DTU Aqua
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Ocean Life
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Adaptive foraging in a size-structured model of marine ecosystem

- M.Sc. thesis report -

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Resumé

I denne afhandling er der lavet en simpel størrelsesstruktur model, der beskriver havets økosystem baseret på det princip at alle arter, som lever i havet – lige fra de små partikler og havdyr som zooplankton til de større fisk som tun og hajer – kan karakteriseres af kun ét karaktertræk, og det er deres maksimum vægt. I denne model er det brugt en antagelse om at alle fisks størrelse er proportional til vægten, og at vægtstørrelsen afgør hvor i det trofiske niveau. Det herskende princip i denne afhandling er at de større fisk spiser de mindre fisk, og hvilken vægtstørrelse fiskene foretrækker at spise er afgjort af den logaritmiske normale vægtfordeling. Dynamik i økosystemet er bestemt af de tre nøglekomponenter; somatisk vækst, frugtbar and dødelighed. Hvor hurtigt fiskene kan vokse er afhængigt af mængden af madenergi, som de har spist. Madenergien skal i første omgang gå til at dække fiskenes strukturelle/metaboliske vedligeholdelse. Når det er dækket går overskuddet af energi til somatisk vækst og reproduktion. I modellen er der også inkluderet en adfærdsanalyse, hvor fisk kan vælge mellem de to forskellige opholdssteder, fortæringssted og beskyttelsessted. Hvert sted har fordele og ulemper. Fortæringsstedet har masser af mad men til gengæld er der en stor risiko for at rovfisk også kommer forbi, mens beskyttelsesstedet yder en beskyttelse til ofrefisk men til gengæld er der ikke så meget mad. Fiskene kan dø af tre forskellige grunde, nemlig død af sult, død af at blive spist af de større fisk og død af andre årsager (baggrundsdødelighed). Formålet med afhandling er at finde ud af, hvad den optimale balance mellem de to opholdssteder er, og undersøge hvilke konsekvenser adfærden har for fiskene. For eksemplet er det fundet, at det optimale opholdssted er afhængigt af mæthedsniveauet (feeding level). Når mæthedsniveauet kommer under det kritiske niveau f_c, så uddør fiskene. Kommer mæthedsniveauet over $\sqrt{f_c}$ (når det antages der ingen baggrund dødelighed er), så betyder det, at fiskene har for meget mad og i princippet kan trække sig lidt tilbage fra fortæringsarenaen. Er mæthedsniveauet mellem f_c og $\sqrt{f_c}$, må fiskene satset hele deres tid på fortæringsarenaen. Det er også fundet, at den optimale adfærd kan findes ved hjælp af ”myopic” ’s analytisk strategi i kombination af den numeriske upwind-metode. Det er yderligere fundet, at tilpasset adfærd har gjort arterne mere følsomme ovenfor tæthedsafhængigheden, idet udsvingene bliver større, når adfærden inkluderes. Kannibalisme synes at dæmpe effekten, hvorfor adfærdsmodellen siges at fremhæve vigtigheden af at inkludere kannibalisme i økologien.

Abstract

A simple size structural model in this thesis is made to describe the marine ecosystem based on the principle that all species living in the sea - from the small particles and sea creatures as zooplankton to the larger fish such as tuna and sharks - can be characterized by only one character trait, and it is their maximum weight. In this model the assumption about all fish size is proportional to the weight and this weight determines which level of the trophic the fish is living, is used. The main principle used in this thesis is that the bigger fish eat the smaller fish and which weight size the predator fish prefer to eat is determined by the logarithmic normal weight distribution. The dynamics of the ecosystem is determined by three key components, somatic growth, fertility and mortality. How quickly the fish can grow depends on the amount of food energy they have eaten. The ingested energy must first go to cover their structural / metabolic maintenance. When the maintenance is covered the excess of energy goes directly to somatic growth and reproduction. The model also includes a behavioral analysis, in which fish can choose between two different habitats, the foraging arena and the refuge. Every habitat has pros and cons. The foraging arena has plenty of food but then there is a high risk to meet the predator fish while the refuge provides protection to prey fish but then there is not as much food. The fish can die of three different reasons: death by starvation, death by being eaten by predators, and death from other causes (background mortality). The aim of the thesis is to find out what the optimal balance between the two habitats is and examine the consequences of this behavior has for the fish. For example it is found that the optimal habitat is depended on the feeding level. When the feeding level falls below the critical level f_c, so the fish dies. The feeding level being above $\sqrt{f_c}$ (assuming no background mortality is), means that the fish has too much food and in principle can spend less time in the foraging arena. If the level of saturation is between f_c and $\sqrt{f_c}$, the fish has to spend their entire time on the foraging arena. It is also found that the optimal behavior can be found by the myopic's analytical strategy in combination of the numerical upwind method. It is further found that the adaptive behavior has made the species more sensitive above density dependence, as the oscillation in the recruitment becomes larger when the behavior is included. Cannibalism seems to lessen the size of oscillation, why the behavioral model is said to highlight the importance of including cannibalism in ecology.

Preface

This thesis has been presented to obtain the Master of Science degree at the Technical University of Denmark (DTU). It was carried out at the National Institute of Aquatic Resource (DTU AQUA / Ocean Life) under supervision by Ken H. Andersen and Uffe H. Thygesen. I am very grateful and wish to thank them for making it possible for me to study the thesis and let me attend the weekly meeting listing to different exciting presentations made by other Ph.D. students, e.g. Julie Sainmont about her work (Dynamic programming vs myopic behavior optimization, 2013) which is very similar to my thesis, and taking an active share in the presentation under the yearly meeting. Working with this thesis has been a very inspiring and instructive experience for me and give me a different view of the biological life cycle.

The presented work marks transition in my areas of interest from the geometry and finance optimization to the marine theoretical ecology. I have had no experience in the field - apart from a course named “Mathematical biology” and a special summer course during last semester. It is at this course I received knowledge about the marine theoretical ecology and acquired a taste for it. It is why I have chosen to work with the thesis. The thesis makes me want to study furthermore about the field and now I hope that the thesis will make it possible for me to take a Ph.D. position in this field and participate in different workshops as part of the knowledge collecting.

The thesis work was carried out with DTU AQUA in Charlottenlund in the period from August 2013 to Januar 2014. The workplace is very international orientation and I like it and have realized that I have to take more active share in the international events if I want to collect more knowledge about the field. Now I am speaking with Ph.D.-student Zablotski from GEOMAR Helmholtz Centre for Ocean Research Kiel about his work (Optimality-based model of marine zooplankton communities, 2013) and Prof. Dr. Agostino Merico from Leibniz Center for Tropical Marine Ecology about my thesis. It has lead to some interesting discussions and I can only give thanks to my supervisors for encouraging me to apply for the international network.

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Contents

1. Introduction 8
    1.1. Objectives 8
    1.2. Thesis Outline 8
2. Theory 11
    2.1. Structured Population Models 11
        2.1.1. The water column: Two habitats 12
        2.1.2. Partial Differential Equation (PDE) 12
        2.1.3. Community spectrum 14
        2.1.4. Size selection of food items 15
        2.1.5. Volumetric search rate 16
        2.1.6. Encountered food 17
        2.1.7. Maximum consumption 18
        2.1.8. Feeding level 18
        2.1.9. Energy to growth and reproduction 19
        2.1.10. Allocation to reproduction 19
        2.1.11. Fecundity 21
        2.1.12. Somatic growth 22
        2.1.13. Reproduction 23
        2.1.14. Mortality 24
        2.1.15. Dynamic resource spectrum 26
        2.1.16. Survival probability 27
        2.1.17. Fitness 27
        2.1.18. Others 32
        2.1.19. Parameters 33
3. Method 34
    3.1. Which method is best to find the optimal behavior? 34
    3.2. The optimal “myopic” behavior and its limit 35
    3.3. The optimal and critical feeding level 39
4. Results 43
        4.1.1. Static model (static encountered food + static predation mortality) 43
    4.2. Examples of the optimized behavior 47

4.3. Cannibalism 52
  4.3.1. Cannibalism’s influence on the oscillation in the system 55
  4.3.2. A possible solution to the oscillation problem 58
5. Discussion 59
  5.1. Pros and cons in the method 59
  5.2. Improvement of the model 60
  5.3. Numerical setup 63
6. Conclusion 64
Glossary 67
Acronyms 68
References 69
A. Appendices 72

1. Introduction

This chapter contains the formal introduction to the thesis. The objectives of the thesis are stated followed by an outline of the structure of the report.

1.1. Objectives

The objective of this thesis is to locate a mechanism that enables adaptive foraging in a size-structured model of marine ecosystem. The ecosystem is based on the model formulation by (Hartvig, Andersen, & Beyer, 2011) with methods from optimization and evolutionary theory, where the fitness and the adaptive behavior have not been demonstrated. The case studied here is a zooplanktivorous forage fish in a water column. The water column provides two habitats: a foraging arena in the surface where there is food available but where there is also risk of predation, and a refuge at depth where there is little or no food but also much smaller risk from visual predators. The decision an individual faces is how much time during a day should it spend on the foraging arena.

