrete time model may be considered a stroboscopic image of an otherwise continuous development. This is particularly apparent, when one looks at mortality.

Since marine fish move mostly in the open sea. The coefficients \( \tau_i, \sigma_i \) should be largely density independent. This will not be so for lake fish. If one considers density dependent coefficients, however, one should assume \( \partial_i \tau_i \leq 0 \) because of competition. These effects, however, will be ignored here, because the evidence for density dependence in the later life stages is at most scant. Since the recruitment is strongly density dependent, we will assume that the \( f_i \) are density dependent. Thus the model will be nonlinear. We will also assume that the \( f_i \) depend only on the total number of eggs (larvae) i.e., the only density dependence arises via the recruitment process, more precisely from the development egg-larva-fish in the first age class.
The matrix $A$ has nonnegative matrix elements, thus we will need a few facts about such matrices as far as the coefficients are constants.

§ 2.2 Some matrix theory

A matrix with nonnegative entries is called *reducible* if a permutation of its rows or columns results in a block triangular matrix i.e., a matrix in the form

$$
\begin{pmatrix}
A & 0 \\
B & C
\end{pmatrix}
$$

otherwise, the matrix is called *irreducible*. A matrix $A$ is called *primitive* if for some positive integer $k$, we have $A^k > 0$. Primitive matrices are obviously irreducible. Irreducibility for a population matrix means that all classes influence each other, at least indirectly.

A remarkable theorem of Perron and Frobenius states that a positive irreducible matrix $A$ has a positive, (algebraically) simple, dominant eigenvalue $\lambda_A$ with corresponding positive eigenvector $x_A$. Gantmacher [9]. Thus we will speak of the P.F. eigenvalue and eigenvector.

The *Perron-Frobenius* theorem applied to population dynamics guarantees the existence of a limiting stable population structure $x_A$, and growth rate $\lambda_A$ that determines the ultimate dynamical behaviour of the population. That is as $t \to \infty$, $x(t)$ aligns itself in the same direction as $x_A$ and changes in magnitude at a rate that approaches $\lambda_A$.

For population matrices of the above form (2.1) one can show:
Theorem 2.1:-

Assume \( f_m > 0 \), then \( A \) is primitive if at least one diagonal element of \( A \) is non zero or if two neighbouring \( f_i \) are positive. If only \( f_m > 0 \) and all diagonal elements of \( A \) vanish, the dynamics of \( x(t+1) = A \cdot x(t) \) is asymptotically periodic.

Proof

In order to prove that \( A^k > 0 \) for some \( k \), we use the associated graph for \( A \) Logofet [19]. Then we have \( A_{ij} > 0 \) if there is a transition from \( j \) to \( i \).

More generally \( (A')_{ij} > 0 \) if one can go from \( j \) to \( i \) in \( r \) steps.

Now use the fact that one can go from 1 to 1 in \( m+r \) steps, for any \( r \), if there is a non zero diagonal element. Thus one can go from \( i \) to \( j \) in \( 2m+r \) steps for any \( r > 0 \).

Assume that all diagonal elements are zero but \( f_j, f_{j+1} > 0 \), then we have cycles from 1 to 1 of length \( j \) and \( j+1 \). From this the result is follows.

Remark:

If \( f_m \) and \( f_{j_1}, f_{j_2}, \ldots, f_{j_i} \) are positive, it would suffice that \( j_1, j_2, \ldots, j_i \) and \( m \) have 1 as a greatest common divisor in order to obtain primitivity. This can be seen by an extension of the above proof.

A simple model with only \( f_m > 0 \) is the one for salmons, which die after spawning. In that case \( m = 4 \).
§ 2.3 The net reproductive value

We had

$$\chi(t+1) = A\chi(t) = (F+T)\chi(t)$$

with the transition matrix $T$ and fertility part $F$

$$T = \begin{pmatrix} \sigma & 0 & \cdots & 0 \\ \sigma_1 & \sigma_2 & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & \tau_{m-1} & \sigma_m \end{pmatrix}, \quad F = \begin{pmatrix} 0 & f_2 & \cdots & f_m \\ 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & 0 & 0 \end{pmatrix}$$ (2.3)

Then $Z = (I - T)^{-1}F$ is a nonnegative matrix whose P.F. eigenvalue “$n$” is called “the net reproductive value” because biologically it gives the expected number of offspring per individual over its lifetime. This concept was introduced by Cushing and Yicang [7]. The following theorem was shown in Cushing and Yicang [7], determined the relationship between net reproductive value $n$ and Perron Frobenius eigenvalue $\lambda_A$. The present proof however is much simpler and shorter.

**Theorem 2.2** :-

a) One has $\lambda_A > 1$ iff $n > 1$. In this case $n > \lambda_A$

b) $\lambda_A = 1$ iff $n = 1$.

c) $\lambda_A < 1$ iff $n < \lambda_A < 1$. 

Proof

We have

\[ A \cdot x_A = (T + F) \cdot x_A = \hat{\lambda}_A \cdot x_A \]

or

\[ (\hat{\lambda}_A - 1) \cdot x_A + (I - T) \cdot x_A = F \cdot x_A \]

or

\[ (\hat{\lambda}_A - 1) \cdot (I - T)^{-1} \cdot x_A + x_A = (I - T)^{-1} \cdot F \cdot x_A = Z \cdot x_A \]

Multiplication by \( x_A^* = x^* \) from the right leads to

\[ \langle (\hat{\lambda}_A - 1) \cdot (I - T)^{-1} \cdot x_A, x^* \rangle + \langle x_A, x^* \rangle = \langle (I - T)^{-1} \cdot F \cdot x_A, x^* \rangle = n \cdot \langle x_A, x^* \rangle \]

\[ \because \langle (\hat{\lambda}_A - 1) \cdot (I - T)^{-1} \cdot I \rangle x_A, x^* \rangle + \langle (\hat{\lambda}_A - 1) x_A, x^* \rangle + \langle x_A, x^* \rangle = (\hat{\lambda}_A - 1) \cdot Q \cdot \langle x_A, x^* \rangle + \hat{\lambda}_A \cdot \langle x_A, x^* \rangle \cdot I \]

\[ = \langle (I - T)^{-1} \cdot F \cdot x_A, x^* \rangle \cdot I = n \cdot \langle x_A, x^* \rangle \cdot I \]

with

\[ Q = (T + T^2 + \cdots) \geq 0 \]

Thus

\[ \hat{\lambda}_A \cdot I + (\hat{\lambda}_A - 1) \cdot Q = n \cdot I \]

From this all results follow.

Since \( F \) is a rank 1 matrix, \( Z = (I - T)^{-1} F \) is of rank 1 too. Indeed

\[ Z_{ij} = (I - T)^{-1}_{ii} \cdot F_{ij} = (I - T)^{-1}_{ii} \cdot f_j \]

thus all column vectors of \( Z \) are multiples of the vector \((I - T)^{-1}_{ii}\). The explicit form for \((I - T)^{-1}\) can easily be computed. One finds for \( T \) as in (2.3) with \( \tau_0 = 1 \)
\[
(I - T)^{-1}_{ij} = \begin{pmatrix}
(1 - \sigma_i)^{-1} \\
\tau_i (1 - \sigma_1)^{-1}(1 - \sigma_2)^{-1} \\
\vdots \\
\prod_{i=1}^{m} (1 - \sigma_i)^{-1} \cdot \tau_{i-1}
\end{pmatrix} = y
\]

One has \(0 \leq \sigma_i < 1, \quad f_i \geq 0, \quad \tau_i > 0 \quad \text{and} \quad \sigma_i + \tau_i < 1\)

These latter assumptions follow from \(\sigma_i + \tau_i = 1 - \mu_i\) with \(\mu_i\) the mortality in class \(i\). Since \(Z = (I - T)^{-1}F\) has rank 1, it has only one nontrivial eigenvalue \(n = \lambda_z\) and \(0\) has multiplicity \(m - 1\). Now \((I - T)^{-1}F y = n y\) leads to

\[n = f_1 y_1 + f_2 y_2 + \cdots + f_m y_m = \sum_{i=1}^{m} f_i \prod_{j=1}^{j-1} \frac{\tau_{j-1}}{1 - \sigma_j}, \quad \tau_0 = 1
\]

The advantage of the net reproductive value lies in the fact that it can be computed explicitly and that it is more sensitive to matrix elements, as theorem (1.2) shows. The growth rate of an equilibrium population \(\lambda_A\) can be determined from the Euler equation

\[\sum_{i=1}^{m} f_i L_i \lambda_A^i = 1 \quad (2.6)\]
**Proof :-**

The number of eggs $P(t)$ at time $t$ arising from all individuals of all age classes is then

$$P(t) = \sum_{i=1}^{m} f_{i} x_{i}(t) \quad (a)$$

Since the number of individuals of age $i$ alive at time $t$, $x(t)$ is equal to the number of viable eggs $i$- years ago times their survival to the present $L_{i}$, we may substitute the expression

$$x_{i}(t) = P(t - i)L_{i} \quad (b)$$

in equation (a), giving

$$P(t) = \sum_{i=1}^{m} P(t - i)f_{i}L_{i} \quad (c)$$

If the age distribution of the population is constant, each age class grows according to the relation

$$x_{i}(t) = \lambda_{i}^{t}x_{i}(0)$$

Then the number of eggs in the past $(t-i)$ can be calculated by

$$P(t-i) = \lambda_{i}^{t}P(t)$$

Substituting this expression into equation (c), we obtain

$$P(t) = \sum_{i=1}^{m} P(t)\lambda_{i}^{t}f_{i}L_{i}$$

Finally, dividing both sides by $P(t)$ gives

$$\sum_{i=1}^{m} f_{i}L_{i}\lambda_{i}^{t} = 1$$

The Euler equation represents the characteristic equation for the Leslie matrix and it determines the dominant eigenvalue $\lambda_{A}$. 
§ 2.4 Nonlinear matrix models and their equilibria

More general nonlinear models can be written as

$$x(t+1) = g(x(t))$$  \hspace{1cm} (2.7)

where $g$ is a function $g: \mathbb{R}^n \rightarrow \mathbb{R}^n$. Equilibrium solutions of equation (2.7) are defined by

$$\bar{x} = g(\bar{x})$$  \hspace{1cm} (2.8)

A standard method to analyze equations like (2.7) near the equilibrium $\bar{x}$ is to linearize it. For this one writes

$$\Delta x(t) = x(t) - \bar{x} \hspace{0.5cm}, \hspace{0.5cm} t=0,1,2,\ldots$$  \hspace{1cm} (2.9)

for the deviation of $x(t)$ from the equilibrium value $\bar{x}$. Then equation (2.7) becomes

$$\Delta x(t+1) = \Delta x(t) \left[ \frac{dg}{dx} \right]_{\bar{x}} + o(\Delta x) = J \cdot \Delta x + o(\Delta x)$$  \hspace{1cm} (2.10)

where

$$J = \frac{dg}{dx} \bigg|_{\bar{x}}$$  \hspace{1cm} (2.11)

is the Jacobian matrix for the map $g$. If the linearized system is either stable (all eigenvalues lie within the unit circle) or unstable (at least one eigenvalue does not lie inside the unit circle), then $\Delta x(t)$ respectively decays to zero or moves away from zero if it is sufficiently small. For stable systems one can thus expect that solutions near $\bar{x}$ will converge to $\bar{x}$. This however holds only locally. Thus one speaks of local stability or instability.
For a more precise analysis the technique of Lyaponov functions gives better results. We will now specify the above matrix model (2.1) and describe its nonlinearity. There is a considerable dependence of the development of larval fish on food and external conditions. Thus the recruitment process is nonlinear and stochastic. In contrast there will be only a small dependence of \( \sigma_i \) and \( \tau_i \) on \( x \) because in the open sea there is a little competition between fish. If nonlinear effects arise, one expects \( \partial x_i \sigma_j, \partial x_i \tau_j \leq 0 \). In fact this dependence has not been observed so far, mainly because the uncertainties and stochastic effects of the recruitment process mask all other effects. For this reason we will consider \( \sigma_i \) and \( \tau_i \) as constant, so that the only nonlinearity of the model arises through the recruitment process.

The number of eggs produced from individuals in the year \( t \) is

\[
P(t) = \sum_{i=1}^{m} f_i x_i(t)
\]

\hspace{1cm} \cdots (2.12)

The dynamics of the fish larvae is highly density dependent and described by the recruitment function \( R \) as follows

\[
x_i(t+1) = R(P) = \alpha P \cdot r(P) = \sum_{i=1}^{m} \alpha \cdot f_i \cdot x_i(t) \cdot r(P)
\]

\hspace{1cm} \cdots (2.13)

Here \( \alpha \) is the probability of an egg to survive to a recruit at low density and \( r(P) \) is the density dependent survival rate of the larval fish already normalized to \( r(0)=1 \). If \( r(P) \) is not constant, this is the only nonlinearity in the model. This assumption implies that the viability of eggs and larvae is class independent. It would be violated if more mature fish produce larger or more viable eggs. The precise reasons for this density dependence are not yet wholly understood.
This description of the recruitment function contains some arbitrariness, because of the definition of \( f_i \), which means the absolute number of eggs or the number of eggs that survive a certain period, e.g. the first year or the time of recruitment. In some cases people choose the time of maturity or catchability. If we use the latter definition, it would allow us to absorb \( \alpha \) into the \( f_i \). Biologically important is the slope of the recruitment function at the origin. It is given by \( n \) in a model in which \( k_i = \alpha f_i r(P) \). It means the number of recruits produced by a young fish during his lifetime at low population density. This factor is thus a measure how fast a population can recover from overfishing. In some models this parameter is also closely connected with stability. The actual density dependence arises from \( r(P) \), which measures competition.