The central questions in this thesis are following:

1) What is the optimal habitat and how does it change during the lifetime of an organism (ontogeny)?
2) How can we find the optimal behavior when we have dynamic processes?
3) How do the fitness and the adaptive behavior change the result?

1.2. Thesis Outline

Chapter 2 is the scientific introduction to this thesis. An introduction to a simple water column and simple size-structured population model is made based on the formulation by (Hartvig, Andersen, & Beyer, 2011) and all parts of the model are elaborately derived.
Within size-structured models the population of a species is described by a density spectrum that includes the composition of different sized individuals in the species population. The assumption about the weight w being proportional to the size is used here.
Within the chapter the Partial Differential Equation (PDE), that links individual-processes of growth, mortality, and reproduction to the population dynamics, is derived. Some parts of the model are modified such that the simple size-structured model can later be used to study the optimal habitat of the population and its ontogeny. The details of how the two habitats are included in the model are also described in the chapter.

The derived model is denoted simple because only one trait, the asymptotic weight W (maximum weight), is used to characterize a species. The adaptive model is also denoted simple because only two habitats, foraging arena and refuge, are used to describe the column water.

Mortality is implemented as predation mortality from size-dependent food intake if the prey is in the foraging arena, starvation mortality is used when acquired energy is insufficient, and ageing mortality (background mortality) is implemented to ensure that the largest individuals are also exposed to a mortality rate.

Size-dependent food intake is realized with a size-selection function that enables a predator to eat of primarily smaller individuals with a given selection width. Due to the size-dependent intake suitable food items are needed for the smallest individuals for which reason background spectrum is included, i.e. (zoo)plankton.
The acquired energy from food intake, which is allocated into somatic growth, maintenance and reproduction, is used to describe the growth by following the principles from the dynamic energy budget (DEB). The DEB theory describes mechanistically the physiological processes involved in the acquisition and use of energy by individual organisms of any given species all along its life cycle. The egg-stage is not modeled explicitly, but egg-mortality is included when the reproduction effort of the matured individuals is routed into production of new recruits. It is assumed that all species has an equal gender distribution.
The details of how the variables in Hartvig's model are used are treated in the chapter. DEB theory allows all the parameters of the individual model to be expressed as simple function of the maximum size of the considered species. The evaluation of individual-level processes is easier than evaluating population-level processes, thus the model is built from the individual-level up to the population-level.
The concept of the community spectrum is also introduced, which is the spectrum consisting of all individuals across all species and the background spectrum. The background spectrum (also called resource spectrum) represents the lower half of the community spectrum, while the spectrum of the species represents the upper half of the community spectrum. The details of how the spectrum is modeled and used are also treated in the chapter.

The methods used to find the optimal habitat are described in chapter 3. In the chapter the pros and cons is discussed using two different strategies, the dynamic programming versus "myopic" decision.
Calculating the optimal strategy is often done using a "myopic" decision, which use an approximate fitness measure and do not account for the entire life of the organism. But under some simple assumptions the "myopic" decision is shown to be an excellent alternative to the "life-story" decision, since "myopic" decision can be solved analytic hence saves a lot of calculation time compared the "life-story" decision.
The "myopic" decision in the model is based on the principle: maximize the fitness expressed as the reproductive value based on the gained energy per mortality rate. When considering the entire life the dynamic programming offers an insight into the optimal strategy. The results by the strategy is illustrated and discussed here.

Chapter 4 treats the results, in which the first section treats "resident" strategy, initially obtained using dynamic programming, to mutants with a slightly different strategy. If the mutants' strategy results in a higher fitness, the mutant strategy will replace the guess. This procedure is repeated until no mutant strategy is able to invade the resident strategy. The strategy provides an idea about how the foraging in the ecosystem is evolved during the generations, i.e. an answer to the question about how the fitness and the adaptive behavior do change the result.
In this chapter it is also discussed when the fish actually optimizes their strategy, i.e. when the mutant strategy is able to replace the resident strategy. In this discussion it is assumed that all fish have intelligence enough to figure out what is the best strategy and that the evolutionary dynamics is much slower than the ecosystem dynamics, i.e. the fish is able to change their strategy when the ecosystem dynamic is calmed down.

Cannibalism also plays a role for the ecosystem and is thus considered in this chapter. In the chapter it is shown that the adaptive behavior increases the importance of the cannibalism's role in the overall fitness, because cannibalism damps the prey-predator cycle (oscillating effect) and thus is an important mechanical part in understanding of the adaptive foraging behavior.

Chapter 5 provides the discussion of the main results along with suggestions for future research. Chapter 6 contains the conclusion, which rounds off the thesis.

2. Theory

The introduction to the model of the community spectrum primarily based on (Hartvig, Andersen, & Beyer, 2011) is introduced here. This chapter focuses on the motivation of using the structured population model. A discussion about how and why the model is linked to the energy budget model is included as this concept is needed for chapter 3 where the dynamic programming is introduced to the model. The dynamic programming is used to find the optimal behavior.

2.1. Structured Population Models

We start this chapter with a discussion about how the ecosystem of the different habitats is described and connected between each other. Some pelagic fish has maturation determined mainly by the weight size and not by the age, e.g. whiting (Marty, Rochet, & Ernande, 2013). Thus we are able to establish a model based on the weight. A simple illustration in **Figure 2.1** shows how the ecosystem for one habitat works; a more detailed description about the ecosystem is presented later on. The core concept in an ecosystem is that the larger fish eat the smaller fish and the energy from the food is used to ensure growth and reproduction for the new offspring. The predators prefer to eat prey with weight β times lesser than their own weight. To ensure that the smallest individuals, e.g. the new offspring with the weight w_0, can still eat something, (zoo)plankton is added in the system as a resource spectrum. The interval of the individual weight of the plankton is covered from the largest w_{cut} to the smallest weight w_0/β^2. It is assumed that the ability to reproduction is good only when the species are matured and that all species always produce the same weight of offspring. All individuals of species i can grow from w_0 to the asymptotic weight W_i (maximum weight). The growth and mortality rate are different depending on the habitats. The individuals can choose freely how much of their daily life should be used in a given habitat. To simplify the model we use only one species in our model and all individuals with the same asymptotic weight size are assumed to have identical behavior, and there are only two habitats in the model which the individuals can choose.

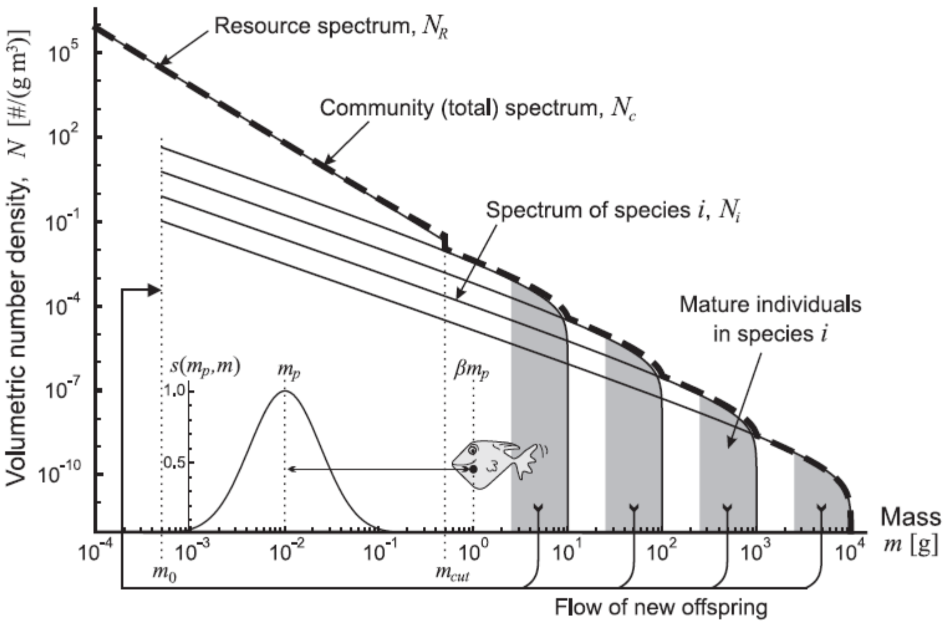


Figure 2.1 An example of how the model is built up.
Illustrated by (Hartvig, Andersen, & Beyer, 2011)

2.1.1. The water column: Two habitats

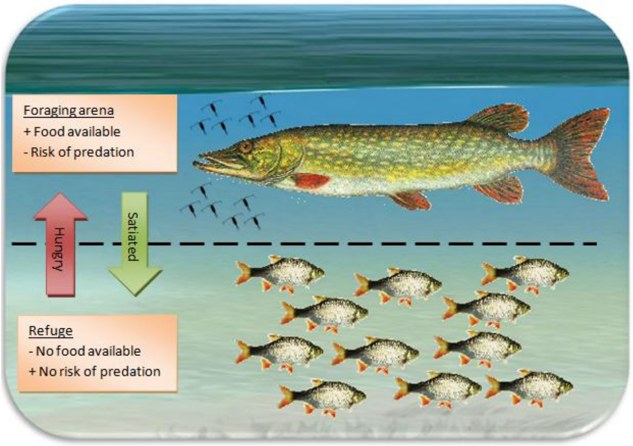


Figure 2.2[1] The water column with two habitats; the foraging arena and the refuge. The hungrier the fish are, the riskier they are willing to run by spending more time τ in the foraging arena, which has food but also predators. The refuge has no food but also no predators, and the time in the refuge is determined by $1 - \tau$.