The general Usher model with nonlinear recruitment is now

\[
\begin{pmatrix}
\sigma_1 & k_2 & k_3 & k_4 & k_5 & \cdots & k_m \\
\tau_1 & \sigma_2 & 0 & 0 & 0 & \cdots & 0 \\
0 & \tau_2 & \sigma_3 & 0 & 0 & \cdots & 0 \\
0 & 0 & \tau_3 & \sigma_4 & 0 & \cdots & 0 \\
0 & 0 & 0 & \tau_4 & \sigma_5 & \ddots & 0 \\
\vdots & \vdots & \vdots & \vdots & \ddots & \ddots & \vdots \\
0 & 0 & 0 & \cdots & 0 & \tau_{m-1} & \sigma_m
\end{pmatrix} \cdot \mathbf{x}(t) = A \cdot \mathbf{x}(t) \quad (2.14)
\]

where

\[
k_i = \alpha f_i \cdot r(P), \quad \sigma_i = (1 - \mu_i) \cdot \left(1 - \frac{1}{T_i}\right), \quad \tau_i = (1 - \mu_i) \cdot \frac{1}{T_i}
\]
There is a considerable variability in the literature in describing the recruitment process. In some cases $P$ is measured in tons and $R$ in number of fish. We will always use number of viable recruits produced by an adult. This corresponds to choosing suitable units to measure the recruits. In order to determine the equilibrium vector $\bar{x}$, we solve $\bar{x} = A \bar{x}$ and get

$$\bar{x}_i = \frac{\tau_1 \cdot \tau_2 \cdots \tau_{i-1} \cdot \bar{x}_1}{(1-\sigma_2) \cdot (1-\sigma_3) \cdots (1-\sigma_i)} = L_i \cdot \bar{x}_1 \quad , i = 2, \ldots, m \quad (2.15)$$

where

$$L_i = \prod_{j=2}^{i} \frac{\tau_{j-1}}{(1-\sigma_j)}$$

$L_i$ is defined as the fraction of fish that survive from age $1$ to age $i$. $L_i$ is also known from the mortality table. To determine $\bar{x}_i$ we use,

$$\bar{x}_1 = \sigma_1 \bar{x}_1 + R(\bar{P})$$

With the abbreviation

$$n = (1-\sigma_1)^{-1} \sum_{i=2}^{m} \alpha f_i \cdot L_i \quad (2.5)$$

this gives

$$\bar{x}_1 = \frac{\left( \bar{x}_1 \cdot \sum_{i=2}^{m} \alpha f_i \cdot L_i \right) \cdot r \left( \bar{x}_1 \cdot \sum_{i=2}^{m} \alpha f_i \cdot L_i \right)}{1-\sigma_1} = \bar{x}_1 \cdot n \cdot (1-\sigma_1) \cdot r \left( \bar{x}_1 \cdot n \cdot (1-\sigma_1) \right)$$

$$\therefore \quad \bar{x}_1 = \frac{1}{(1-\sigma_1) \cdot n} \cdot r^{-1} \left( \frac{1}{n} \right) \quad (2.16)$$
The components of the equilibrium vector are then

\[ \bar{x}_i = \frac{L_i}{(1-\sigma_i)n} \cdot r^{-1} \left( \frac{1}{n} \right), \quad i = 1, 2, \ldots, m \quad (2.17) \]

Even though the Usher models may be simpler because they have fewer classes, they are not that well suited to discuss harvesting, because the values

\[ \tau_i = 1 - \mu_i - \sigma_i \]

are too small. So we will study Leslie model i.e., \( \sigma_i = 0 \) for all \( i \).

\section*{2.5 Stability properties for nonlinear Leslie matrix model}

The stability of the equilibrium \( \bar{x} \) for the nonlinear Leslie matrix model depends on the eigenvalues of the Jacobian at the equilibrium \( \bar{x} \)

\[
J = \begin{pmatrix}
\nu_1 & \nu_2 & \nu_3 & \cdots & \nu_m \\
\tau_1 & 0 & 0 & \cdots & 0 \\
0 & \tau_2 & 0 & \cdots & 0 \\
\vdots & \ddots & \ddots & \ddots & \vdots \\
0 & \cdots & 0 & \tau_{m-1} & 0
\end{pmatrix}
\]

where

\[
v_i = \frac{\partial x_i}{\partial x_i} \bigg|_{\bar{x}} = f_i \left. \frac{d(\alpha \cdot P \cdot r(P))}{dP} \right|_{\bar{x}} = f_i \left[ \alpha [r(\bar{P}) + \bar{P} \cdot r'(\bar{P})] \right] \quad (2.18)
\]
**Theorem 2.3:**

A sufficient condition for the local stability of system of nonlinear Leslie matrix at an equilibrium \( \bar{x} \) is

\[
\left| \frac{d}{dP} R(P) \right| \sum_{i=1}^{m} \alpha f_i L_i < 1 \quad (2.19)
\]

**Proof:**

The Jacobian \( J \) at the equilibrium \( \bar{x} \) is similar to a matrix \( M \) in Frobenius normal form i.e., \( J \) can be written as

\[
J = \left. \frac{\partial A}{\partial x} \right|_{x=\bar{x}} = C^{-1}MC,
\]

where \( C = \text{diag} (L_1, L_2, \cdots, L_m) \) and

\[
M = \begin{pmatrix}
M_1 & M_2 & M_3 & \cdots & M_m \\
1 & 0 & 0 & \cdots & 0 \\
0 & 1 & 0 & \cdots & 0 \\
\vdots & \ddots & \ddots & \ddots & \vdots \\
0 & \cdots & 0 & 1 & 0
\end{pmatrix}
\]

with

\[
M_i = \alpha f_i L_i R'(\bar{P}) \quad (2.21)
\]

From (2.20) it follows that \( M \) and \( J \) have the same characteristic roots.

Now all the \( M_i, (i=1,2,\ldots,m) \) are of the same sign, and also

\[
\sum_{i=1}^{m} |M_i| = \left| R'(\bar{P}) \sum_{i=1}^{m} \alpha f_i L_i \right|.
\]
It follows from Jury condition Lewis [17] that if (2.19) holds then all characteristic roots of $M$ and therefore of $J$ lie within the unit circle. which completes the proof.

**Theorem 2.4 :-**

An inequality (2.19) is a sufficient condition for the local stability of system of nonlinear Usher matrix at an equilibrium $\bar{x}$.

**Proof :-**

The Jacobian $J$ at the equilibrium $\bar{x}$ can be written as

$$ J = \frac{\partial A}{\partial x} \bigg|_{x=\bar{x}} = C^{-1}MC, \quad (2.22) $$

where $C = \text{diag} (L_1, L_2, \ldots, L_m)$ and

$$ M = \begin{pmatrix} 0 & M_2 & M_3 & \cdots & M_m \\ \tilde{\tau}_1 & \tilde{\sigma}_2 & 0 & \cdots & 0 \\ 0 & \tilde{\tau}_2 & \tilde{\sigma}_3 & \cdots & 0 \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ 0 & \cdots & 0 & \tilde{\tau}_{m-1} & \tilde{\sigma}_m \end{pmatrix} $$

with

$$ M_i = \alpha f_i L_i R'(\bar{P}) \quad (2.23) $$

and

$$ \tilde{\tau}_i = L_{i+1}^{-1} \tau_i L_i = \tau_i \frac{1 - \sigma_{i+1}}{\tau_i}, \quad \tilde{\sigma}_{i+1} = \sigma_{i+1} $$

so

$$ \tilde{\tau}_i + \tilde{\sigma}_{i+1} = 1 $$

From (2.19) it follows that $M$ and $J$ have the same characteristic roots.

Now all the $M_i, (i=1,2,\ldots,m)$ are of the same sign, and so

$$ \sum_{i=1}^m |M_i| = \left| R'(\bar{P}) \sum_{i=1}^m \alpha f_i L_i \right|. $$

It follows that if (2.19) holds then all characteristic roots of \( M \) and therefore of \( J \) lie within the unit circle. which completes the proof.

If \( n = \alpha \sum_{i=1}^{m} f_i L_i < 1 \) the population dies out.

**Theorem 2.5:**

Assume \( R \) is monotonically increasing as in the *Beverton-Holt* model then the nontrivial equilibrium is stable.

**Proof:**

By assumption that \( R \) is monotonically increasing means \( r < 0 \) but \( \partial_r R \geq 0 \).

Thus \( \alpha f_i r(\bar{P}) > \upsilon_i \). By assumption the largest eigenvalue of \( A \) at equilibrium \( P \) is 1. By the Perron Frobenius theory the largest eigenvalue of \( J \) is strictly less than the largest eigenvalue of \( A(P) \). So the model is stable which completes the proof.

**Stability condition when Ricker recruitment is used:**

Now we assume the Ricker recruitment model \( R(P) = \alpha P e^{-\beta P} \).

At equilibrium,

\[
\bar{P} = \sum_{i=1}^{m} f_i L_i \bar{x}_i
\]

and

\[
\bar{x}_i = -\frac{\ln \left( \alpha \sum_{i=1}^{m} f_i L_i \right)}{\beta \sum_{i=1}^{m} f_i L_i}
\]

Thus

\[
\bar{P} = \frac{\ln \left( \alpha \sum_{i=1}^{m} f_i L_i \right)}{\beta}
\]
in Jacobian matrix (2.18) are given by

\[ u_i = f_i \alpha \left[ 1 - \beta P \right] e^{-\beta \tau} = f_i \alpha \left[ 1 - \ln \left( \alpha \sum_{i=1}^{m} f_i L_i \right) \right] e^{-\ln \left( \alpha \sum_{i=1}^{m} f_i L_i \right)} \]

\[ \therefore u_i = \frac{f_i \alpha \left[ 1 - \ln \left( \alpha \sum_{i=1}^{m} f_i L_i \right) \right]}{\alpha \sum_{i=1}^{m} f_i L_i} = \frac{f_i \left[ 1 - \ln \left( \alpha \sum_{i=1}^{m} f_i L_i \right) \right]}{\sum_{i=1}^{m} f_i L_i} \]

Let \( \hat{\alpha} = \alpha \sum_{i=1}^{m} f_i L_i \), then

\[ u_i = \frac{f_i \left( 1 - \ln(\hat{\alpha}) \right)}{\sum_{i=1}^{m} f_i L_i} \]

The eigenvalues of \( J \) are the roots of the characteristic equation

\[ \frac{1}{1 - \ln(\hat{\alpha})} = \sum_{j=1}^{m} a_j \lambda^{-j} \]

where

\[ a_j = \frac{f_j L_j}{\sum_{i=1}^{m} f_i L_i} \]

A necessary condition for stability according to Jury condition Lewis [17] is

\[ \frac{1}{1 - \ln(\hat{\alpha})} < \left( a_2 + a_4 + \cdots \right) - \left( a_1 + a_3 + \cdots \right) \quad (2.24) \]
And if \( n = 1 \) at equilibrium, then the Ricker recruitment model has a stable nontrivial biological equilibrium whenever the inequality

\[
0 < \ln \left( \alpha \sum_{i=1}^{m} f, L_i \right) < 2
\]

is satisfied. Otherwise the dynamics is unstable. Generally this implies the existence of periodic or chaotic dynamics Levin, Goodyear [18] though this will have to be shown separately in all cases.
Chapter 3

Harvesting theory

§ 3.1 The semicontinuous description

The most critical point is to model the sequence of harvesting, spawning and survival. It is immediately clear that harvesting should follow spawning in order to allow fish to procreate before being caught. In practice this can be achieved by closing the spawning season and spawning areas to fishing. Further measures could be restrictions on gear to protect young fish or larvae. The EU has species specific restrictions in all these domains. We have noted above that in general, the spawning season is rather short. The main reason for this seems to be the saturation of predators on eggs and larvae. It cannot be too short, however, because it has to match plankton growth. Thus we have schematically

\[
\begin{array}{c|c|c|c}
& & & \\
\text{Harvesting} & \text{Survival} & \text{Spawning}
\end{array}
\]

\[T_H \rightarrow t\]

For simplicity we assume that spawning is restricted to an instant, which also marks the beginning of the year. In contrast to this survival and harvesting occur over an extended period. In order to model the interference of these processes, consider a fixed population class \(x\). Then

\[
\frac{dx}{dt} = \begin{cases} 
-\mu x & 0 \leq t \leq T_H \\
-(\mu + h)x & T_H < t \leq 1 
\end{cases}
\]

(3.1)

Here \(\mu\) is the mortality rate and \(h\) is the harvesting intensity.
The above equation has the solution

\[ x(t) = \begin{cases} x_0 e^{-\mu t} & 0 \leq t \leq T_H \\ x_0 e^{-\mu t (t - T_H/h)} & T_H \leq t \leq 1 \end{cases} \]  
(3.2)

The harvested amount is then

\[ \int_{t_n}^{1} h \cdot x(t) \cdot w(t) \ dt = h x_0 \beta \omega e^{-\mu T_H} \left[ \frac{1 - e^{-\mu t}}{\mu} + \frac{e^{K t}}{\mu + h + K} + \frac{3 e^{K t}}{\mu + h + 2 K} \right] \]

where

\[ \hat{t} = 1 - T_H \]

A similar formula is obtained if one considers pulse harvesting in (3.1). In this case a fixed amount \( h \) of the population is removed at an instant after spawning.

The interference of fishing and harvesting has a considerable negative effect.