The water column is a conceptual column of water from sea surface to bottom. Habitat is where a fish lives and must contain: adequate oxygen, tolerable temperature, adequate food and hiding places and much more. The water column provides different type habitats. On the water surface in sea, lakes and ponds there is good food available, fine light, highly oxygen but there is also a risk of predation because this arena provides poor hiding places. It is assumed that the predators also depend on the light in the sea to find the prey. The deeper, the lesser light at the water, hence the harder predators are at finding the prey.

In this study we assume for simplicity there are only two habitats in the water column, *foraging arena* and *refuge*. As mentioned above a foraging arena is an arena in the surface where there is food available but also there is also a risk of predation, and a refuge is a area at depth where there may be too little oxygen and light to sustain life, especially plankton, so there is no food but the refuge provides many hiding places hence much smaller risk from visual predators. A simple example of the water column is illustrated in **Figure 2.2**. The concept is used chiefly for adaptive studies. The decision that an individual in species i faces is how much time $\tau(w)$ during a day it should spend on the foraging arena, where $\tau(w)$ is expressed as a percentage, i.e. $\tau(w) \in [0,1]$. The time spend during a day in the refuge is hereby $1 - \tau(w)$. The decision-making is based on how much risk an individual is willing to take. More about the decision-making is described in chapter 3, but the core conceptual in the behavioral adaption is that the individual is more willing to take risk if starving.

2.1.2. Partial Differential Equation (PDE)

The size-structured model of the ecology system can be stated as an advection equation, where the population structure is described by size-spectrum N. The size-spectrum represents the volumetric abundance density distribution of individuals. The population dynamic is obtained from individual somatic growth rate g and mortality rate μ. One central assumption of the model is that the most important trait of a fish species is its asymptotic size W. The trait dimension is split into discrete asymptotic size classes. The number of individuals in the size range $[w, w + dw]$ is therefore $N(w,t)dw$. The dynamics of the spectrum is generated by the advection equation:

Equation (McKendrick-von Foerster):	**Unit:**
$\frac{\partial N(w,t)}{\partial t} + \frac{\partial g(w,t)N(w,t)}{\partial w} = -\mu(w,t)N(w,t)$	$N = \# \cdot (mass \cdot volume)^{-1} = [\# \cdot (g \cdot m^3)^{-1}]$ $g = mass \cdot time^{-1} = [g \cdot year^{-1}]$

---

[1] This figure is manipulated in programs Paint and PowerPoint and is made by several pictures taking from different homepages, e.g. http://www.mikandersen.dk/GeddeW.jpg, http://www.mikandersen.dk/Aborre.jpg, http://www.travelsworlds.com/wp-content/uploads/2013/12/miami-beach-party-wallpaperbeachx2--blue-and-white-beach-wallpaper-en9kccxd.jpg,

	$\mu = time^{-1} = [year^{-1}]$

The first term expresses the dynamic of the spectrum throughout time, while the second term expresses the growth of the spectrum through weight. The last term describes the mortality of the spectrum. The advection equation is formulated by (McKendrick, 1926) and later by (von Foerster, 1959). A simple interpretation of the equation is illustrated in **Figure 2.3**.

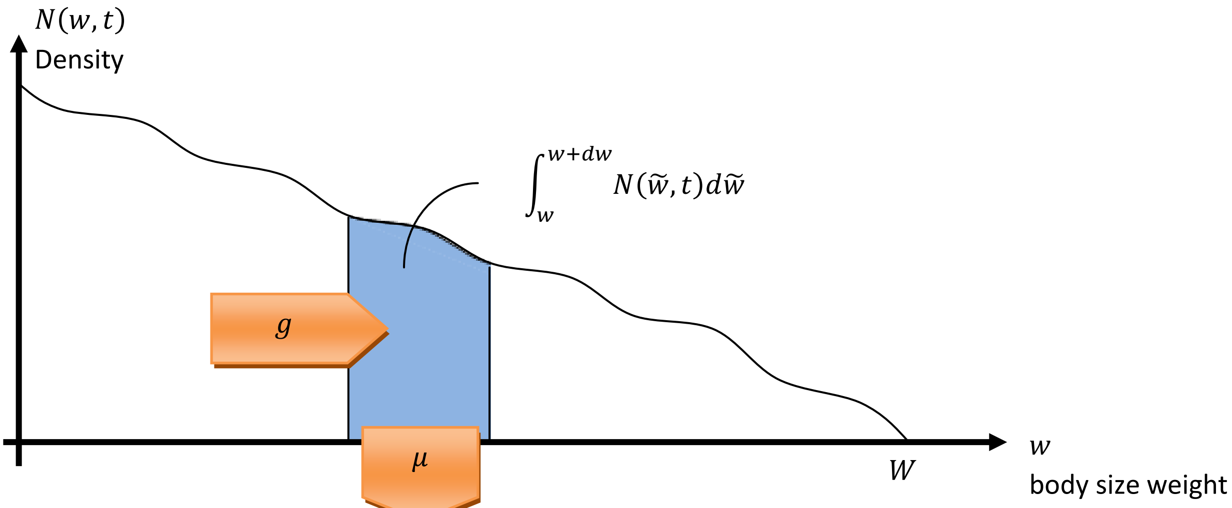


Figure 2.3 A very simple example plot of the population spectrum N with the individual somatic growth g, the individual total mortality μ and the asymptotic weight W, where w is the individual weight and t is time.

In fact the model is formulated as a partial integro-differential equation (PIDE), because of the individual somatic growth and the individual total mortality is included as integrals. To solve the PIDE a numerical method is needed. Since the somatic growth g is a non-negative function in the interval $w \in [0, W]$ for all t, we can use the upwind method as the numerical setup of the model. More details about the numerical setup of the model are described in **appendix A.1**.

The model is too complicated to analytically, but we can analyze the model when the system is in steady state. The model is in a steady state when $\frac{\partial N(w,t)}{\partial t} = 0$ for all weight w, time t and behavior τ, which means the PDE problem becomes to

$$\begin{aligned}
\frac{\partial g(w,t)N(w,t)}{\partial w} &= -\mu(w,t)N(w,t) \\
\frac{\partial g(w,t)N(w,t)}{\partial w} &= -\frac{\mu(w,t)}{g(w,t)}g(w,t)N(w,t) \\
\frac{\partial \ln\big(g(w,t)N(w,t)\big)}{\partial w} &= -\frac{\mu(w,t)}{g(w,t)} \\
\int_{\ln(g(w_0,t)N(w_0,t))}^{\ln(g(w,t)N(w,t))} d\ln\big(g(\tilde{w},t)N(\tilde{w},t)\big) &= -\int_{w_0}^{w}\frac{\mu(\tilde{w},t)}{g(\tilde{w},t)}d\tilde{w} \\
\ln\left(\frac{g(w,t)N(w,t)}{g(w_0,t)N(w_0,t)}\right) &= -\int_{w_0}^{w}\frac{\mu(\tilde{w},t)}{g(\tilde{w},t)}d\tilde{w}
\end{aligned}$$

where w_0 is the weight of new offspring.

Using the equation of the recruitment (also called reproduction) $R(t) = g(w_0, t)N(w_0, t)$ the population of the fish in the steady state of the system can be expressed as

$$N(w,t) = \frac{R(t)}{g(w,t)} \exp\left(- \int_{w_0}^{w} \frac{\mu(\tilde{w},t)}{g(\tilde{w},t)} d\tilde{w} \right)$$

As previously stated we need to include functions for the growth, mortality, and reproduction in order to describe the population. The reproduction should be included as a boundary condition. More about these functions is described in later sections.

2.1.3. Community spectrum

In this section we change the focus. Instead of looking at size distribution of individuals within in a species we will now look at the summation of all species' size spectra. The so-called community size spectrum N_c is a sum of the community size spectrum in the foraging arena $N_{c,f}$ and the community size spectrum in the refuge $N_{c,r}$. Due to the size-dependent intake suitable food items are needed for the smallest individuals, there is included a resource spectrum N_R, i.e. (zoo)plankton. The resource spectrum is also called background spectrum. The plankton can only exist up to a certain weight size w_{cut} and live in the foraging arena only. Thus the spectrum in the foraging arena $N_{c,f}$ is denoted as a sum of all the size spectra in the foraging arena $N_f = \tau N$ and resource spectrum N_R, while the community spectrum in the refuge $N_{c,r}$ is denoted as a sum of all size spectra in the refuge $N_r = (1 - \tau)N$.