The harvesting intensity \( h \) will be measured by capacity of boat \( x \) days or simply boat days, if all boats in the fleets have a comparable fishing capacity. The harvesting acts mainly through an increase of mortality.
§ 3.2 *Discrete Harvesting model* :-

§ 3.2.1 *Selective Harvesting*

In the literature selective harvesting has been discussed in great detail. We will discuss the question of exploitation in the context of proportional harvesting under equilibrium conditions. In this case one assumes that the harvesting rates for each class can be fixed arbitrarily. This assumption is clearly an unrealistic idealization. Assume that harvesting occurs in all classes separately with harvesting intensity $h_i$ for class $i$. Thus $h_i x_i$ represents the proportion of individuals removed from the $i$-th age class, $i= 2,3,\ldots,m$ at the end of each time period. We assume that there is no harvesting in the first class. Thus harvesting can be described by the escapement matrix

$$
(I - H) = \begin{pmatrix}
1 & 0 & 0 & \cdots & 0 \\
0 & 1-h_2 & 0 & \cdots & 0 \\
0 & 0 & 1-h_3 & \ddots & \vdots \\
\vdots & \vdots & \ddots & \ddots & 0 \\
0 & 0 & \cdots & 0 & 1-h_m
\end{pmatrix}
$$

(3.3)

Since $h_i$ describes a proportion, its value ranges between 0 and 1. The matrix $(I - H) A$ has again the same structure as $A$. With the replacement

$$
\tau_{i-1} \rightarrow (1-h_i) \cdot \tau_{i-1} \quad \text{and} \quad \sigma_i \rightarrow (1-h_i) \cdot \sigma_i, \quad i = 2, \ldots, m
$$

the components of the nontrivial equilibrium vector are given by :-

$$
-\frac{x_i(h_i)}{n(h_i)} = \frac{L_i(h_i)}{s_i(h_i)} \cdot r^{-1} \left( \frac{1}{n(h_i)} \right), \quad i = 1,2,\ldots,m : j = 2,3,\ldots,m
$$

(3.4)

where

$$
L_i(h_i) = \prod_{j=1}^{i} \frac{\tau_{j-1}(1-h_j)}{1 - \sigma_j (1-h_j)}, \quad n(h_i) = \sum_{i=2}^{m} a_i f_i \cdot L_i(h_i)
$$
The yield is then

\[ Y(h) = \langle HA \bar{x},w \rangle = \langle H(I-H)^{-1}(I-H)A \bar{x},w \rangle = \langle H(I-H)^{-1} \bar{x},w \rangle \]

where \( <,> \) is the inner product and \( w = (w_i) \) is the average weight or the price of a fish in class \( i \). Explicitly

\[ Y(h_j) = r^{-1} \left( \frac{1}{n(h_j)} \right) \left\{ \sum_{j=2}^{m} w_j \cdot h_j \cdot \prod_{k=2}^{j} \frac{\tau_{k-1}^{\sigma_{k-1}}(1-h_{k-1})}{1-\sigma_k(1-h_k)} \right\} , h_1 = 0 \quad (3.5) \]

The value \( \prod_{k=2}^{j}(1-h_k) \) represents the proportion of individuals that escaped harvesting up to age \( i \) in the Leslie model.

It is advantageous to discuss harvesting only in the Leslie model frame work, because the coefficients in (3.5) decay too rapidly if \( \sigma_i \neq 0 \).

The maximal sustainable yield is now

\[ \max_h Y(h) = Y_{\text{max}} \]

Since \( Y = Y(h) \) depends continuously on \( h \) and since \( h \in [0,1]^{m-1} \), the maximum exists.

It has been shown by Getz and Haight [10], Reed [27] that the optimal strategy for the Leslie type model is the two age class policy. This will be elaborated upon in the following section.
Equation (3.5) for Leslie models where \( \sigma_j = 0 \) can be simplified as in the paper of Reed [27]

\[
Y = \phi(n) \cdot \sum_{i=1}^{m} w_i \cdot (v_{i-1} - v_i) \quad \sigma_1 = 0 \quad n = \sum_{i=1}^{m} \alpha f_i L_i v_i
\]

where

\[
\phi(n) = \frac{r^{-1} \left( \frac{1}{n} \right)}{n}, \quad and, \quad v_i = \prod_{j=1}^{i} (1 - h_j)
\]

The harvest \( Y \) is expressed as the product of the total number of recruits \( \phi(n) \) and the average yield per recruit as determined by

\[
\eta(v) = \sum_{i=1}^{m} w_i \cdot (v_{i-1} - v_i)
\]

§ 3.2.2 Harvesting policy

In order to obtain the maximum sustainable yield, we must maximize the harvested amount

\[
\phi(n) \cdot \sum_{i=1}^{m} w_i \cdot (v_{i-1} - v_i)
\]

subject to

\[
1 = v_0 \geq v_1 \geq \cdots \geq v_m \geq 0
\]

This nonlinear programming problem can be transformed into a linear problem as in Reed [27] as follows :-

\[
\sum_{i=1}^{m} w_i L_i z_i \rightarrow \max \quad (3.6)
\]
subject to
\[ \sum_{i=1}^{m} c_i z_i = c_1 - n \quad (3.7) \]
\[ \sum_{i=1}^{m} z_i \leq 1 \quad (3.8) \]

and
\[ z_j \geq 0 \quad \forall i = 1, 2, \ldots, m \quad (3.9) \]

where
\[ c_j = \sum_{i=j}^{m} f_i L_i, \quad z_i = v_{i-1} - v_i = h_i \prod_{j=1}^{i} (1 - h_{j-1}), \quad n = \sum_{i=1}^{m} \alpha f_i L_i v_i \]

**Theorem 3.1 :- Reed [27]**

For selective harvesting in the Leslie model, the optimal policy is of the “two-age” type. For this we define \( j(t) \) recursively by

\[ j(1) = \arg \max_j \frac{w_j L_j}{\sum_{i=j}^{m} f_i L_i} \]

and

\[ j(t+1) = \arg \max_j \frac{w_j L_j - w_{j(t)} L_{j(t)}}{\sum_{i=j}^{m} f_i L_i} \]

for \( t=1,2,\ldots \)

a) If \( \sum_{i=1}^{m} \alpha f_i L_i > n \geq \sum_{i=1}^{j(1)-1} \alpha f_i L_i \), there is a partial harvest at age \( j(1) \) with proportional escapement

\[ 1 - h_{j(1)} = \frac{n - \sum_{i=1}^{j(1)-1} \alpha f_i L_i}{\sum_{i=j(1)}^{m} \alpha f_i L_i} \]
with no other harvesting.

b) If \( \sum_{i=1}^{j(1)} \alpha_i f_{j_i} L_i \geq n \geq \sum_{i=1}^{j(2)} \alpha_i f_{j_i} L_i \), there is a partial harvest at age \( j(2) \) with proportional escapement

\[
1 - h_{j(2)} = \left( n - \sum_{i=1}^{j(2)-1} \alpha_i f_{j_i} L_i \right) / \sum_{i=j(2)}^{j(1)-1} \alpha_i f_{j_i} L_i
\]

and a total harvest at age \( j(1) \).

c) In general, if \( \sum_{i=1}^{j(t)} \alpha_i f_{j_i} L_i \geq n \geq \sum_{i=1}^{j(t+1)} \alpha_i f_{j_i} L_i \), there is a partial harvest at age \( j(t+1) \) and a total harvest at age \( j(t) \) where \( j(t) > j(t+1) \).

**Proof:**

The key idea of Reed’s proof is to do the optimization in two steps. In step 1, linear programming is used to determine the pattern of harvesting, here the two age class harvesting. In a second step, the optimization has to be done with respect to the single variable \( \Phi \). An optimal policy must exist, because we maximize a continuous function (3.6) over a compact set.
Now we will prove the first part of the theorem:

The dual problem for the linear programming (3.6)-(3.9) is:

$$\min \ (c_1 - n)y_1 + y_2$$

such that

$$c_i y_1 + y_2 \geq w_i L_i \quad \forall i = 1, 2, \ldots, m$$

with $y_2 \geq 0$ and $y_1$ unconstrained in sign. Since the problem has only two constraints, the dual problem can be realized in $R^2$.

We want to determine two indices with associated lines $j(t)$ and $j(t+1)$ which intersect in an optimal solution. Since $j(t) > j(t+1)$, this means $c_{j(t)} < c_{j(t+1)}$, $n < c_1$.

Let

$$y'_1 = y_1' - y_1$$

where

$$y'_1, y'_1 \geq 0$$

so the dual problem becomes

$$\min \ (c_1 - n)y'_1 - (c_1 - n)y_1' + y_2$$

such that

$$c_{j(t)} y'_1 - c_{j(t)} y_1' + y_2 \geq w_{j(t)} L_{j(t)}$$

$$c_{j(t+1)} y'_1 - c_{j(t+1)} y_1' + y_2 \geq w_{j(t+1)} L_{j(t+1)}$$
By transforming to standard form, we get

$$\max \quad -(c_1 - n)y_1^* + (c_1 - n)y_1 - y_2$$

such that

$$-c_{j(t)}y_1^* + c_{j(t)}y_1^* - y_2 + s_1 = -w_{j(t)}L_{j(t)}$$

$$-c_{j(t+1)}y_1^* + c_{j(t+1)}y_1^* - y_2 + s_2 = -w_{j(t+1)}L_{j(t+1)}$$

$$y_1^*, y_2^*, s_1, s_2 \geq 0$$

where $s_1$ and $s_2$ are slack variables. We will use the two phase method for solving the dual problem Taha [29]:-

**Initial table 1:**

$$\begin{bmatrix}
  y_1^* & y_1^* & y_2 & s_1 & s_2 & |
  = & = & = & = & = & =
  -c_{j(t)} & c_{j(t)} & -1 & 1 & 0 & | -w_{j(t)}L_{j(t)}
  -c_{j(t+1)} & c_{j(t+1)} & -1 & 0 & 1 & | -w_{j(t+1)}L_{j(t+1)}
  = & = & = & = & = & =
  c_1 - n & -c_1 + n & 1 & 0 & 0 & | 0
\end{bmatrix}$$

Since the values in the right hand column are negative, phase 1 has to be used to find an initial solution

Assume the pivot row is row $j(t)$-th and the pivot element is $-c_{j(t)}$.

Pivoting now leads to
Table 2:-

\[
\begin{bmatrix}
  y_1 & y_2 & s_1 & s_2 \\
  1 & -1 & \frac{1}{c_{j(t)}} & \frac{-1}{c_{j(t)}} & 0 & w_{j(t)}L_{j(t)} \\
  0 & 0 & \frac{c_{j(t+1)}}{c_{j(t)}} & 1 & \frac{w_{j(t)}L_{j(t)}}{c_{j(t)}} - w_{j(t+1)}L_{j(t+1)} \\
  0 & 0 & 1 & \frac{c_1 - n}{c_{j(t)}} & \frac{c_1 - n}{c_{j(t)}} & 0 & \frac{w_{j(t)}L_{j(t)}}{c_{j(t)}}(c_1 - n) \\
\end{bmatrix}
\]

Since

\[
\frac{w_{j(t)}L_{j(t)}}{c_{j(t)}} > 0 \text{ and } \frac{w_{j(t)}L_{j(t)}}{c_{j(t)}} - \frac{w_{j(t+1)}L_{j(t+1)}}{c_{j(t+1)}} > 0
\]

phase 1 is completed and phase 2 applies

Phase 2 :-

In phase 2, the pivot element is found using two rules:-

Rule 1- pivot column:-

The pivot column is selected by locating the most negative entry in the objective row. In our problem this is the $y_2$ column because

\[
1 - \frac{c_1 - n}{c_{j(t)}} < 0 \quad \text{and} \quad \frac{c_1 - n}{c_{j(t)}} > 0
\]
Rule 2- pivot row:–

In order to determine the pivot row, divide each entry in the last right-hand column by the corresponding positive entry (from the same row) in the pivot column. (Ignore any rows in which the pivot column entry is less than or equal to zero). The row, with the smallest positive ratio, is the pivot row. In our problem the pivot row is given by

\[
\max_i \frac{w_i L_i - w_j(L_{j(t)})}{c_i - c_{j(t)}}
\]

Assume this maximum occurs at \( i = j(t+1) \), this means \( j(t+1) \) is given by

\[
\max_{j = j(t+1)} \frac{w_j L_j - w_j(L_{j(t)})}{c_j - c_{j(t)}},
\]

Applying the pivoting process in table 2 we get

**Table 3:**

\[
\begin{pmatrix}
  y_1 & y_1 & y_2 & s_1 & s_2 & | & = & = & = & = & = \\
  1 & -1 & 0 & 1 & -1 & | & \frac{w_{j(t+1)}L_{j(t+1)} - w_{j(t)}L_{j(t)}}{c_{j(t+1)} - c_{j(t)}} & c_{j(t+1)} - c_{j(t)} \\
  0 & 0 & 1 & -c_{j(t+1)} & c_{j(t+1)} & | & \frac{c_{j(t+1)} - c_{j(t)}}{c_{j(t+1)} - c_{j(t)}} & c_{j(t+1)} - c_{j(t)} \\
  0 & 0 & 0 & \frac{c_{j(t+1)} - c_{j(t)} + n}{c_{j(t+1)} - c_{j(t)}} & \frac{c_{j(t+1)} - c_{j(t)} - n}{c_{j(t+1)} - c_{j(t)}} & | & \frac{w_{j(t)}L_{j(t)}(c_{j(t)} - c_{j(t+1)} - n) + w_{j(t+1)}L_{j(t+1)}(c_{j(t)} - c_{j(t+1)} + n)}{c_{j(t+1)} - c_{j(t)}} & c_{j(t+1)} - c_{j(t)} \\
\end{pmatrix}
\]

Since there are no negative row entries in the objective row, the pivot process (phase 2) is completed and the optimal solution has been found.
From the previous tables we get the following results:-

1) The two lines corresponding to $j(t)$ and $j(t+1)$ determine the optimal solution (total and partial age class harvesting respectively). They are determined from

$$ j(1): \quad \arg \max_j \quad \frac{w_j L_j}{c_j} \quad (3.10) $$

and recursively

$$ j(t+1) = \arg \max_j \quad \frac{w_j L_j - w_j(1) L_j(t)}{c_j - c_j(t)} \quad , \quad t = 1, 2, \cdots \quad (3.11) $$

2) The optimal solution is

$$ z_{j(t)} = \frac{c_j(t) - c_j}{c_j(t+1) - c_j(t)} $$$$ z_{j(t+1)} = \frac{c_i - c_j(t)}{c_j(t+1) - c_j(t)} $$

and the maximum of the primal objective function is

$$ w_j L_j \frac{c_j(t+1) - c_j + n}{c_j(t+1) - c_j(t)} + w_j(1) L_j(t) \frac{c_i - c_j(t) - n}{c_j(t+1) - c_j(t)} $$

Now we will prove the second part of the theorem :-

Since

$$ \sum_{i=1}^{m} \alpha f_j L_i > n \geq \sum_{i=1}^{j-1} \alpha f_j L_i, \quad (3.12) $$

and

$$ n = \sum_{i=1}^{m} \alpha f_j L_i \prod_{j=1}^{l} (1-h_j) $$
then \( n \) must be of the form
\[
n = \sum_{i=1}^{j(1)-1} \alpha f_i L_i + (1 - h_{j(1)}) \sum_{i=j(1)}^{m} \alpha f_i L_i, \quad 0 < h_{j(1)} < 1
\]
this means that a partial harvest occurs at age \( j(1) \) with no other harvesting
\[
i.e., h_{j(1)} < 1, \quad h_i = 0 \forall i \neq j(1)
\]
Substitute this into (3.7) we get
\[
c_{j(1)} z_{j(1)} = c_1 - n
\]
or
\[
z_{j(1)} = \frac{c_1 - n}{c_{j(1)}}
\]
Proportional escapement is
\[
1 - z_{j(1)} = 1 - h_{j(1)} = \frac{n - \sum_{i=1}^{j(1)-1} \alpha f_i L_i}{\sum_{i=j(1)}^{m} \alpha f_i L_i}
\]
which proves part (a) of the theorem.

In the case of (b), there are two age classes, \( j(1), j(2) \) and the value of \( n \) is smaller than it’s value in case (a).
Since
\[
\sum_{i=1}^{j(1)-1} \alpha f_i L_i \geq n \geq \sum_{i=j(1)}^{j(2)-1} \alpha f_i L_i, \quad (3.13)
\]
then $j(1) > j(2)$ and

$$n = \sum_{i=1}^{j(2)-1} \alpha f_i L_i + (1 - h_{j(2)}) \sum_{i=j(2)}^{j(1)-1} \alpha f_i L_i + (1 - h_{j(2)}) \cdot (1 - h_{j(1)}) \sum_{i=j(1)}^{m} \alpha f_i L_i$$

$n$ satisfies inequality (3.13) only when $h_{j(1)} = 1$ and $h_{j(2)} < 1$, this means that a total harvest occurs at $j(1)$ and a partial harvest at $j(2)$.

Substitute $h_{j(1)} = 1$ and $h_{j(2)}$ in (3.7) we get

$$c_{j(1)} z_{j(1)} + c_{j(2)} z_{j(2)} = c_1 - n$$

and

$$z_{j(1)} = h_{j(1)} (1 - h_{j(2)}) = (1 - h_{j(2)}), \quad z_{j(2)} = h_{j(2)}$$

then

$$c_{j(1)} (1 - h_{j(2)}) + c_{j(2)} h_{j(2)} = c_1 - n \Rightarrow \left[ c_{j(2)} - c_{j(1)} \right] h_{j(2)} = c_1 - c_{j(1)} - n$$

$$\therefore h_{j(2)} = \frac{c_1 - c_{j(1)} - n}{c_{j(2)} - c_{j(1)}}$$

Thus the proportional escapement is given by

$$1 - h_{j(2)} = \frac{n - \sum_{i=1}^{j(2)-1} \alpha f_i L_i}{\sum_{i=j(2)}^{j(1)-1} \alpha f_i L_i}$$

which completes the prove of part (b).

The condition

$$1 - \frac{c_1 - n}{c_{j(1)}} < 0 \quad \text{and} \quad \frac{c_1 - n}{c_{j(2)}} > 0$$

is equivalent to

$$n \leq c_1 - c_{j(1)} = \sum_{i=1}^{j(1)-1} \alpha f_i L_i$$
So, if \( \sum_{i=1}^{j(t+1)-1} \alpha f_i L_i \geq n \geq \sum_{i=1}^{j(t+1)-1} \alpha f_i L_i \), there is a partial harvest at age \( j(t+1) \) and a total harvest at age \( j(t) \) where \( j(t) > j(t+1) \) which completes the prove of theorem (3.1).

This result of Reed reduces the computation of the maximal sustainable yield to:

i) determination of \( j(1), j(2), \ldots \)

ii) determination of the optimal harvesting pair \( j(t), j(t+1) \) and \( h = h_{j(t+1)} \).

Thus, in effect the search for \( Y_{\text{max}} \) has been reduced to an optimization with respect to \( h \).

We will study two examples as applications of theorem 3.1 which are:-

1) fecundity is proportional to weight with constant mortality ( theorem 3.2 ) as a simple example.

2) fecundity is proportional to weight and the price is proportional to \( P_i = w_i^{1,1} \) with variable and constant mortality. This assumption about the price is based on the fact that bigger fish are more valuable.
**Theorem 3.2** :-

If the fecundity is proportional to weight and if the mortality is constant, then

\[ j(t) = m(t-1), \quad t = 1,2,\ldots \]

**Proof** :-

In order to prove the theorem, we must show that

\[ \frac{w_i L_i}{\sum_{j=1}^{m} f_j L_j} \]

is increasing when \( f_i = w_i \) and when the mortality \( \mu \) is constant.

Let

\[ a_i = \frac{w_i L_i}{\sum_{j=1}^{m} w_j L_j} = \frac{w_i (1-\mu)^{i-1}}{\sum_{j=1}^{m} w_j (1-\mu)^{j-1}} \]

divide the last equation by \( (1-\mu)^{i-1} \). We get

\[ a_i = \frac{w_i}{\sum_{j=1}^{m} w_j (1-\mu)^{j-i}} \quad (3.14) \]

Similarly

\[ a_{i+1} = \frac{w_{i+1}}{\sum_{j=1}^{m} w_j (1-\mu)^{j-(i+1)}} \quad (3.15) \]
From (3.14) and (3.15) we get

\[
\frac{a_{i+1}}{a_i} = \frac{w_i \sum_{j=i+1}^{m} w_j (1-\mu)^{j-i}}{w_i \sum_{j=i+1}^{m} w_j (1-\mu)^{j-i-1}} = 1 + \frac{w_i \sum_{j=i+1}^{m} w_j (1-\mu)^{j-i-1}}{w_i \sum_{j=i+1}^{m} w_j (1-\mu)^{j-i-1}}
\]

The last equation can be written as

\[
\frac{a_{i+1}}{a_i} = 1 + \frac{\sum_{j=i+1}^{m-1} (w_{i+1} w_j - w_i w_{j+1}) (1-\mu)^{j-i} + w_i w_m (1-\mu)^{m-i}}{w_i \sum_{j=i+1}^{m} w_j (1-\mu)^{j-i-1}}
\]

From the behaviour of weight function, we get for \( j > i \)

\[w_{i+1} w_j \geq w_i w_{j+1}\]

Thus \( a_i \) is increasing and thus \( j(1) = m \).

By the same technique we will prove that

\[
\frac{w_i L_i - w_{j(1)} L_{j(1)}}{\sum_{j=i}^{j(1)-1} f_j L_j}
\]

is increasing when \( f_i = w_i \) and the mortality is constant :-

Let

\[
b_i = \frac{w_i L_i - w_{j(1)} L_{j(1)}}{\sum_{j=i}^{j(1)-1} w_j L_j} = \frac{w_i (1-\mu)^{j-i} - w_{j(1)} (1-\mu)^{j(1)-i}}{\sum_{j=i}^{j(1)-1} w_j (1-\mu)^{j-i}} = \frac{w_i - w_{j(1)} (1-\mu)^{j(1)-i}}{\sum_{j=i}^{j(1)-1} w_j (1-\mu)^{j-i}}
\]

As before,

\[
b_{i+1} = \frac{w_{i+1} - w_{j(1)} (1-\mu)^{j(1)-i-1}}{\sum_{j=i+1}^{j(1)-1} w_j (1-\mu)^{j-i-1}}
\]
The ratio between \( b_{i+1} \) and \( b_i \) is

\[
\frac{b_{i+1}}{b_i} = \frac{\left[ \sum_{j=d}^{j(t)-1} w_j (1-\mu)^{j(t)-j-1} \right] \sum_{j=d+1}^{j(t)} w_j (1-\mu)^{j-1} \left( w_{j(D)} - w_{j(D)} (1-\mu)^{j(D)-1} \right) \sum_{j=d+1}^{j(D)} w_j (1-\mu)^{j-1}}{\left[ \sum_{j=d}^{j(t)-1} w_j (1-\mu)^{j(t)-j-1} \right] \sum_{j=d+1}^{j(t)} w_j (1-\mu)^{j-1} \left( w_{j(D)} - w_{j(D)} (1-\mu)^{j(D)-1} \right) \sum_{j=d+1}^{j(D)} w_j (1-\mu)^{j-1}}
\]

this ratio can be written as

\[
\frac{b_{i+1}}{b_i} = 1 + \frac{\sum_{j=d}^{j(t)-1} w_{j(D)} - w_{j(D)} (1-\mu)^{j(D)-1}}{\left[ \sum_{j=d}^{j(t)-1} w_j (1-\mu)^{j(t)-j-1} \right] \sum_{j=d+1}^{j(t)} w_j (1-\mu)^{j-1} \left( w_{j(D)} - w_{j(D)} (1-\mu)^{j(D)-1} \right) \sum_{j=d+1}^{j(D)} w_j (1-\mu)^{j-1}}
\]

from the last equation and the behaviour of the weight function, we get that \( b_i \) is increasing. This means that if \( t=1 \) we get \( j(2) = m-1 = j(1) - 1 \) i.e., by iteration method, \( j(t) \) satisfies the equation

\[
j(t) = m-(t-1), \quad t = 1, 2, \ldots
\]

and the proof is completed.

If the mortality increases in the second half of a fish life, e.g.,

\[
\mu_i = \begin{cases} 
0.2 & i \leq \frac{m}{2} \\
0.4 \times \frac{i}{m} & i > \frac{m}{2}
\end{cases}
\]

(3.16)

then \( j(1)=m \) and \( j(2), j(3) \) depend on the maximum age \( m \) and Bertalanffy growth parameter \( K \).
**Proof :-**

Since mortality is defined by (3.16), the value $L$ is defined as

$$
L_i = \begin{cases} 
0.8^{-i} & i \leq \frac{m}{2} \\
0.8^{-i} \times \left(1 - \frac{0.4 \times i}{m}\right)^{-1} & i > \frac{m}{2}
\end{cases}
$$ (3.17)

Let $a_i = w_i, L_i$, we get for $j(1)$ that

$$
1 = \frac{a_m}{a_m} \geq \frac{a_j}{\sum_{i=j}^{m} a_i}
$$

is always holds so $j(1) = m$.

Numerically one finds for $j(2)$:

**Table 3.1: Dependence of $j(2)$ on $m$ and $K$ when $L$ is defined by (3.17):**

<table>
<thead>
<tr>
<th>m</th>
<th>K</th>
<th>0.08</th>
<th>0.16</th>
<th>0.24</th>
<th>0.32</th>
<th>0.4</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>9</td>
<td>9</td>
</tr>
<tr>
<td>15</td>
<td>14</td>
<td>7</td>
<td>7</td>
<td>7</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>20</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>25</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
</tr>
<tr>
<td>30</td>
<td>15</td>
<td>15</td>
<td>15</td>
<td>15</td>
<td>15</td>
<td>15</td>
</tr>
</tbody>
</table>

From table 3.1 we get that $j(2) = j(1) - 1 = m - 1$ for small values of $m$ ($m \leq 10$) and in this case $j(2)$ is independent of $K$ but at large values of $m$ ($m > 10$), $j(2)$ depends on $K$ i.e., for small $K$ and $m \leq 15$, $j(2) = j(1) - 1 = m - 1$, otherwise $j(2) = m/2$ if $m$ is even and $j(2) = (m-1)/2$ if $m$ is odd. Thus roughly, $j(2) \approx m/2$ and below this value, $j(t)$ decreases in integer steps. This follows from the proof of theorem 3.2.
**Maximum sustainable yield:**

Finally, we will determine the maximum sustainable yield for selective harvesting. The total harvest occurs at \( j(t) \) i.e., \( h_{j(t)} = 1 \) and partial harvest at \( j(t+1) \) i.e., \( 0 < h_{j(t+1)} < 1 \) and otherwise \( h_i = 0 \)

\[
Y \left( h_{j(t+1)} \right) = \frac{r^{-1} \left( 1 \right)}{n(h_{j(t+1)})} \prod_{j=t}^{j(t+1)} \tau_{j-1} \{ w_{j(t)}(1-h_{j(t+1)})\tau_{j(t)-1} + w_{j(t+1)}h_{j(t+1)} \} \cdots \quad (3.18)
\]

where \( r^{-1}(x) \) is given from the stock-recruitment relationships.

We will use the Ricker and Beverton-Holt recruitment functions as an example. Thus if we use Ricker model, we have

\[
r(P) = e^{-\beta P}, \quad r^{-1} \left( \frac{1}{n(h)} \right) = \frac{\ln \left( n(h) \right)}{\beta}
\]

while if we use Beverton-Holt model, we have

\[
r(P) = \frac{1}{1 + \beta P}, \quad r^{-1} \left( \frac{1}{n(h)} \right) = \frac{n-1}{\beta}
\]

Note that in all cases, we use a normalized expression for \( r(P) \) i.e., \( r(0) = 1 \).
§ 3.2.3 Harvesting with nets

If one wants to model fishing with nets, one has to translate the width of fishing nets into this model. This will be done as follows. We write \( H = h \text{ diag}(0,0,\ldots, \gamma,1,\ldots,1) \) to describe the situation where all fish from class \( k+1 \) or more are caught, while all fish of class \( k-1, k-2, \ldots \) can escape. Of class \( k \) only a fraction \( \gamma \) is retained. By this we mean that the mesh width is too small for fish from class \( k+1 \). With the term \( \gamma \), we can thus model the fact that the mesh width is a continuous variable.