The naturally cannibalism is a special case of predation, meaning the density of the food in the foraging arena $N_{f,food} = N_f + N_R$ if cannibalism is included, or $N_{f,food} = N_R$ if cannibalism is not included. The same holds for the refuge, but as there is no plankton available then $N_{r,food} = N_r$ if cannibalism occurs, otherwise $N_{r,food} = 0$.

Equation:	**Unit:**
$N(w,t) = N_f(w,t) + N_r(w,t)$	$N = \# \cdot (mass \cdot volume)^{-1} = [\# \cdot (g \cdot m^3)^{-1}]$
$N_f(w,t) = \tau(w)N(w,t)$ $N_r(w,t) = \big(1 - \tau(w)\big)N(w,t)$	$N_f = \# \cdot (mass \cdot volume)^{-1} = [\# \cdot (g \cdot m^3)^{-1}]$ $N_r = \# \cdot (mass \cdot volume)^{-1} = [\# \cdot (g \cdot m^3)^{-1}]$
$N_{c,f}(w,t) = N_f(w,t) + N_R(w,t)$ $N_{c,r}(w,t) = N_r(w,t)$	$N_{c,f} = \# \cdot (mass \cdot volume)^{-1} = [\# \cdot (g \cdot m^3)^{-1}]$ $N_{c,r} = \# \cdot (mass \cdot volume)^{-1} = [\# \cdot (g \cdot m^3)^{-1}]$
$N_c(w,t) = N_{c,f}(w,t) + N_{c,r}(w,t)$ $= N_R(w,t) + N(w,t)$	$N_c = \# \cdot (mass \cdot volume)^{-1} = [\# \cdot (g \cdot m^3)^{-1}]$
$N_{f,food}(w,t) = \begin{cases} N_f(w,t) + N_R(w,t), & Cannibalism \\ N_R(w,t), & Noncannibalism \end{cases}$ $N_{r,food}(w,t) = \begin{cases} N_r\big(w,t,\tau(w)\big), & Cannibalism \\ 0, & Noncannibalism \end{cases}$	$N_{f,food,} = \# \cdot (mass \cdot volume)^{-1} = [\# \cdot (g \cdot m^3)^{-1}]$ $N_{r,food} = \# \cdot (mass \cdot volume)^{-1} = [\# \cdot (g \cdot m^3)^{-1}]$
	$N_R = \# \cdot (mass \cdot volume)^{-1} = [\# \cdot (g \cdot m^3)^{-1}]$

We now know how the populations and the resource are distributed among the two habitats, but what about growth, reproduction and mortality? From the PDE we thus see that we need to determine functions for the growth, reproduction, and mortality of the individuals. To describe these we use the so-called energy budget model that reduces the complexity of the bioenergetic anatomically system. This is the topic of the eleven following sections.

2.1.4. Size selection of food items

To describe the growth we need to know how the food is selected. In the model the food is selected on the basis of the size difference between individuals. The individuals naturally cannot eat everything in the environment, so we introduce a selection function that gives a percentage of how likely a predator of weight w consumes a prey of size w_{prey}. The selection is a logarithm distribution with the weight size of the prey w_{prey}, that is β times lesser than the weight size of the predator w, as mean. The width of the selection is σ. The smaller σ the fussier eater the predators are about the weight of the prey. The selection φ generates a value between 0 (don't eat it) and 1 (love to eat it). The fixed log-normal function is adopted from the model by (Pedersen M. , 2006) which is again adopted from the North Sea model (Andersen & Ursin, 1977). The parameters in the model are set to be $\beta = 100$ and $\sigma = 1.3$. According to (Pedersen M. , 2006) the parameters are based on investigations of cod and dab (Ursin, 1973) and copepods (Ursin, 1974).

Equation:	**Unit:**
$\varphi(w_{prey}, w) = \exp\left[-\frac{\left(\ln\left(\frac{\beta w_{prey}}{w}\right)\right)^2}{2\sigma^2}\right]$	$\varphi = no\ unit = [1]$

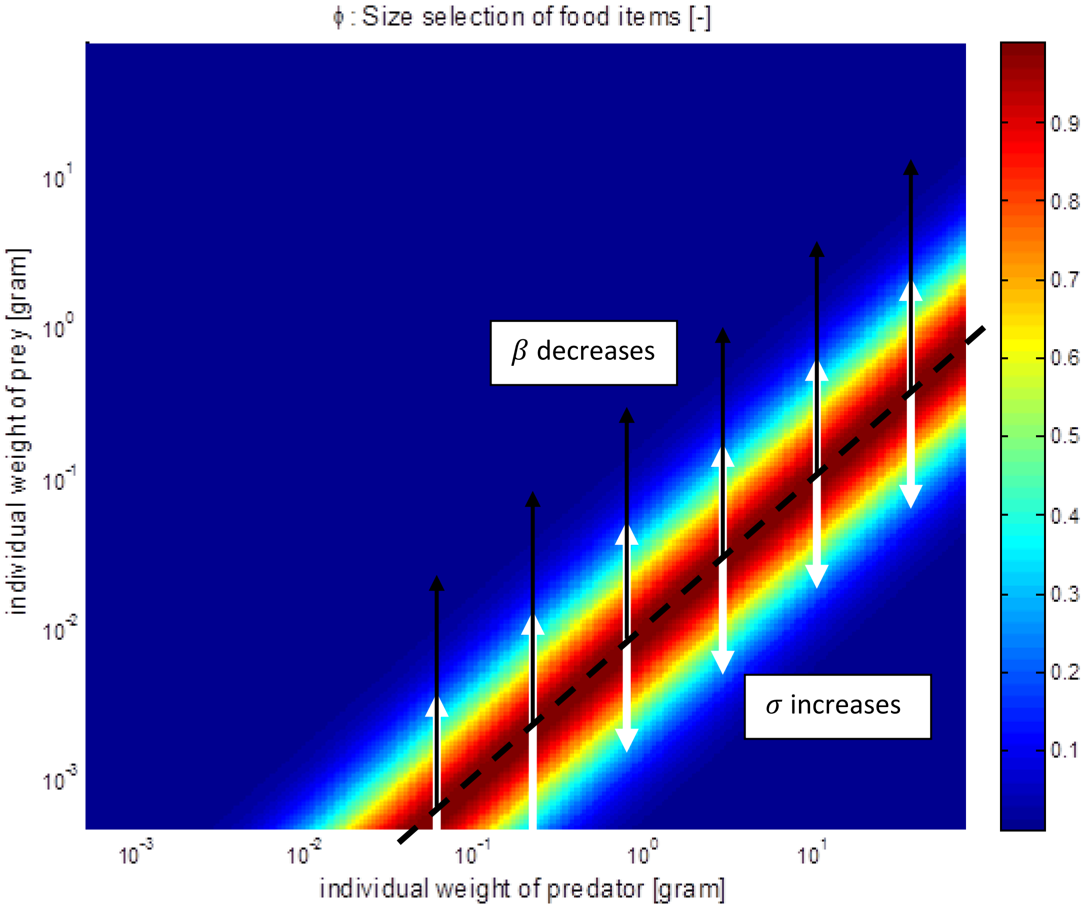


Figure 2.4 Logarithm food selection function with β preferred predator-prey weight ratio and σ width of selection function. All values are between 0 (don't eat it) and 1 (love to eat it). The smaller value β, the larger prey fish the predator fish prefers to eat. The larger σ, the lesser choosy the predators are about what they eat.

2.1.5. Volumetric search rate

A predator needs to search for food. How large area per unit time (search rate) a predator can cover by searching after the food can logically describes as a product of the individuals' circular cross sectional area πr^2 with the radius r and the foraging speed v: $V = \pi r^2 v$. In the model the radius is assumed to be proportional to the body weight size w, and the empirical results (Hunter, 1981; 1980; Ware, 1978) have shown that the larger individuals has high swimming speed, hence a large volume per unit time. In other words we assume that the search rate is scaled with the search volume factor γ and the positively exponent of search volume q. The search volume factor γ differs according to which habitat the individual is living in. Let γ_f and γ_r be the search volume factor for the foraging arena and the refuge respectively, and then define V_f and V_r as volumetric search rate for the foraging arena and the refuge respectively. From the model (Hartvig, Andersen, & Beyer, 2011) we set the exponent $q = 0.8$. The higher q, the bigger signification the weight has for the search volume.

Equation:	**Unit:**
$V_f(w) = \gamma_f w^q$ $V_r(w) = \gamma_r w^q$	$V_f = V_r = volume \cdot (time \cdot \#)^{-1} = [m^3 \cdot (year \cdot \#)^{-1}]$

In the model we assume the refuge has no food/predation and the search volume factor in the refuge γ_r is initialized to be zero in the habitat, hence the volumetric search rate for the refuge is zero $V_r = 0$.