Now we can use the formulae from selective harvesting with

\[
\begin{align*}
   h_i &= \begin{cases} 
   0 & 1 \leq i \leq k-1 \\
   \gamma h & i = k \\
   h & k < i \leq m 
   \end{cases} 
\end{align*}
\]

so

\[
(I - H) = \begin{pmatrix}
1 & 0 & 0 & \cdots & \cdots & \cdots & 0 \\
0 & 1 & 0 & \cdots & \cdots & \cdots & 0 \\
0 & 0 & \ddots & 0 & \cdots & \cdots & \vdots \\
\vdots & \vdots & \ddots & 1 - \gamma \cdot h & \ddots & \cdots & \vdots \\
\vdots & \vdots & \ddots & 1 - h & \ddots & \cdots & \vdots \\
\vdots & \vdots & \ddots & \ddots & \ddots & \ddots & 0 \\
0 & 0 & \cdots & \cdots & \cdots & 0 & 1 - h 
\end{pmatrix} \quad \overleftarrow{k-th \ class} \quad \cdots (3.19)
\]

and the dynamic equation becomes \( \chi(t+1) = (I - H)A\chi(t) \). This amounts to the replacements

\[
\begin{align*}
   \tau_{k-1} &\rightarrow (1 - \gamma \cdot h) \cdot \tau_{k-1} \\
   ; \sigma_k &\rightarrow (1 - \gamma \cdot h) \cdot \sigma_k \\
   \tau_{i-1} &\rightarrow (1 - h) \cdot \tau_{i-1} \\
   ; \sigma_i &\rightarrow (1 - h) \cdot \sigma_i \quad , i = k+1, k+2, \ldots, m
\end{align*}
\]
with this replacement, the components of equilibrium vector are:-

\[ \bar{x}_i(h) = \frac{L_i(h)}{n(h)} \cdot r^{-1} \left( \frac{1}{n(h)} \right) \quad , i = 1, 2, \cdots, m \]

where

\[ n(h) = \sum_{i=1}^{m} \alpha f_i \cdot L_i(h) \quad \text{and} \]

\[ L_i(h) = \begin{cases} 
\prod_{j=1}^{i} \tau_{j-1}, & 1 \leq i \leq k - 1 \\
\prod_{j=1}^{k-1} \tau_{j-1} \tau_{k-1} (1 - \gamma h), & i = k \\
\prod_{j=1}^{k-1} \tau_{j-1} \tau_{k-1} (1 - \gamma h) \prod_{j=k+1}^{i} \tau_{j-1} (1 - h)^{i-j}, & k < i \leq m
\end{cases} \]

This holds for a general Usher model. However as stated above we will use the Leslie model for harvesting only. As before the yield is given by

\[ Y(h) = \langle H A \bar{x}, w \rangle = \langle (I - H)^{-1} (I - H) A \bar{x}, w \rangle = \langle H (I - H)^{-1} \bar{x}, w \rangle \]

where \(<, >\) is the inner product and \(w = (w_i)\) is the average weight or the price of a fish in class \(i\). Explicitly the yield is given by

\[ Y(h) = \sum_{i=k}^{m} w_i \cdot \frac{\bar{x}_i}{1 - h_i} \]
Substituting the components of the equilibrium vector into the formula for the yield one gets with some simplifications

\[ Y(h) = \frac{C \cdot h \cdot r^{-1}\left(\frac{1}{n(h)}\right)}{[1-\sigma_k(1-\gamma \cdot h)] \cdot n(h)} \left\{ w_k \cdot \gamma + \sum_{i=k+1}^{m} w_i \cdot (1-\gamma \cdot h) \prod_{j=k+1}^{i} \frac{\tau_{i-j} \cdot (1-h)^{j-k-1}}{1-\sigma_j(1-h)} \right\} \ldots (3.20) \]

where

\[ C = \left( \prod_{i=k}^{1} \frac{\tau_i}{1-\sigma_i} \right) \]

We will only consider the case \( \gamma = 0 \) for simplicity in our numerical computations. Thus equation (3.20) becomes

\[ Y(h) = \sum_{i=k+1}^{m} \frac{C^* \cdot h \cdot r^{-1}\left(\frac{1}{n(h)}\right)}{n(h)} \cdot w_i \cdot \prod_{j=k+1}^{i} \frac{\tau_{i-j} \cdot (1-h)^{j-k-1}}{1-\sigma_j(1-h)} \ldots (3.21) \]

where

\[ C^* = \left( \prod_{i=k}^{1} \frac{\tau_{i-j}}{1-\sigma_i} \right) \]

For the Leslie model, \( Y(h) \) is a continuous function of \( \gamma \) and \( h \).

\[ Y(h) = \frac{h \cdot r^{-1}\left(\frac{1}{n(h)}\right)}{n(h)} \left[ w_{k+1} l_{k+1} + \sum_{i=k+2}^{m} w_i l_i (1-h)^{i-k-1} \right] \]

where

\[ n(h) = \sum_{i=1}^{k} \alpha f_i l_i + \sum_{i=k+1}^{m} \alpha f_i l_i (1-h)^{i-k} \]
and

\[ l_{i+1} = \prod_{j=0}^{i} \tau_j, \quad l_1 = \tau_0 = 1 \]

To see that this function has a unique maximum, consider the individual terms \( Y_{k+s} \) as

\[ \therefore Y_{k+s}(h) = r^{-1} \left( \frac{1}{n(h)} \right) \left[ w_{k+s} l_{k+s} h (1-h)^{-k} \right], \quad s = 1, 2, \ldots, m-k \]

Now write

\[ \therefore n(h) = \sum_{i=1}^{k+s} \alpha f_i l_i + \sum_{i=k+s+1}^{m} \alpha f_i l_i (1-h)^{i-k} = a + \sum_{i=k+s+1}^{m} \alpha f_i l_i (1-h)^{i-k} \]

The first and second derivatives of \( n(h) \) are

\[ n'(h) = \frac{dn(h)}{dh} = -\alpha f_{k+s} l_{k+s} - \sum_{i=k+2}^{m} \alpha f_i l_i (i-k)(1-h)^{i-k-1} < 0 \]

\[ n''(h) = \frac{d^2n(h)}{dh^2} = \sum_{i=k+2}^{m} \alpha f_i l_i (i-k)(i-k-1)(1-h)^{i-k-2} > 0 \]

Also the first derivative of \( Y_{k+s}(h) \) w.r.to \( h \) with the Ricker recruitment function is

\[ \frac{dY_{k+s}(h)}{dh} = n'(1-\ln(n))(h(1-h)^{-1}) + \ln(n) \left( \frac{1}{(1-sh)(1-h)^{-2}} \right) \]

\[ \frac{dA_s}{dh} = (1-h)^{-2} \left( \frac{n''(1-\ln(n) - n'\ln(1-sh))}{n^2} - \frac{n'^2 h(1-h)(3-\ln(n))}{n^3} \right) < 0 \]

\[ \frac{dB_s}{dh} = (1-h)^{-3} \left[ \frac{n'(1-sh)(1-h)(1-\ln(n))}{n^2} - \frac{\ln(n) \{ (s-2)(1-sh) \}}{n} \right] < 0 \]
If Beverton-Holt recruitment function is used, we get

\[
\frac{dY_{k+s}(h)}{dh} = \frac{n' h (1-h)^{i-1}}{n^2} + \frac{(n-1)(1-sh)(1-h)^{i-2}}{n}
\]

\[
\frac{dA_{B-H}}{dh} = (1-h)^{i-2} \left( \frac{n'' h (1-h) + n'(1-sh)}{n^2} - \frac{2n'^2 h (1-h)}{n^3} \right) < 0
\]

\[
\frac{dB_{B-H}}{dh} = (1-h)^{i-3} \left[ \frac{n'(1-sh)(1-h)}{n^2} - \frac{(n-1)(1-s)(hs-2)(1-h)}{n} \right] < 0
\]

Finally the second derivative w.r.to \( h \) is

\[
\frac{d^2Y_{k+s}}{dh^2} = \frac{dA}{dh} + \frac{dB}{dh} = \frac{dA_{B-H}}{dh} + \frac{dB_{B-H}}{dh} < 0
\]

All individual terms satisfy \( Y'_{k+s} < 0 \). Hence \( Y''(h) \leq 0 \), so \( Y(h) \) is a continuous function with a unique maximum.
§ 3.3 Semicontinuous Harvesting model :-

§ 3.3.1 Selective Harvesting

In this part, we treat time, $t$, as a continuous variable and harvesting as a continuous process with intensity $\"h\"$ in class $i$. Assume that the natural mortality for the age class $i$ is $\"\mu\"$ which is time independent. Assume that each year is divided into two seasons Getz [11]:-

1) A spawning season of length $t_c$ before harvesting.
2) A harvesting season of length $\hat{t} = 1 - t_c$.

Let $x_i(t)$ be the number of individuals in the $i$-th age class at time $t$.

The growth equation is given by the following differential equation

$$
\frac{dx_i(t)}{dt} = \begin{cases} 
-\mu_i x_i(t), & t_0 \leq t \leq t_0 + t_c \\
-(\mu_i + h_i)x_i(t), & t_0 + t_c \leq t \leq 1 + t_0 .
\end{cases} \quad t_0 = 0, 1, 2, \ldots, m - 1 \quad \text{(3.22)}
$$

The solution of this equation is

$$
x_i(t) = x_i(t_0) \begin{cases} 
e^{-\mu_i(t-t_0)}, & t_0 \leq t \leq t_0 + t_c \\
e^{-\mu_i t} \cdot e^{-(\mu_i + h_i)(t-t_0 + t_c)}, & t_0 + t_c \leq t \leq 1 + t_0
\end{cases} \quad \text{(3.23)}
$$

Introducing a stock - recruitment function $R(P) = P r(P)$ as before we get with

$$
P(t) = \sum_{j=2}^{m} \alpha_j x_j(t) \quad \text{(3.24)}
$$

the number of eggs produced in the year $t$, the number of recruits $R(P)$. 
Under these assumptions, the spawning season model is:

**Spawning season.**

\[ t \in [t_0, t_0 + t_c] \]

\[ x_1(t + 1) = R \left( P(t) \right) \]

\[ x_{i+1}(t + 1) = e^{-\mu_i} x_i(t), \quad i = 1, 2, \ldots, m - 1 \quad (3.25) \]

Thus if \( x(t_0+t_c) \) is the state of the population at the beginning of the \((t_0+1)\)-th harvesting season, then

**Harvesting season.**

\[ t \in [t_0 + t_c, t_0 + 1], \quad \hat{t} = 1 - t_c \]

\[ x_1(t + 1) = R \left( P(t) \right) = \alpha \sum_{i=2}^{m} f_i \cdot x_i(t) + \left( \alpha \sum_{i=2}^{m} f_i \cdot x_i(t_c) \right) \]

\[ x_{i+1}(t + 1) = e^{-\mu_{i+1}} x_i(t), \quad i = 1, 2, \ldots, m - 1 \quad (3.26) \]

With this the Leslie matrix model should be modified to

\[
\bar{x}(t + 1) = \begin{pmatrix}
0 & k_2 & k_3 & k_4 & k_5 & \cdots & k_m \\
\tau_1 & 0 & 0 & 0 & 0 & \cdots & 0 \\
0 & \tau_2 & 0 & 0 & 0 & \cdots & 0 \\
0 & 0 & \tau_3 & 0 & 0 & \cdots & 0 \\
0 & 0 & 0 & \tau_4 & 0 & \cdots & 0 \\
\vdots & \vdots & \vdots & \ddots & \ddots & \ddots & \vdots \\
0 & 0 & 0 & \cdots & 0 & \tau_{m-1} & 0
\end{pmatrix} \cdot \bar{x}(t) \quad (3.27)
\]

where

\[ \tau_i = e^{-\mu_i - h_i} \hat{t} \quad (3.28) \]
For the equilibrium vector \( \vec{x} \) we get as before

\[
\vec{x}_j = \prod_{j=1}^{i-1} r_j \cdot \vec{x}_1 \quad , i = 2, \ldots , m
\]

where \( r_i \) is given by (3.28) and where \( \vec{x}_i \) is a solution of the equation

\[
\vec{x}_1 = R(\vec{p}) = R \left( \sum_{i=2}^{m} \alpha f_i \cdot \vec{x}_i \right) = \left( \sum_{i=2}^{m} \alpha f_i \right) \prod_{j=1}^{i-1} r_j \vec{x}_1 \cdot \left( \sum_{i=2}^{m} \alpha f_i \right) \prod_{j=1}^{i-1} r_j \vec{x}_1
\]

This leads to

\[
\vec{x}_1 = \vec{x}_1 \cdot n \cdot r \left( \vec{x}_1 \cdot n \right)
\]

The components of the equilibrium vector are then

\[
\therefore \vec{x}_1 = \frac{1}{n} \cdot r^{-1} \left( \frac{1}{n} \right)
\]

\[
\vec{x}_1 = \frac{L_i}{n} \cdot r^{-1} \left( \frac{1}{n} \right) \quad , i = 1, 2, \ldots , m\quad (3.29)
\]

where

\[
n = \sum_{i=2}^{m} \alpha f_i \cdot L_i; \quad L_i = \prod_{j=1}^{i-1} e^{-h_j} , L_i = 1 \quad , i = 2, 3, \ldots , m
\]

The yield for the harvesting vector \( h \) in harvesting season is then

\[
Y(h) = \sum_{i=2}^{m} h_i \cdot \int_{t_0}^{t_0+\tau_i} w_i(t) \cdot x_i(t)dt \quad (3.30)
\]

where \( x_i(t) \) is given by (3.23).
If the weight function is derived from the Von-Bertalanffy growth function

\[ w(t) = w_0 \left(1 - e^{-K(t-t_0)}\right)^3 \]

one gets

\[ Y(h_i) = \sum_{i=2}^{m} h_i w_{x_i(t_0)} e^{\mu_i t_0 + h_i(t_0 + t_i)} \int_{t_0}^{1+t_i} (1-e^{-K(t-t')})^3 e^{-\mu_i + h_i} dt \]

After some simplifications, the integral becomes

\[ \int_{t_0}^{1+t_i} (1-3e^{-K(t-t')}) + 3e^{-2K(t-t')} - e^{-3K(t-t')}) e^{-(\mu_i + h_i)} \ dt = \]

\[ e^{-(\mu_i + h_i)} \left\{ \frac{1 - e^{-(\mu_i + h_i) t_i}}{\mu_i + h_i} - \frac{3e^{-K(t_0 + t_i - t')}}{\mu_i + h_i + K} \left(1 - e^{-(\mu_i + h_i + K) t_i}\right) \right\} \]

Altogether this gives

\[ Y(h_i) = w \sum_{i=2}^{m} h_i x_i(t_0) e^{-\mu_i t_i} \left\{ \frac{1 - e^{-(\mu_i + h_i) t_i}}{\mu_i + h_i} - \frac{3e^{-K(t_0 + t_i - t')}}{\mu_i + h_i + K} \left(1 - e^{-(\mu_i + h_i + K) t_i}\right) \right\} \]
Maximum Sustainable Yield:-

By definition (MSY) is the maximal yield at equilibrium so,

\[
Y(h_i) = w \sum_{i=2}^{m} h_i \varpi_i \cdot e^{-\mu_i h_i} \cdot \left[ \frac{1-e^{-(\mu_i + h_i) \varpi_i}}{\mu_i + h_i} - \frac{3e^{-K(t_i, 1, \varpi_i, -\varpi_i)} \left(1-e^{-(\mu_i + h_i + K) \varpi_i} \right)}{\mu_i + h_i + K} + \frac{3e^{-2K(t_i, 1, \varpi_i, -\varpi_i)} \left(1-e^{-(\mu_i + h_i + 2K) \varpi_i} \right)}{\mu_i + h_i + 2K} - \frac{e^{-3K(t_i, 1, \varpi_i, -\varpi_i)} \left(1-e^{-(\mu_i + h_i + 3K) \varpi_i} \right)}{\mu_i + h_i + 3K} \right]
\]

where the equilibrium vector components are given by (3.29). It is important to note that now \( h_i \) is not anymore restricted to the interval [0,1] but is free to vary in [0,\( \infty \)). Nevertheless one can still show the existence of a maximum.