The search volume factor for the foraging arena γ_f is very difficult to assess, and we know that there are many other factors which influence the search volume factor, e.g. the pickiness σ, the preferred predator-prey weight ratio β, the factor for the maximum intake h, the feeding level f and so on.
We also keep in mind that the model is derived for the cruising predator, as most of the pelagic species do actually search for food. A sit-and-wait (ambush strategy) predator can have a lower γ, but also the advantage of a lower metabolism. It might however be so that different strategies have different functional responses so different variants of the feeding level concepts have to be implemented. The different variants complicate the matter further unnecessarily. Thus we make use of the assumption that all individuals in the model are cruising predator.

A formula for the seach volume factor γ is taken from Hartvig's model (2011):

$$\gamma = \frac{f_0 h \beta^{2-\lambda}}{(1-f_0)\sqrt{2\pi}\kappa_r \sigma}$$

Where κ_r is the carrying capacity of the resource spectrum and $\lambda = 2$ is the exponent of the resource spectrum. More about these are explained in **section 2.1.15**. The symbol f_0 is the initial feeding level.

However, since the feeding level f of small individuals is determined by the amount of encountered food from the resource spectrum, we may use initial feeding level f_0 as a physiological measure of food encountered. The initial feeding level is used as a control parameter for food availability (enrichment), through which the value of γ_f can be calculated. According to (Hartvig, Andersen, & Beyer, 2011) the initial feeding level $f_0 = 0.6$ seems to be a reasonable value.

It is noted that the higher maximum intake h has a positively correlated influence on the search volume factor, and the choosier (lesser value of σ) the individuals are, the larger volume they are willing to search for food, i.e. higher γ. More information about the parameters h is described in **section 2.1.7**.

2.1.6. Encountered food

With knowledge of the preferred food φ, the volumetric search rate V and the density of preys in the foraging arena $N_{f,food}$ the encountered food can be calculated. The encountered food in foraging arena E_f is expressed as the available food in the foraging arena $\int w_{prey} N_{f,food}(w_{prey}, t)\varphi(w_{prey}, w) dw_{prey}$ multiplied by the volumetric search rate in foraging arena V_f, while the encountered food in the refuge E_r is expressed as the available food in the refuge $\int w_{prey} N_{r,food}(w_{prey}, t)\varphi(w_{prey}, w) dw_{prey}$ multiplied by the volumetric search rate in the refuge V_r. The individuals spends their average daytime in the foraging arena with the strategy τ, hence $1-\tau$ in the refuge. The encountered food for the individuals is therefore a sum balanced on the encountered food in foraging arena τE_f and the refuge $(1-\tau)E_r$.

Due to the integration term in the encountered food the lately calculation of the differential with respect to the behavior τ is very complex to make the calculation easier we assume the encountered foods E_f and E_r are both ”independently” of the behavior τ.

Equation (Dynamic):	**Unit:**
$E_f(w,t) = V_f(w) \int w_{prey} N_{f,food}(w_{prey},t)\varphi(w_{prey},w)dw_{prey}$ $E_r(w,t) = V_r(w) \int w_{prey} N_{r,food}(w_{prey},t)\varphi(w_{prey},w)dw_{prey}$	$E_f = mass \cdot (time)^{-1} = [g \cdot year^{-1}]$ $E_r = mass \cdot (time)^{-1} = [g \cdot year^{-1}]$
$E(w,t) = \tau(w)E_f(w,t) + (1-\tau(w))E_r(w,t)$	$E = mass \cdot (time)^{-1} = [g \cdot year^{-1}]$

Assuming no predation in the refuge $V_r = 0$ the equation of the encountered food simplify to

$$E(w,t) = \tau(w)E_f(w,t)$$

The expression means there is no food in the refuge.

A simpler and static expression of the encountered food is also made. The static expression is used to demonstrate the mechanics behind the adaptive behavior, and when understood we can continue to examine the model furthermore by making use of the advanced dynamic equation of the encountered food. In the static model it is assumed that all fish encounters always the food in an amount which is corresponding to the size of their stomach C_{max}. Still only in the foraging arena the fish can find food.

Equation (Static):	**Unit:**
$E_f(w,t) = C_{max}(w) = hw^n$ $E_r(w,t) = 0$	$E_f = mass \cdot (time)^{-1} = [g \cdot year^{-1}]$ $E_r = mass \cdot (time)^{-1} = [g \cdot year^{-1}]$

2.1.7. Maximum consumption

No individuals can eat unlimited. It will be limited by size of in their stomach. It is assumed that the distribution of the size of the individuals’ stomach, limiting its maximum intake C_{max}, is proportional to the body size w with the exponent n. According to Jobling (1994) it is stated that the ecosystem is most realistic when the exponent satisfies the inequality $\frac{2}{4} < n < \frac{3}{4}$. In our model we use the exponent $n = \frac{3}{4}$. The distribution is also dependent on the factor for maximum intake h. Similar to Hartvig’s model (2011) we assume the model is realistic when using the factor $h = 85\ g^{1-n}/year$.

Equation:	**Unit:**
$C_{max}(w) = hw^n$	$C_{max}(w) = mass \cdot (time)^{-1} = [g \cdot year^{-1}]$

2.1.8. Feeding level

With the knowledge of the maximum intake C_{max} and the encountered food E we can calculate how satiated the individuals are. In other words the feeding level f is the distribution of food in the stomachs at individual level. The value of the feeding level is between 0 (very hungry) and 1 (satiated). When the encountered food is very high, the predators will have no problem to find food for filling their stomach C_{max}. In the model the equation of the feeding level corresponds to a type II functional response.

Equation:	Unit:
$f(w,t) = \frac{E(w,t)}{E(w,t) + C_{max}(w)}$	$f = no\ unit = [1]$

By assuming no predation in the refuge $V_r(w) = 0$ the feeding level can simplify to

$$f(w,t) = \frac{\tau(w)E_f(w,t)}{\tau(w)E_f(w,t) + C_{max}(w)}$$

The plankton are lived in the foraging arena only, then the feeding level for the resource spectrum is

$$f_R(w,t) = \frac{E_f(w,t)}{E_f(w,t) + C_{max}(w)}$$

2.1.9. Energy to growth and reproduction

Now we can calculate how much energy the individuals have gathered and allocated to the growth and reproduction. But before the allocating process can be clarified, the energy cost of the metabolism and activity must be stated. It is assumed that distribution of the size of the individuals' activity and metabolism is proportional to the body size w and there is an effective loss converting from food to energy. In other words the ingested food $f(w,t)C_{max}(w)$ is in the model assimilated by an efficiency $\alpha \in [0,1]$ and used to fuel the needs for standard metabolism and activity, also called structural maintenance E_{meta}. Empirical data (Kleiber, 1932; 1947) validates that the metabolic rate follows the power law $k_s w^p$. The remaining available energy E_{energy} is divided between growth and reproduction by an allocation function ψ. From Hartvig's model (2011) we use the efficiency $\alpha = 0.1$ and the exponent for the standard metabolism $p = \frac{3}{4}$ and the factor $k_s = 10\ gram^{1-p} \cdot year^{-1}$.

Equation(s):	Unit:
$E_{cf}(w,t) = \alpha f(w,t)C_{max}(w)$ $E_{meta}(w) = k_s w^p$ $E_{energy}(w,t) = E_{cf}(w,t) - E_{meta}(w)$	$E_{cf} = mass \cdot (time)^{-1} = [g \cdot year^{-1}]$ $E_{meta} = mass \cdot (time)^{-1} = [g \cdot year^{-1}]$ $E_{energy} = mass \cdot (time)^{-1} = [g \cdot year^{-1}]$

2.1.10. Allocation to reproduction

The reproduction allocation function ψ is a function of weight changing between 0 (around the offspring weight where all available energy is used for growth) to 1 (at the asymptotic weight where all available energy is used for reproduction). The weight at maturation ηW is assumed to be proportional to the asymptotic weight, where $\eta \in [0,1]$. The term in the square bracket is a function which varies smoothly from 0 to 1 with width of maturation transition u. The last term describes how the relative amount of energy invested in reproduction increases as the weight approaches the asymptotic weight. In the model it is assumed that all species follow the same relative allocating function, i.e. they have the same size relative to the asymptotic weight, same width of maturation transition and so on. From Hartvig' model (2011) we use the following parameters $u = 10$, $\eta = 0.25$ and $n = 3/4$.

Equation:	**Unit:**
$\psi(w) = \left[1 + \left(\frac{w}{\eta W}\right)^{-u}\right]^{-1} \left(\frac{w}{W}\right)^{1-n}$	$\psi = no\ unit = [1]$

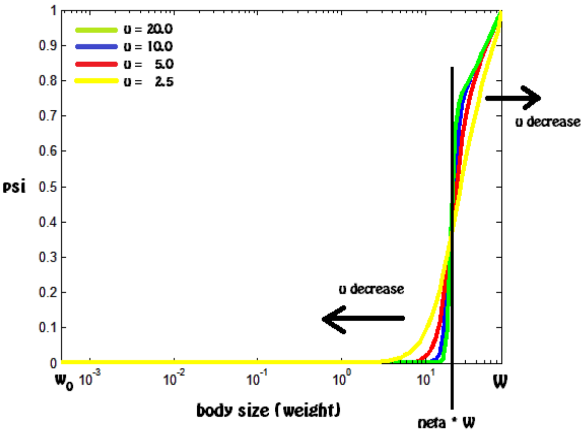


Figure 2.5 An illustration of how the allocation function must be understand.