It is quite obvious now that the Reed result cannot be valid any more, because this problem is highly nonlinear in the harvesting variable \( (h_i) \).

Since selective harvesting is rather unrealistic, we shall only consider the semicontinuous harvesting approach in conjunction of harvesting with nets, which will be considered in the next section.

§ 3.3.2 Harvesting with nets

If one wants to model continuous harvesting with nets, one has to proceed as follows. We write \( H= h \text{ diag}(0,0,\ldots, \gamma,1,\ldots,1) \) to describe the situation where all fish from class \( k+1, \ldots \) are caught, while all fish of class \( k-1, k-2, \ldots \) can escape and of class \( k \) only a fraction \( \gamma \) is retained. By this we mean that the mesh width is too small for fish from class \( k+1 \).

Now we can use the formulae from selective harvesting with

\[
h_i = \begin{cases} 
0 & 1 \leq i \leq k - 1 \\
\gamma h & i = k \\
h & k < i \leq m 
\end{cases}
\]
The components of the equilibrium vector are:

\[ x_i(h) = \frac{L_i(h)}{n(h)} \cdot r_i \left( \frac{1}{n(h)} \right), i = 1, 2, \ldots, m \]  

(3.31)

where

\[ n(h) = \sum \alpha f_i \cdot L_i(h) \]

and

\[
L_i(h) = \begin{cases} 
\prod_{j=1}^{i-1} e^{-\mu_j / \gamma_i}, & 2 \leq i \leq k \\
\prod_{j=1}^{k} e^{-\mu_j / \gamma_i} \prod_{j=k+1}^{i-1} e^{-\mu_j / h_i}, & i = k + 1 \\
\prod_{j=1}^{k} e^{-\mu_j / \gamma_i} \prod_{j=k+1}^{i-1} e^{-\mu_j / h_i}, & k + 2 \leq i \leq m 
\end{cases}
\]

Substituting the components of the equilibrium vector to the formula for the yield we get with some simplification and \( \gamma = 0 \)

\[
Y(h) = w_h \sum_{i=k+2}^{m} \bar{x}_i \cdot e^{-\mu_i / \gamma_i}, \quad \left\{ \begin{array}{l}
1 - e^{-(\mu_i + h / \gamma_i)} \frac{3e^{-K (\mu_i + h / \gamma_i)}}{\mu_i + h} - \frac{3e^{-K (\mu_i + h + 2K / \gamma_i)}}{\mu_i + h + 2K} \\
+ \frac{3e^{-K (\mu_i + h + 2K / \gamma_i)}}{\mu_i + h + 2K} = e^{-3K (\mu_i + h + 3K / \gamma_i)} \left( 1 - e^{-(\mu_i + h + 3K / \gamma_i)} \right) \end{array} \right.
\]

where the equilibrium vector components are given by (3.31) with

\[
n(h) = \sum_{i=2}^{k+1} \alpha f_i \prod_{j=1}^{i-1} e^{-\mu_j / \gamma_i} + \sum_{i=k+2}^{m} \alpha f_i \prod_{j=1}^{i-1} e^{-\mu_j / \gamma_i} \times \prod_{j=k+1}^{i-1} e^{-\mu_j / h_i}
\]
Alternatively, if each $w_i(t)$ is taken as a constant $w_i$ (independent on time) over a harvesting season, then the yield (3.30) reduces to the much simpler expression

$$Y(h) = \sum_{i=k+2}^{m} \frac{w_i h x_i}{\mu_i + h} \cdot e^{-\mu_i h} \left(1-e^{-\mu_i (h+h)}\right)$$

$Y(h)$ is a highly non-linear function of $h$. It is clear that $Y(0)=0$ and $Y(h)$ remains positive for $h > 0$. The graph of $Y(h)$ against $h$ can be used to find the value of $h_{\text{max}}$ for which $Y(h)$ is a maximum.
Chapter 4
Numerical Examples and Influence of parameters on Harvesting Models

§ 4.1 Numerical Examples :-

Now, we will study the optimal harvesting for haddock and cod using the Leslie model with $\gamma=0$ for simplicity. The aim is to determine the optimal mesh width $k$ and the maximum sustainable yield (MSY). $k$ is a discrete parameter for the width of the meshes. Large $k$ corresponds to large width. All classes from $k$ on are harvested with intensity $h$. In addition we will compare selective harvesting, harvesting with nets and semicontinuous harvesting. We showed in section (3.2.2) that partial harvesting $h_{j(t+1)}$ cannot be determined analytically, so we will determine it numerically.

**Example 1. Haddock**

From Beverton-Holt [2], the maximum age of haddock is $m = 20$ years and it has approximately a constant natural mortality of 0.2 per year. Weight of haddock is approximately given by

$$w(t) = 1.34 \times \left(1 - e^{-0.26(t+0.75)}\right)^3 \text{ kg}$$

The fecundity is determined from

$$f(t) = w(t) \times 10^5$$
The stock-recruitment parameters for haddock are approximately **Beverton-Holt** [2]

\[ \beta = \frac{1}{61.4}, \quad \alpha = 1.53 \times 10^{-8} \]

In the following discussion, these parameters will not be changed. We will allow, however, different recruitment functions, namely **Beverton-Holt** or **Ricker**.

**Beverton-Holt:**

\[ R(P) = \frac{\alpha P}{1 + \beta P} \]

**Ricker:**

\[ R(P) = \alpha P e^{-\beta P} \]

--- Beveryton Holt

--------- Ricker

Fig 4.a: Recruitment functions for haddock
If we want to discuss the influence of mortality, we consider either constant mortality or variable mortality, which we define as

$$
\mu(i) = \begin{cases} 
0.2 & i \leq \frac{m}{2} \\
0.4 \times \frac{i}{m} & i > \frac{m}{2}
\end{cases}
$$

For animals and men, it is well known that, mortality increases with age at higher age, so this is a more realistic form than just constant mortality Hoenig [14].

1. **Selective harvesting** :-

   Since in general, larger fish are more valuable, we will model the price of fish by

   $$
p(w) = w^{1.1}
$$

   when we study the influence of price as harvesting.
When weight is used

fig.4.1.1: optimal value of $h$ in Ricker = 0.8, $j(t+1)$ = 7 years and MSY = 4567 gm
while optimal value of $h$ in B-H = 0.8, $j(t+1)$ = 8 years and MSY = 6334 gm
When price is used

Fig. 4.1.2: optimal value of \( h \) in Ricker = 0.8, \( j(t+1) = 7 \) years and MSY = 4888 gm while optimal value of \( h \) in B-H = 0.8, \( j(t+1) = 8 \) years and MSY = 6786 gm

Fig. 4.1.3: Comparison between constant and variable mortality in selective harvesting. \( j(t+1) = 7, h_{\text{max}} = 0.8 \) and MSY = 4567 gm

Influence of variable mortality is ignored in selective harvesting because \( j(t+1) < m/2 \).
2. Net harvesting: -

2.1 Ricker recruitment function

Fig. 4.2.1: mortality = 0.2, weight is used. Optimal mesh width $k = 6$. $h_{max} = 0.85$ with MSY = 4564 gm

Fig. 4.2.2: mortality = 0.2, price is used. Optimal mesh width $k = 6$. $h_{max} = 0.85$ with MSY = 4884 gm

MSY when price is used > MSY when weight is used.
2.2 Beverton-Holt recruitment function

From previous figures we found that $Y_{max}$ for selective harvesting is greater than $Y_{max}$ for net harvesting whatever recruitment function is used.
Influence of increasing mortality is small and then ignored at height values of harvesting because increasing mortality means the numbers of individuals are decreasing and MSY in this case is decreasing. At high values of harvesting, the yield curves in constant and variable mortality are coincide.
3. **Semicontinuous harvesting** :-

![Graph of Yield vs Harvesting h](image1)

Fig 4.3.1: Comparison between net and semicontinuous harvesting

- Semicontinuous, optimal mesh width $k = 6$, $h_{\text{max}} = 2.22$, MSY = 3246 gm
- Net harvesting, optimal mesh width $k = 7$, $h_{\text{max}} = 0.68$, MSY = 3448 gm

This figure shows that MSY in net harvesting is greater than MSY in semicontinuous harvesting because all functions in semicontinuous harvesting are continuous in their arguments.

![Graph of Yield vs Harvesting h](image2)

Fig. 4.3.2: Comparison between constant and variable mortality in semicontinuous harvesting. Optimal mesh width $k = 6$.

The same influence of mortality is holds in semicontinuous harvesting.
Example 2. Cod

From Law-Grey [15], the maximum age of cod is $m = 30$ years and it has approximately a constant natural mortality of 0.18 per year Hoenig [14]. The weight of cod is approximately given by

$$w(t) = 17 \times (1 - e^{-0.12t})^3 \text{ kg}$$

The fecundity is determined from

$$f(t) = 0.2 \times 10^6 \times w(t)$$

The stock-recruitment parameters for cod are approximately Ricker [28]

$$\beta = \frac{1}{53.7}, \quad \alpha = 5.89 \times 10^{-6}$$

In the following discussion, these parameters will not be changed. We will allow, however, different recruitment functions, namely Beverton-Holt or Ricker.

**Beverton-Holt**:-

$$R(P) = \frac{\alpha P}{1 + \beta P}$$

**Ricker**:-

$$R(P) = \alpha Pe^{-\beta P}$$
Also we will discuss the influence of variable mortality which we model as

\[
\mu(i) = \begin{cases} 
0.18 & i \leq \frac{m}{2} \\
0.44 \times i - 0.04 & i > \frac{m}{2} 
\end{cases}
\]

Fig 4.b: ---- Beverton Holt _______ Ricker
1. **Selective harvesting**

Constant mortality, weight

![Graph showing yield vs. h](image)

Fig. 4.4.1: Ricker recruitment is used. Optimal value of \( h = 0.8, j(t+1) = 7 \) years and MSY = 18.7 Kg

![Graph showing yield vs. h](image)

Fig. 4.4.2: B-H. recruitment is used. Optimal value of \( h = 0.85, j(t+1) = 8 \) years and MSY = 28 Kg
Variable mortality, weight

Fig. 4.4.3: Ricker recruitment is used. Optimal value of $h = 0.8$, $j(t+1) = 7$ years and $\text{MSY} = 18.7$ Kg

Fig. 4.4.4: B-H. recruitment is used. Optimal value of $h = 0.85$, $j(t+1) = 8$ years and $\text{MSY} = 28$ Kg
Constant mortality, price

Fig. 4.4.5: Ricker recruitment is used. Optimal value of $h = 0.8$, $j(t+1) = 7$ years and
$\text{MSY} = 18.9 \text{ Kg}$

Fig. 4.4.6: B-H. recruitment is used. Optimal value of $h = 0.85$, $j(t+1) = 8$ years and
$\text{MSY} = 28.4 \text{ Kg}$
Variable mortality, price

Fig. 4.4.7: Ricker recruitment is used. Optimal value of $h = 0.8$, $j(t+1) = 7$ years and $\text{MSY} = 18.9 \text{ Kg}$

Fig. 4.4.8: B-H. recruitment is used. Optimal value of $h = 0.85$, $j(t+1) = 8$ years and $\text{MSY} = 28.4 \text{ Kg}$

There is no difference between constant and variable mortality because $j(t+1) < m/2$ whatever the recruitment function is used.
2. **Net harvesting**

Constant mortality, weight

![Graph showing yield vs. harvesting rate](image)

\[ \ldots k = 5, \quad \ldots h_{\text{max}} = 0.92 \quad \text{with MSY} = 18.66 \text{ Kg} \]

Variable mortality, weight

![Graph showing yield vs. harvesting rate](image)

\[ \ldots k = 5, \quad \ldots h_{\text{max}} = 0.92 \quad \text{with MSY} = 18.6 \text{ Kg} \]
Constant mortality, price

Fig. 4.5.3: Optimal mesh width $k = 6$. $h_{\text{max}} = 0.91$ with MSY = 18.9 Kg

Variable mortality, price

Fig. 4.5.4: Optimal mesh width $k = 6$. $h_{\text{max}} = 0.91$ with MSY = 18.7 Kg

MSY in variable mortality is smaller than MSY in constant mortality.
3. **Semicontinuous harvesting**

**Constant mortality**

![Graph showing yield $Y(h)$ vs. harvesting $h$ for different mesh widths $k$.](image)

*Fig. 4.6.1: Optimal mesh width $k = 5$. $h_{max} = 5.8$ with MSY = 13.44 Kg*

**Variable mortality**

![Graph showing yield $Y(h)$ vs. harvesting $h$ for different mesh widths $k$.](image)

*Fig. 4.6.2: Optimal mesh width $k = 5$. $h_{max} = 5$ with MSY = 13 Kg*
§ 4.2 Influence of parameters

There are three independent parameters acting on our models (mortality $\mu$, Von-Bertalanffy growth parameter $K$, which are approximately linearly dependent on the maximum age $m$ (see Fig.1.3 chapter 1) and finally recruitment parameter $\alpha$). $\beta$ is a scaling parameter i.e., it does not influence the results. Now, we will study the influence of these parameters in yield using the linear regression formula which obtained in chapter 1 (section 1.3). We will use Ricker recruitment function as an example.

1 Mortality $\mu$ :-

1. Selective harvesting

Fig. 4.7.1: Influence of mortality in selective harvesting when mortality depends on max age $m$. 
Table 4.1. Results of fig. 4.7.1:-

<table>
<thead>
<tr>
<th>Mortality</th>
<th>$h_{max}$</th>
<th>Optimal k</th>
<th>$Y_{max}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.47</td>
<td>1</td>
<td>3</td>
<td>5451</td>
</tr>
<tr>
<td>0.37</td>
<td>0.93</td>
<td>4</td>
<td>5365</td>
</tr>
<tr>
<td>0.27</td>
<td>0.8</td>
<td>5</td>
<td>4890</td>
</tr>
<tr>
<td>0.17</td>
<td>0.6</td>
<td>6</td>
<td>4768</td>
</tr>
<tr>
<td>0.07</td>
<td>0.6</td>
<td>7</td>
<td>4635</td>
</tr>
</tbody>
</table>

Increasing mortality means the numbers of individual at high age classes are decreasing and MSY in this case is decreasing because the probability of dying is increasing.

2. Net harvesting

Fig. 4.7.2: Influence of mortality in net harvesting when mortality depends on max age $m$. 
Table 4.2. Results of fig. 4.7.2:-

<table>
<thead>
<tr>
<th>Mortality</th>
<th>$h_{max}$</th>
<th>$J(t+1)$</th>
<th>$Y_{max}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.47</td>
<td>0.9</td>
<td>3</td>
<td>4925</td>
</tr>
<tr>
<td>0.37</td>
<td>0.8</td>
<td>4</td>
<td>4367</td>
</tr>
<tr>
<td>0.27</td>
<td>0.7</td>
<td>5</td>
<td>4230</td>
</tr>
<tr>
<td>0.17</td>
<td>0.6</td>
<td>6</td>
<td>2428</td>
</tr>
<tr>
<td>0.07</td>
<td>0.5</td>
<td>7</td>
<td>2901</td>
</tr>
</tbody>
</table>

$Y_{max}$ in selective harvesting is always greater than $Y_{max}$ in net harvesting.

3. Semicontinuous harvesting

![Influence of mortality when it depends on $m$ in the semicontinuous model](image)

Fig. 4.7.3: Influence of mortality in semicontinuous harvesting when mortality depends on max age $m$.

Table 4.3. Results of fig. 4.7.3:-

<table>
<thead>
<tr>
<th>Mortality</th>
<th>$h_{max}$</th>
<th>$Optimal\ k$</th>
<th>$Y_{max}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.47</td>
<td>0.3</td>
<td>1</td>
<td>319.8</td>
</tr>
<tr>
<td>0.37</td>
<td>0.4</td>
<td>2</td>
<td>458</td>
</tr>
<tr>
<td>0.27</td>
<td>0.4</td>
<td>3</td>
<td>605</td>
</tr>
<tr>
<td>0.17</td>
<td>0.5</td>
<td>4</td>
<td>860</td>
</tr>
<tr>
<td>0.07</td>
<td>0.5</td>
<td>4</td>
<td>1576</td>
</tr>
</tbody>
</table>
2. Von Bertalanffy growth parameter $K$

2.1 Selective harvesting

Fig. 4.8.1 Influence of $K$ in selective harvesting when $K$ depends on max age $m$.

Table 4.4. Results of fig. 4.8.1:-

<table>
<thead>
<tr>
<th>$K$</th>
<th>$h_{\text{max}}$</th>
<th>Optimal $k$</th>
<th>$Y_{\text{max}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.76</td>
<td>0.6</td>
<td>4</td>
<td>12146</td>
</tr>
<tr>
<td>0.61</td>
<td>0.7</td>
<td>5</td>
<td>12046</td>
</tr>
<tr>
<td>0.46</td>
<td>0.8</td>
<td>6</td>
<td>11418</td>
</tr>
<tr>
<td>0.31</td>
<td>0.9</td>
<td>7</td>
<td>10460</td>
</tr>
<tr>
<td>0.16</td>
<td>0.92</td>
<td>10</td>
<td>9414</td>
</tr>
</tbody>
</table>
2.2 Net harvesting

Fig. 4.8.2: Influence of $K$ in net harvesting when $K$ depends on max age $m$.

Table 4.5. Results of fig. 4.8.2:

<table>
<thead>
<tr>
<th>$K$</th>
<th>$h_{\text{max}}$</th>
<th>$J(t+1)$</th>
<th>$Y_{\text{max}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.76</td>
<td>0.6</td>
<td>2</td>
<td>11989</td>
</tr>
<tr>
<td>0.61</td>
<td>0.7</td>
<td>3</td>
<td>11166</td>
</tr>
<tr>
<td>0.46</td>
<td>0.8</td>
<td>3</td>
<td>9767</td>
</tr>
<tr>
<td>0.31</td>
<td>0.9</td>
<td>4</td>
<td>8910</td>
</tr>
<tr>
<td>0.16</td>
<td>0.9</td>
<td>6</td>
<td>7169</td>
</tr>
</tbody>
</table>
2.3 Semicontinuous harvesting

![Graph showing influence of K in semicontinuous harvesting when K depends on max age m.]

Table 4.6. Results of fig. 4.8.3:-

<table>
<thead>
<tr>
<th>K</th>
<th>$h_{max}$</th>
<th>$Optimal \ k$</th>
<th>$Y_{max}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.76</td>
<td>0.4</td>
<td>2</td>
<td>11910</td>
</tr>
<tr>
<td>0.61</td>
<td>0.6</td>
<td>3</td>
<td>9236</td>
</tr>
<tr>
<td>0.46</td>
<td>0.7</td>
<td>4</td>
<td>8748</td>
</tr>
<tr>
<td>0.31</td>
<td>1</td>
<td>5</td>
<td>8685</td>
</tr>
<tr>
<td>0.16</td>
<td>2</td>
<td>5</td>
<td>7138</td>
</tr>
</tbody>
</table>

Figures 4.8.1, 4.8.2 and 4.8.3 show that when $m$ decreases, the value of $K$ is increasing and the growth function raises to its asymptotic value more quickly. This means that the weight is increasing more quickly too. Since the larger fish are more catchable, so the values of $j(t+1)$, optimal mesh width $k$ are decreasing while the MSY is increasing.
3. Recruitment parameter $\alpha$

3.1 Selective harvesting

Fig. 4.9.1. Comparison between different values of $\alpha$ in selective harvesting

- $\alpha$: $h_{max} = 0.9$, $j(t+1) = 4$ and $Y_{max} = 13139$
- 1.5 $\alpha$: $h_{max} = 0.4$, $j(t+1) = 3$ and $Y_{max} = 14327$
- 2 $\alpha$: $h_{max} = 0.3$, $j(t+1) = 2$ and $Y_{max} = 15176$

3.2 Harvesting with nets

Fig. 4.9.2. Comparison between different values of $\alpha$ in net harvesting

- $\alpha$, optimal mesh width $k = 3$, $h_{max} = 0.9$ and MSY = 13133 gm
- 1.5 $\alpha$, optimal mesh width $k = 2$, $h_{max} = 0.7$ and MSY = 14126 gm
- 2 $\alpha$, optimal mesh width $k = 1$, $h_{max} = 0.6$ and MSY = 14595 gm
3.3 Semicontinuous harvesting

Fig. 4.9.3. Comparison between different values of $\alpha$ in semicontinuous harvesting

- $\alpha$, optimal mesh width $k = 3$, $h_{\text{max}} = 1.2$ and MSY = 12432 gm
- $1.5\alpha$, optimal mesh width $k = 2$, $h_{\text{max}} = 2.2$ and MSY = 13792 gm
- $2\alpha$, optimal mesh width $k = 1$, $h_{\text{max}} = 3$ and MSY = 14106 gm

Figures 4.9.1, 4.9.2 and 4.9.3 indicate that MSY is increasing as the recruitment parameter $\alpha$ is increasing because $\alpha$ is the probability of an egg to develop into a viable larva and when this probability increases, the recruitment function increases i.e., the number of eggs is increasing so MSY increases as $\alpha$ increases.
§ 4.3 Sensitivity of parameters

Sensitivity analysis Tomovic [31] was employed to determine the relative importance of misspecification of the biological variables in the model to the predicted evolutionary stable solution. Now we will study the sensitivity of mortality, Von Bertalanffy growth parameter $K$ and recruitment parameter $\alpha$ in each harvesting model.

1. Mortality

Selective harvesting:-

![Graph](image)

Fig. 4.10.1a. Sensitivity for mortality parameter in selective harvesting
(Dotted): mortality = 0.19, (Solid): mortality = 0.2 and (Dashed): mortality = 0.21
Net harvesting:-

![Graph showing yield Y(h) against harvesting h for net harvesting with different mortality parameters (Dotted: mortality = 0.19, (Solid): mortality = 0.2 and (Dashed): mortality = 0.21).

Fig. 4.10.1b. Sensitivity for mortality parameter in net harvesting (Dotted): mortality = 0.19, (Solid): mortality = 0.2 and (Dashed): mortality = 0.21

Semicontinuous harvesting:-

![Graph showing yield Y(h) against harvesting h for semicontinuous harvesting with different mortality parameters (Dotted: mortality = 0.19, (Solid): mortality = 0.2 and (Dashed): mortality = 0.21).

Fig. 4.10.1c. Sensitivity for mortality parameter in semicontinuous harvesting (Dotted): mortality = 0.19, (Solid): mortality = 0.2 and (Dashed): mortality = 0.21

From figures 4.10.1, we get that increasing in mortality parameter by 0.01 makes decreasing in MSY of selective and net harvesting by approximately 600 units and decreasing by 100 units in semicontinuous harvesting.
2. Von Bertalanffy Growth parameter $K$

Selective harvesting:-

Fig. 4.10.2 a. Sensitivity for parameter $K$ in selective harvesting
(Dotted): $K = 0.69$, (Solid): $K = 0.7$ and (Dashed): $K = 0.71$

Net harvesting:-

Fig. 4.10.2 b. Sensitivity for parameter $K$ in net harvesting
(Dotted): $K = 0.47$, (Solid): $K = 0.46$ and (Dashed): $K = 0.48$
Semicontinuous harvesting:-

Fig. 4.10.2 c. Sensitivity for parameter $K$ in semicontinuous harvesting
(Dotted): $K = 0.69$, (Solid): $K = 0.7$ and (Dashed): $K = 0.71$

From figures 4.10.2, we get that increasing in $K$ parameter by 0.01 makes increasing in MSY by approximately 50 units.

3. Recruitment parameter $\alpha$

Selective harvesting:-

Fig. 4.10.3 a. Sensitivity for recruitment parameter $\alpha$ in selective harvesting
(dashed) 0.9 $\alpha$, (Solid) 1.1 $\alpha$ and (dotted) $\alpha$
Net harvesting:

![Net harvesting graph](image)

**Fig. 4.10.3 b.** Sensitivity for recruitment parameter $\alpha$ in net harvesting (dashed) 0.9 $\alpha$, (Solid) 1.1 $\alpha$ and (dotted) $\alpha$

Semicontinuous harvesting:

![Semicontinuous harvesting graph](image)

**Fig. 4.10.3 c.** Sensitivity for recruitment parameter $\alpha$ in semicontinuous harvesting (dashed) 0.9 $\alpha$, (Solid) 1.1 $\alpha$ and (dotted) $\alpha$

From figures 4.10.3, we get that increasing in recruitment parameter $\alpha$ by 0.1 makes increasing in MSY by 50 units.
§ 4.4 Influence of Cost in semicontinuous harvesting

In this section, we will study influence of cost function in semicontinuous harvesting because we found that semicontinuous harvesting is more realistic harvesting models.

For simplicity assume that cost function is a linear function in fishing effort as

\[ C(h) = a + b\ h \]

Where, \( a \) is the fixed cost and \( b \) is the cost of fishing effort \( h \).

In order to determine the cost parameters \( a \) and \( b \), let us consider

\[ a + bh_{\text{max}} = c \cdot Y_{\text{max}}, \quad a = bh_{\text{max}} \]

\[ \therefore b = \frac{c \cdot Y_{\text{max}}}{2h_{\text{max}}}, \quad a = \frac{c \cdot Y_{\text{max}}}{2} \]

where \( 0 \leq c \leq 1 \) is measure the percentage of cost and \( 1-c \) is measure the percentage of gain.

The net revenue is the difference between the Yield \( Y(h) \) and the cost function \( C(h) \) i.e.,

\[ N(h) = Y(h) - (a + bh)(1 + \delta) \]

where, \( \delta \) is the interest rate.
We are now in a situation, where the population levels are far below the equilibrium, due to overfishing. In order to describe this situation, we assume

\[ x_i(0) = d \cdot \bar{x}_i \]

Now we will determine the values of \( c, d \) and \( \delta \) such that the net revenue \( N(h) \geq 0 \) because when \( N(h) < 0 \), the fishing is uneconomical.