There is an interesting case which we may take a closer look at. We will need below theorem in connection with the derivation of a property of the fecundity and growth (see **chapter 2.1.9-11**).

Theorem:

Let the individual weight and the asymptotic weight be expressed as w and W respectively.

Assume $W_1 \leq W_2$ and the allocating function

$$\psi_W(w) = \left[1 + \left(\frac{w}{\eta W}\right)^{-u}\right]^{-1} \left(\frac{w}{W}\right)^{1-n}$$

where the exponent of maximum intake as $n \in [0,1]$, the size at maturation relative to asymptotic weight W as $u \geq 0$ and the width of maturation transition as $\eta \in [0,1]$, then

$$\psi_{W_2}(w) \leq \psi_{W_1}(w)$$

For all w.

Proof:

Assume the two different species in which the one has higher asymptotic weight than the second $W_1 \leq W_2$. Then we have

$$wW_1 \leq wW_2$$

$$\frac{w}{W_2} \leq \frac{w}{W_1}$$

Thus

$$\left(\frac{w}{W_2}\right)^{1-n} \leq \left(\frac{w}{W_1}\right)^{1-n}, \qquad n \in [0,1]$$

Hence under the assumption $u \geq 0$ and $\eta \in [0,1]$ we have

$$\left(\frac{w}{\eta W_2}\right)^{u} \leq \left(\frac{w}{\eta W_1}\right)^{u}$$
$$\left(\frac{w}{\eta W_2}\right)^{-u} \geq \left(\frac{w}{\eta W_1}\right)^{-u}$$
$$\left[1+\left(\frac{w}{\eta W_2}\right)^{-u}\right]^{-1} \leq \left[1+\left(\frac{w}{\eta W_1}\right)^{-u}\right]^{-1}$$
$$\left[1+\left(\frac{w}{\eta W_2}\right)^{-u}\right]^{-1}\left(\frac{w}{W_2}\right)^{1-n} \leq \left[1+\left(\frac{w}{\eta W_1}\right)^{-u}\right]^{-1}\left(\frac{w}{W_1}\right)^{1-n}$$
$$\psi_{W_2}(w) \leq \psi_{W_1}(w) \quad \blacksquare$$

2.1.11. Fecundity

Let F be the fecundity for the individual. Out of the available energy E_{energy} a fraction ψ is used for reproduction but if the intake is insufficient to cover respiratory cost ($E_{Energy} < 0$) they become infertile, thus the fecundity is defined as:

Equation:	**Unit:**
$F(w,t) = \begin{cases} \psi(w)E_{energy}(w,t), & E_{energy}(w,t) > 0, w \in [w_0, W] \\ 0, & otherwise \end{cases}$	$F = mass \cdot time^{-1} = [g \cdot year^{-1}]$

The consequence for the fecundity if using the allocating function described in the previous section is underlined in the theorem below:

Theorem:

Let the offspring weight, the individual weight and the asymptotic weight be expressed as w_0, w and W respectively.

Let the available energy E_{energy} be independent of asymptotic weight W, in other words $\frac{\partial E_{energy}}{\partial W} = 0$. And let the allocation function ψ be a function of weight that allocates the available energy to reproduction and the fecundity function be defined as

$$F(w,t) = \begin{cases} \psi(w)E_{energy}(w,t), & E_{energy}(w,t) > 0, w \in [w_0, W] \\ 0, & otherwise \end{cases}$$

If $w_0 \leq W_1 \leq W_2$ and $\psi_{W_2} \leq \psi_{W_1}$, then we have

$$F_{W_2}(w,t) \le F_{W_1}(w,t), \qquad w \in [w_0, W_1]$$
$$F_{W_2}(w,t) \ge F_{W_1}(w,t) = 0, \qquad w \in [W_1, W_2]$$

For all w.

Proof:

Let there be two species with different asymptotic weight $W_1 \le W_2$. The one species can only grow to weight W_1, while the second can continue growing to weight W_2, thus we have to break the interval $w \in [w_0, W_2]$ into two intervals $w \in [w_0, W_1]$ and $w \in [W_1, W_2]$. We define the fecundity for the smallest species (W_1) to be zero in the interval $w \in [W_1, W_2]$. Or more simply

$$F_{W_2}(w,t) \ge F_{W_1}(w,t) = 0, \qquad w \in [W_1, W_2]$$

When the available energy E_{energy} is independent of asymptotic weight W ($\frac{\partial E_{energy}}{\partial W} = 0$), the available energy can be multiplied by the allocating function without changing the inequality relation, i.e. due to the theorem in the previous section ($\psi_{W_2} \le \psi_{W_1}$ when $W_1 \le W_2$) we can conclude that when $\frac{\partial E_{energy}}{\partial W} = 0$ and $w \in [w_0, W_1]$ where $W_1 \le W_2$, then

$$\psi_{W_2}(w) \le \psi_{W_1}(w)$$
$$\psi_{W_2}(w) E_{energy,W_2}(w,t) \le \psi_{W_1}(w) E_{energy,W_1}(w,t)$$
$$F_{W_2}(w,t) \le F_{W_1}(w,t)$$

Said in another way the small species allocates larger or equivalent amount of the available energy to fecundity compared to the large species in the interval $w \in [w_0, W_1]$. ■

The species independent available energy being $\frac{\partial E_{energy}}{\partial W} = 0$ can happen if all species have for example the same behavior and the same encountered food, e.g. the static encountered food hw^n.

2.1.12. Somatic growth

Out of the available energy a fraction ψ is used for reproduction, and the rest for somatic growth. If the intake is insufficient to cover respiratory cost ($E_{Energy} < 0$) growth is halted. Body size doesn't shrink when the costs cannot be covered, but instead individuals are starving and exposed to starvation mortality. More about the starvation mortality is explained later.

Equation:	**Unit:**
$g(w,t) = \begin{cases} (1-\psi(w))E_{energy}(w,t), & E_{energy}(w,t) > 0 \\ 0, & otherwise \end{cases}$	$g = mass \cdot (time)^{-1} = [g \cdot year^{-1}]$

The consequence for the growth if using the allocating function described in its section is underlined in the theorem below:

Theorem:

Let the individual weight and the asymptotic weight be expressed as w and W respectively.

Let the available energy E_{energy} be independent of asymptotic weight W, in other words $\frac{\partial E_{energy}}{\partial W} = 0$. And let the allocation function ψ be a function of weight that allocates the available energy to reproduction and the growth function be defined as

$$g(w,t) = \begin{cases} (1-\psi(w))E_{energy}(w,t), & E_{energy}(w,t,\tau(w)) > 0 \\ 0, & otherwise \end{cases}$$

If $W_1 \leq W_2$ and $\psi_{W_2} \leq \psi_{W_1}$, then we have

$$g_{W_2}(w,t) \geq g_{W_1}(w,t)$$

For all w.

Proof:

When the available energy E_{energy} is independent of asymptotic weight W ($\frac{\partial E_{energy}}{\partial W} = 0$), the available energy can be multiply with the allocating function without change the inequality relation, i.e. by a theorem in the allocating function section ($\psi_{W_2} \leq \psi_{W_1}$ when $W_1 \leq W_2$) we can conclude

$$\begin{gathered} \psi_{W_2}(w) \leq \psi_{W_1}(w) \\ 1-\psi_{W_2}(w) \geq 1-\psi_{W_1}(w) \\ \left(1-\psi_{W_2}(w)\right) E_{energy,W_2}(w,t) \geq \left(1-\psi_{W_1}(w)\right) E_{energy,W_1}(w,t) \\ g_{W_2}(w,t) \geq g_{W_1}(w,t) \end{gathered}$$

when $W_1 \leq W_2$ and $\frac{\partial E_{energy}}{\partial W} = 0$. Expressed in another way it can be said that the large species grow faster or equally fast compared to the small species. ■

2.1.13. Reproduction

In this section we look at the total reproduction of a given species. It is assumed that all species are diploid and reproduce sexually, and there are no demographic differences between males and females. The assumption makes the calculation of the total flux of offspring easier. The total flux of offspring is found by integrating the population N and its fecundity F over all individual sizes, where w_0 is the egg size and ϵ is the egg survival factor. It is multiplied with 1/2 to take into account that only females spawn (equal gender distribution). The individual reproduces only if the fecundity is positive, in other word only the positive available energy rate can invest in the reproduction.

The total flux of offspring is:

Equation:	**Unit:**
$R(t) = \frac{\epsilon}{2w_0}\int_{w_0}^{W} N(w,t,\tau(w))F(w,t)dw$	$R = \# \cdot (time \cdot volume)^{-1} = [\# \cdot (year \cdot m^3)^{-1}]$

The egg size and the egg survival factor are adopted from model by Hartvig (2011), i.e. they are defined as $w_0 = 0.5 \cdot 10^{-3}$ gram and $\epsilon = 0.1$.