**Example 1: Haddock**

![Graph showing influence of cost function in semicontinuous harvesting](image)

Fig. 4.11.1: Influence of cost function in semicontinuous harvesting

- \( \_\_\_\_ \): \( c = 0.3 \) \( d = 0.2 \) and \( \delta = 0.1 \)
- \( \----- \): \( c = 0.3 \) \( d = 0.2 \) and \( \delta = 0.07 \)
From these figures we found that the fishing must be begin when 30% for haddock population are in the sea (\(d=0.3\)) with 30% cost and 70% gain (\(c=0.3\)).
Now we will study the influence of cost on $h_{\text{max}}$ for haddock

![Graph](image)

**Fig. 4.11.3: Influence of cost function on $h_{\text{max}}$**

--- Yield with cost function, $c = 0.3$, $d = 0.3$, $\delta = 0.1$ and $h_{\text{max}} = 1.1$

----- Yield without cost function, $h_{\text{max}} = 2.2$

From figure 4.11.3, the cost function causes decreasing in $h_{\text{max}}$

**Example 2: Cod**

![Graph](image)

**Fig. 4.11.5: Influence of cost function in semicontinuous harvesting**

--- $c = 0.2$, $d = 0.2$, and $\delta = 0.1$

----- $c = 0.2$, $d = 0.2$, and $\delta = 0.07$
From these figures we found that the fishing must be begin when 30% for cod population are in the sea ($d=0.3$) with 20% cost and 80% gain ($c=0.2$) because MSY when $d=0.2$ is smaller than MSY when $d=0.3$
Now we will study the influence of cost on $h_{\text{max}}$ for cod

![Graph showing the influence of cost function on $h_{\text{max}}$.](image)

Fig. 4.11.7: Influence of cost function on $h_{\text{max}}$

- : Yield with cost function, $c = 0.2$ $d = 0.3$ $\sigma = 0.1$ and $h_{\text{max}} = 2.4$

- : Yield without cost function, $h_{\text{max}} = 5.8$

From figure 4.11.7, the cost function also causes decreasing in $h_{\text{max}}$

Finally, below the value of $d$, the fishing is uneconomical.
§ 4.5 Conclusion and Results:

The role of harvesting in nonlinear age-structured fish population models is studied. We compare different harvesting models (selective harvesting, harvesting with nets and semicontinuous harvesting). We used the overcompensatory Ricker and Beverton-Holt recruitment functions in our models. The comparison between MSY in Ricker and Beverton-Holt recruitment is studied. When Ricker recruitment is used, the maximum sustainable yield (MSY) is approximately 25% less than that in the Beverton-Holt model because the number of recruits in the Ricker model is less than that in the Beverton-Holt description. This can be seen clearly in Figs. 4.a,b.

The important parameters in our model are mortality, the von Bertalanffy growth parameter $K$, maximum age $m$ and finally recruitment parameters $\alpha$ and $\beta$. There exists an approximate linear relationship between Von Bertalanffy growth parameter $K$ and maximum age $m$ (see Fig. 1.3). Also there exists an approximate linear relationship between mortality and maximum age $m$ Hoenig [14], so we studied the influence of mortality, Von Bertalanffy growth parameter $K$ and recruitment parameter $\alpha$ on harvesting models. Note that parameter $\beta$ is a scaling parameter i.e., it has no influence on harvesting models.

1) The influence of mortality is that, in general, increasing mortality means the numbers of individual at high age classes are decreasing and MSY in this case is decreasing because the probability of dying is increasing. In our particular example, Figure 4.1.3 indicates that the influence of mortality in selective harvesting is ignored because $j(t+1)$ is less than $m/2$ and mortality is constant in this case.
If one uses a more realistic form of mortality, where mortality increases with age, the higher age classes will be smaller. However, since these are small any way the influence of such an increasing mortality is rather small. This holds in particular, when the largest part of the harvest comes from the low age classes.

In Fig. 4.2.5, the influence of mortality in net harvesting is that the values of MSY in variable mortality is slightly smaller than those in constant mortality because when mortality is increasing, the survival probability $L_i$ is decreasing i.e., the number of fish which arrive to fishable age is also decreasing. At high values of harvesting, the yield curves in constant and variable mortality are coincide. So the sensitivity of mortality parameter on our models is small (about 5%) and we can use a constant mortality as a simplification of our discrete models (selective harvesting and harvesting with nets).

2) **The influence of the Von-Bertalanffy growth parameter $K$** is that when $m$ decreases, the value of $K$ is increasing and the growth function raises to its asymptotic value more quickly. This means that the weight is increasing more quickly too. Since the larger fish are more catchable, so the values of $j(t+1)$, optimal mesh width $k$ are decreasing while the MSY is increasing.

3) Since the bigger fish are more valuable, we can use the price instead of weight proportional to $p_i = w_i^{1.1}$ as an example. In this case, the MSY increases by a factor of $w_{\infty}^{0.1}$. In haddock example, the factor of increasing $(1.34)^{0.1} = 1.03$ which means a small increment occurs when we used the price instead of weight.
There is a direct relationship between the values of optimal mesh width \( k \) in net harvesting and the values of partial age class harvested in selective harvesting \( j(t+1) \) this means that when optimal mesh width \( k \) is decreasing, the smaller age fish are catching so \( j(t+1) \) is decreasing and vice versa.

4) The influence of the recruitment parameter \( \alpha \):
Figures 4.9.1, 4.9.2 and 4.9.3 indicate that MSY is increasing as the recruitment parameter \( \alpha \) is increasing because \( \alpha \) is the probability of an egg to develop into a viable larva and when this probability increases, the recruitment function increases i.e., the number of eggs is increasing so MSY increases as \( \alpha \) increases.

5) MSY in selective harvesting is greater than MSY in net harvesting because in selective harvesting, the MSY is over a cube with \( m-1 \) dimension (the values of \( h_i, h_f = 0 \)) but in harvesting with nets, the MSY is over a subset of the cube in selective harvesting, these subsets are lines of diagonal of that cube so, selective harvesting is always greater than harvesting with nets but the results are very close.

Selective harvesting is the simplest harvesting strategy because the equations which describe selective harvesting are very simple. But it is unrealistic so we can not use it as a harvesting strategy.
MSY in selective harvesting policy involves a partial or a total harvest of only one age class or a partial harvest of one age class and a total harvest of a second (of course older) age class. The bimodality of the MSY policy was first derived for the Leslie matrix model by Beddington and Taylor [1].

Harvesting with nets is more realistic than selective harvesting but its equations are more complicated and it is impossible to determine the optimal harvesting analytically, so we determined it numerically. We can use harvesting with nets as a discrete model to determine MSY in fish populations.

The semicontinuous harvesting model is more realistic than harvesting with nets because in semicontinuous harvesting, the harvesting intensity is a continuous process vary in \([0, \infty)\). Fig. 4.3.1 shows that MSY in harvesting with nets is greater than those in semicontinuous harvesting because in semicontinuous harvesting, the probabilities of surviving from age class \(i\) to age class \(i+1\) \((\tau_i)\) are decreasing function of harvesting intensity \(h\) in an exponential form. Of course all functions (weight, mortality and surviving probabilities) are continuous in their arguments.

When we use the cost function on semicontinuous harvesting, we found that \(h_{\text{max}}\) must be decreasing.

Equations in semicontinuous harvesting are more complicated than harvesting with nets and also determination of an optimal harvesting strategy is very complicated too. So we can not determine it analytically any more and rather use numerical methods.
Chapter 5
Dynamical model for fish population and stability

In chapter 2, we studied the static model for fish population and determined the equilibrium vector. In this chapter we will analyze the dynamics for some concrete models because in reality we are far from the equilibrium.

§ 5.1 Description of the model

Let $P(t)$ be the number of recruits of fish from all age classes at time $t$. $x_i(t)$ be the population density (number of fish) of $i$-th age class at time $t$. The model will be

$$x(t+1) = A x(t)$$  \hspace{1cm} (5.1)

where $A$ is a Leslie matrix described in equation (3.27).

The general solution of a matrix equation (5.1) is given by

$$x(t+1) = A(t) A(t-1) \cdots A(1) x(0)$$  \hspace{1cm} (5.2)

We will determine the state vector $x(t)$ if $x(0)$ is given.

Let

$$x(1) = \begin{bmatrix} x_1(1) \\ x_2(1) \\ \vdots \\ x_m(1) \end{bmatrix} = \begin{bmatrix} x_1(0) \\ \tau_1 x_1(0) \\ \vdots \\ \tau_{m-1} \cdots \tau_1 x_1(0) \end{bmatrix}$$

Since the initial value of individual is undetermined, we assume that this initial value is far from the equilibrium i.e., let

$$x_i(0) = 0.1 \bar{x}_i(0) \hspace{1cm} \forall i = 1, \cdots, m$$

where $\bar{x}_i(0)$ are components of equilibrium vector determined by equation (2.17).
Since

\[ P(0) = \sum_{i=1}^{m} f_i x_i(0) \]

then \( P(0) \) is also determined.

For \( t = 1 \) one obtains

\[
x(2) = \begin{pmatrix}
x_1(2) \\
x_2(2) \\
\vdots \\
x_m(2)
\end{pmatrix} = \begin{pmatrix}
\alpha P(1) r(P(1)) \\
\tau x_1(1) \\
\vdots \\
\tau_{m-1} x_{m-1}(1)
\end{pmatrix}
\]

where

\[ P(1) = \sum_{i=1}^{m} f_i x_i(1) \]

is also determined

Continuing this method for all \( t \), we can determine all values of \( x(t) \) in terms of \( x(0) \).

By using this method, we can get

\[
P(t) = \alpha \sum_{i=1}^{t} L_{i} f_{i} P(t-i) r(P(t-i)) + \sum_{i=m+1}^{m} L_{m} f_{i} x_i(0), \quad t < m \quad (5.3a)
\]

and

\[
P(t) = \alpha \sum_{i=1}^{m} L_{i} f_{i} P(t-i) r(P(t-i)), \quad t \geq m \quad (5.3b)
\]

Here \( \alpha \) is as before the density-independent probability of survival from egg to age 1. Equations (5.3) describes the number of eggs at time \( t \) which are spawned by mature fish of age \( t-i \). Since

\[ x_i(t+1) = \alpha P(t) r(P(t)) \quad (5.4) \]

we can determine the population \( x(t) \) for all values of time \( t \).
§ 5.2 Stability for concrete fish species

Now we will determine numerically the stable age distribution for haddock and cod for several values of $\alpha$. We will use Ricker and Beverton-Holt recruitment models.

1) Haddock

Specifically we have for haddock $m = 20$ years, $\mu = 0.2$ and

$$w(t) = 1.34 \times \left(1 - e^{-0.26(t + 0.75)}\right)^3 \text{ kg}$$

As before the fecundity is determined from

$$f(t) = w(t) \times 10^5$$

and the stock-recruitment parameters are

$$\beta = \frac{1}{61.4}, \quad \alpha = 1.53 \times 10^{-8}$$
**a) Ricker recruitment model:**

By using these parameters for haddock, we can determine the stable age distribution from the following figure.

![Graph showing stable age distribution for haddock as a function of $\alpha n$]({"alt": "Fig. 5.2: Stable age distribution for haddock as a function of $\alpha n$"})

From Fig. 5.2, we see that, when the values ($\alpha n$) are increasing, this means that the expected number of offspring per individual over its lifetime is also increasing, so the values of the stable age distribution are also increasing. In all cases the solution approaches the stable age distribution because ($\ln \alpha n < 2$). After one generation, the population will be stable.
Now, we will introduce harvesting and discuss the influence of harvesting on stable age distribution

Fig. 5.3: Influence of harvesting for haddock when $\alpha n = 15$
In long time ignoring the first 50 years, we get the figure of periodicity as:-

As expected, periodic solutions occur beyond the stability. Vertical axis in number $\times 10^{-7}$ of individuals in first age class.
From previous Figures, without harvesting and $ln(\alpha n) < 2$, the haddock population are periodic with periodicity $m/2$ where $m$ is the maximum age. Increasing harvesting rate causes more stable in population.
\textit{b) Beverton-Holt recruitment model :–}

Fig. 5.5: Stable age distribution for haddock as a function of $(αn)$

Fig. 5.6: Influence of harvesting for haddock when $(αn=15)$
From Figures 5.5 to 5.7, we found as expected that when we use Beverton-Holt recruitment model, stability of population always holds whatever the values of $(\alpha n)$.  

Fig. 5.7: Influence of harvesting for haddock when $(\alpha n =30)$
2) Cod

For cod the parameters are \( m = 30 \) years, \( \mu = 0.18 \) and

\[
 w(t) = 17 \times \left(1 - e^{-0.12t}\right)^3 \text{ kg}
\]

As before the fecundity is determined from

\[
 f(t) = 0.2 \times 10^6 \times w(t)
\]

and the stock-recruitment parameters are

\[
 \beta = \frac{1}{53.7}, \quad \alpha = 5.89 \times 10^{-6}
\]
Ricker recruitment model:-

Fig. 5.9: Stable age distribution for cod as a function of \((a_n)\)

As expected, the stability holds because \(\ln (a_n) < 2\). After approximately one generation, the cod population will be stable. The maximum value of gibbs phenomena is increasing when \((a_n)\) is increasing because the expected number of offspring per individual over its lifetime is increasing.
From previous Figures, without harvesting and $\ln(\alpha n) < 2$, cod population is periodic with periodicity $m/2$ where $m$ is the maximum age. Increasing harvesting rate causes more stable in population.
Finally, if we use Ricker recruitment function, the densities of haddock and cod approximately return to their previous values (periodic behaviour) every 10 years for haddock and 15 years for cod i.e., every $m/2$ years where $m$ is the maximum age. The unstability in these cases holds because of the discretization of time.

The simulations shown in Figs. 5.3, 5.4 and 5.10 examine the behaviour of the system of haddock and cod as $(a n)$ is fixed with harvesting intensity $h$ is varied.

The simulations shown in Figs. 5.2 and 5.9 examine the behaviour of the system of haddock and cod as $(a n)$ is varied with no harvesting intensity.

Figures 5.5 – 5.7 show that the system is stable when we use Beverton-Holt recruitment function.
References