2.1.14. Mortality

In this section we look at how the total mortality rate for the individuals must be defined.

2.1.14.1. Total mortality

In the model the mortality rate μ of an individual is assumed to have three main sources: predation mortality μ_p, starvation mortality μ_s and background mortality μ_b, which can be disease, ageing and so on. The total mortality is a sum of all sources.

Equation:	**Unit:**
$\mu(w,t) = \mu_p(w,t) + \mu_s(w,t) + \mu_b$	$\mu = time^{-1} = [year^{-1}]$

2.1.14.2. Predation mortality

The size-dependent predation mortality rate is calculated such that all that is eaten translates into predation mortalities on the ingested prey individuals. The predation mortality rate depends on about the encountered food is static or dynamic. If dynamic then it is depended on how hungry the predators are $1 - f(w,t)$. The lower the feeding level, the hungrier the predators are. This leads to higher predation mortality rate for the individual of the prey with bodyweight size w_{prey}. The predation mortality depends naturally also on the predators' search rate in this habitat (e.g. V_f for the foraging arena and V_r for the refuge) times their preferred intake φ. The total intake is then $\left(1 - f(w,t)\right)V_f(w)\varphi\left(w_{prey}, w\right)$ for the foraging arena or $\left(1 - f(w,t)\right)V_r(w)\varphi\left(w_{prey}, w\right)$ for the refuge, both are multiplied with the predator density in this habitat (e.g. $N_{f,food}$ for the foraging arena and $N_{r,food}$ for the refuge) integrated over weight of predators w. The predation mortality rate in a given habitat is expressed as $\mu_{p,f}$ for the foraging arena and $\mu_{p,r}$ for the refuge. The foraging arena is also populated by the (zoo)planktons, thus the predation mortality rate in this habitat is a sum of the predation mortality from the fish in foraging arena and the predation mortality from the planktons $\mu_{p,f,R}\left(w_{prey}, t\right) = \int \left(1 - f_R(w,t)\right)V_f(w)N_{c,f}(w,t)\varphi\left(w_{prey}, w\right)dw$. In short the predation mortality rate experienced by the prey in a given habitat is the probability of being consumed at a given time-step in this habitat.

With the behavior τ the prey can adjust its total predation mortality μ_p from the two habitats, $\tau\mu_{p,f}$ for the foraging arena and $(1 - \tau)\mu_{p,r}$ for the refuge.

Due to the integration term in the predation mortality the lately calculation of the differential of that with respect to the behavior τ is very complex. It can be made easier by assuming that the predation mortalities $\mu_{p,f}$ and $\mu_{p,r}$ are both ”independently” of the behavior τ.

It is also made a simpler and static expression of the predation mortality. Like the encountered food the static expression of the predation mortality is used to demonstrate the mechanics behind the adaptive behavior, and when we have understood the mechanics we can continue to examine the model furthermore by making use of the advanced dynamic equation of the predation mortality. In the static model we assume that the predation mortality is proportionality to the size of their stomach C_{max} but inversely proportionality to the weight w. The bigger they are, the easier they are funded at a long distance but harder to kill. Let the kill be performed with the efficiency a (predation mortality factor). Still only in the foraging arena the predation exists.

Equation:	**Unit:**
(Non-cannibalism / static) $\mu_{p,f}(w_{prey},t) = ahw_{prey}^{n-1}$ $\mu_{p,r}(w_{prey},t) = 0$	$\mu_{p,f} = time^{-1} = [year^{-1}]$ $\mu_{p,r} = time^{-1} = [year^{-1}]$
(Cannibalism / dynamic) $\mu_{p,f}(w_{prey},t) = ahw_{prey}^{n-1} + \int (1-f(w,t))V_f(w)N_f(w,t)\varphi(w_{prey},w)dw$ $\mu_{p,r}(w_{prey},t) = \int (1-f(w,t))V_r(w)N_r(w,t)\varphi(w_{prey},w)dw$	
$\mu_p(w_{prey},t) = \tau(w_{prey})\mu_{p,f}(w_{prey},t) + \left(1-\tau(w_{prey})\right)\mu_{p,r}(w_{prey},t)$	$\mu_p = time^{-1} = [year^{-1}]$
<u>Dynamic predation mortality for the resource spectrum - (zoo)plankton:</u> $\mu_{p,f,R}(w_{prey},t) = \int (1-f(w,t))V_f(w)N_{c,f}(w,t)\varphi(w_{prey},w)dw$	$\mu_{p,f,R} = time^{-1} = [year^{-1}]$

It should noted that when assuming zero search volume factor in the refuge γ_r hence $V_r(w) = 0$ the dynamic predation mortality can simplify to

$$\mu_p(w,t) = \tau(w)\mu_{p,f}(w,t)$$

which means no predation in the refuge.

2.1.14.3. Starvation mortality

The starvation mortality may occur when food abundance is sparse. In other words when the food supply doesn't cover respiratory cost ($E_{Energy} < 0$), starvation mortality kicks in. We may assume that starvation mortality is proportional to the deficiency energy -E_{Energy} multiplied with a fraction of energy reserves $\xi \in [0,1]$ and inversely proportional to lipid reserves, which are assumed proportional to bodyweight size w.

As discussed above starvation mortality should play a significant role for the resulting total mortality, hence the choice of the foraging strategy, so we select a low value for the fraction of the energy reserves, e.g. $\xi = 0.1$. We have to mention that the energy reserves and the lipid reserves is difficult to estimate, because of it is hard to obtain data to validate the model. So the states having a strong dependence on starvation in our model should hence be interpreted with caution. Thus the value $\xi = 0.1$ is chosen based on the parameter from other similar models, e.g. (Hartvig, 2011).

Equation:	**Unit:**

$\mu_s(w,t) = \begin{cases} 0, & E_{energy}(w,t) \geq 0 \\ -\frac{E_{energy}(w,t)}{\xi w}, & otherwise \end{cases}$	$\mu_s = time^{-1} = [year^{-1}]$

It is noted, that the predation mortality actually can be interpreted - as an indirect effect of starvation mortality: if individuals cannot grow due to insufficiently food then they will not able to escape predation mortality, and thus will be more vulnerable to predation.

2.1.14.4. Background mortality

Other causes of mortality, e.g. diseases or ageing are more difficult to assess and are therefore included in a non-dominating constant background mortality. The background mortality is used to ensure that the largest individuals in the community spectrum also experience mortality as they are not predated upon by any individuals from the community spectrum. The background mortality is assumed to be constant μ_0 within a species multiplied with the inversely proportional to asymptotic weight W. Reason for the inversely proportional is that the large species have experienced lower background mortality compared to the smaller species.

The background mortality factor μ_0 is adopted from the model (Hartvig, 2011), i.e. it is assumed to be $\mu_0 = 0.84\ g^{n-1}/year$.

Equation:	**Unit:**
$\mu_b = \mu_0 W^{n-1}$	$\mu_b = time^{-1} = [year^{-1}]$

2.1.15. Dynamic resource spectrum

The resource spectrum N_R are the food items which are needed for the smallest individuals. We introduce the community spectrum as the spectrum of everything in the sea. Naturally the resource spectrum is included in this spectrum, but since we are interesting at the higher trophic species, we do not model the resource spectrum explicitly, i.e. we don't model the life histories of species in the resource spectrum (it is why we call it as a background spectrum) like the fish. If we have to model the life histories the model will get very complicated because we will have to model several small species, e.g. detritus and particles such as phosphorous. In the articles by (Pedersen & Andersen, 2009; Hartvig, Andersen, & Beyer, 2011) they suggest that the dynamics of each size group in the resource spectrum shall be described as a semi-chemostatic growth with $\kappa_r w^{-\lambda}$ as carrying capacity and $r_0 w^{p-1}$ as the population regeneration rate. It is preferred semi-chemostatic to logistic growth because planctionic resources rebuild from depletion locally due to both population growth and invasion. The resource spectrum over time is expresses as:

<u>Dynamic</u>

$$\frac{\partial N_R(w,t)}{\partial t} = r_0 w^{p-1} \left(\kappa_r w^{-\lambda} - N_R(w,t) \right) - \mu_{p,f,R}(w,t) N_R(w,t)$$

But to make the investigation of the mechanism behind the adaptive behavior easier to understand we have make a part of the investigation used the static resource spectrum, i.e. a constant background spectrum. It allows us to examine the model without the influence of the background spectrum.

Static

$$N_R(w,t) = \kappa_r w^{-\lambda}$$

Regardless whether the resource spectrum is dynamic or static it is only valid for sizes up to a certain weight w_{cut}. An study (Pedersen M. , 2006) has shown that if w_{cut} is given as a small weight then the individuals of a small species can reach the size of maturation solely on background resources and thus maintain the species population. Large species cannot do so, and need the possibility of predation on larger food items as i.e. the smaller species. Larger species thus uses the smaller species as a trophic ladder to reach the size of maturation. Thus in the model w_{cut} is setup to be as large as possible, e.g. the largest weight which is used in the stimulation of the model is the asymptotic weight $W = 100g$.

2.1.16. Survival probability

When all details about the individuals' bioenergetic growth and the ecosystem has been raised, then we can raise the question; what is the survival probability of the individuals if they are living in this ecosystem? The survival rate dS/dw for the individuals with the weight w at the time t falls directly proportional to the total mortality rate per growth rate μ/g multiplied with the survival probability S (Pitman, 1992; Hartvig, 2011). The higher the growth, the better the survival probability. The higher the mortality, the worse the survival probability. In short the survival rate can denote mathematically as:

$$\frac{\partial S(w,t)}{\partial w} = -\frac{\mu(w,t)}{g(w,t)} S(w,t)$$

which can reformulate to the following expression:

$$\int_{S(w_0,t)}^{S(w,t)} \frac{1}{S(\widetilde{w},t)} dS(\widetilde{w},t) = -\int_{w_0}^{w} \frac{\mu(\widetilde{w},t)}{g(\widetilde{w},t)} d\widetilde{w}$$

$$\frac{S(w,t)}{S(w_0,t)} = \exp\left(-\int_{w_0}^{w} \frac{\mu(\widetilde{w},t)}{g(\widetilde{w},t)} d\widetilde{w}\right) = S(w_0,w,t)$$

where w_0 is the weight of new offspring. $S(w_0,w,t)$ describes the current survival probability for living from the weight w_0 to weight w - provided that growth and mortality does not change in time.
The survival probability is in other words defined as the percent of individuals which will survive. E.g. if the survival probability for an individual with a particular growth and mortality is 60 %, this means that 60 out of 100 initially individuals would be alive after growing from the weight w_0 to weight w.

2.1.17. Fitness

In this section we look at the definition of fitness in the simplest possible case and then discuss how the definition needs to be modified to deal with more general and realistic situations.

The fitness is a central idea in the evolution theory. It can be defined in different ways, but here in our basic model we define the fitness as the ability of the species to survive and dominate the ecology system. It does not refer to whether an individual is "physically fit" – bigger, faster or stronger – or "better" in any subjective sense. It refers solely to their ability to transmit their genes from one generation to the next. It is assumed that it is no mutant genetic inheritance. We quantify it with the reproductive value, i.e. the ability depends on the total amount of energy an individual expects to invest in reproduction over the rest of its life (Houston & McNamara, 1999).

Let V be the reproductive value cf., with reference to the definition above, of an individual. We use the reproductive value V as the possible measure of the fitness, where the choice of the foraging options always is based on the maximum of the reproductive value. The reproductive value depends on its weight w (and time t if non-steady state), but it also depends on the foraging strategy τ. But what is the optimal foraging strategy?

Derivation of the Hamilton-Jacobi-Bellman equation

Our model of the optimal foraging strategies is based on the Bellman equation, also known as a dynamic programming equation. In other words the optimal reproductive value is decided on the basis of the equation. The equation is an important condition for the mathematical optimization method known as dynamic programming. More about the dynamic programming is described later. Now we are going to demonstrate, how the equation is derived and how it affects the decision.

Let τ^* be the optimal foraging strategy. If the individual chooses a foraging option that delivers energy to growth a smooth flow with growth rate g between t and $t+\Delta t$, its weight at time $t+\Delta t$ is $w+g\Delta t$, provided it is not killed during the interval. Its reproductive value if it survives until $t+\Delta t$ is thus $V(w+g\Delta t, t+\Delta t)$. By using Taylor expansion series and assuming Δt is small and ignoring terms of order $(\Delta t)^2$ we can write

$$V(w+g(w,t)\Delta t, t+\Delta t)$$
$$\cong$$
$$V(w,t)+g(w,t)\Delta t\frac{\partial V(w,t)}{\partial w}+\Delta t\frac{\partial V(w,t)}{\partial t}$$

Let μ be the total mortality rate under the option; then the probability that the individual dies the time interval of length Δt is $\mu\Delta t$ or in other words: the probability for the individual to survive the same time interval is $1-\mu\Delta t$. The reproductive value is lost when an individual is dead. Thus under this option its reproductive value at time t is $(1-\mu\Delta t)V(w+g\Delta t, t+\Delta t)$, which gives

$$V(w,t)+\Delta t\frac{\partial V(w,t)}{\partial t}+\Delta t\left(g(w,t)\frac{\partial V(w,t)}{\partial w}-\mu(w,t)V(w,t)\right)$$

where terms of order Δt in the Taylor expansion series of $\mu\Delta t\ V(w+g\Delta t, t+\Delta t)$ is ignored.

Let F be the fecundity; then it is the increase in rate of reproduction value as a result of the available energy which is allocated to the reproduction. Thus under this option its reproductive value at time t is

$$V(w,t)+\Delta t\frac{\partial V(w,t)}{\partial t}+\Delta t\left(g(w,t)\frac{\partial V(w,t)}{\partial w}-\mu(w,t)V(w,t)+F(w,t)\right)$$

We suppose that the individuals always follow the optimal choice of the foraging behavior. When using the optimal strategy, the reproductive value is maximized, i.e.

$$V(w,t) = \max_{\tau(w)\in[0,1]} \left\{ V(w,t) + \Delta t \frac{\partial V(w,t)}{\partial t} + \Delta t \left(g(w,t) \frac{\partial V(w,t)}{\partial w} - \mu(w,t)V(w,t) + F(w,t) \right) \right\}$$

Cancelling $V(w,t)$ at both sides of this equation and dividing through by Δt gives

Equation (Hamilton-Jacobi-Bellman equation):

$$-\frac{\partial V(w,t)}{\partial t} = \max_{\tau(w)\in[0,1]} \left\{ g(w,t) \frac{\partial V(w,t)}{\partial w} - \mu(w,t)V(w,t) + F(w,t) \right\}$$

(Bellman R. E., 1957; Houston & McNamara, 1999)

$\partial V / \partial w$ is the rate at which the reproductive value increases with weight w, so $g\, \partial V / \partial w$ is the rate of increase of the reproductive value as a result of the growth. μ is the rate of mortality and V is the loss in reproductive value as a result of being killed, so μV is the rate of decrease of reproductive value as a result of total mortality. ψ is the allocation function and E_{energy} is the gain of energy, so F is the net rate at which the gain of energy is distributed to the reproduction. Thus $g\, \partial V / \partial w - \mu V + F$ is the net rate at which foraging increases reproductive value. The best option maximizes the net rate.

To simplify the model it is assumed that the evolutionary dynamics is much slower than the ecosystem dynamics, i.e. the individual is able to optimize their strategy when the ecosystem dynamic is calmed down. In other words the reproductive value should be independent of time $\partial V / \partial t = 0$ (steady state).

To what extent fish actually optimize when the population is not in steady state is a very complex issue, for which reason this is not in clear focus in the report.

Theorem:

Let the two functions be defined $p(w,t) = -\frac{\mu(w,t)}{g(w,t)}$ and $q(w,t) = -\frac{F(w,t)}{g(w,t)}$.

Assume steady state then the complete solution to the Hamilton-Jacobi-Bellman equation (HJB) is

$$V(w,t) = \begin{cases} e^{-P(w,t)} \left(\int e^{P(w,t)} q(w,t) dw + c \right), & g(w,t) \neq 0 \\ \dfrac{F(w,t)}{\mu(w,t)}, & g(w,t) = 0 \end{cases}$$

Where $c \in \mathbb{R}$ and $P(w,t) = \int p(w,t) dw$.

Proof:

When background mortality exists for all species $\mu_b > 0$ and the starvation mortality and the predation mortality are both nonnegative, the assumption about the inequality $\forall \tau(w): \mu(w,t) > 0$ is true. So letting Q be the expression in the braces of the HJB equation:

$$Q(w,t) = g(w,t)\frac{\partial V(w,t)}{\partial w} - \mu(w,t)V(w,t) + F(w,t)$$

it is noted that

$$\max_{\tau(w)\in[0,1]}\{Q(w,t)\} = 0 \Leftrightarrow \max_{\tau(w)\in[0,1]}\left\{\frac{Q(w,t)}{\mu(w,t)}\right\} = 0$$

which means that the steady state of the HBJ equation can reformulated to the "life-history" strategy:

Equation (Reproduction value by following the "life-history" strategy):	**Unit:**
$$V(w,t) = \max_{\tau(w)\in[0,1]}\left\{\frac{g(w,t)\frac{\partial V(w,t)}{\partial w} + F(w,t)}{\mu(w,t)}\right\}$$	$V = mass = [g]$

When the growth is zero $g(w,t) = 0$, then the reproductive value is simplified to

$$V(w,t) = \frac{F(w,t)}{\mu(w,t)}$$

But what if $g \neq 0$? Since $\frac{\partial V(w,t)}{\partial w}$ is unknown, we can reformulate steady state HBJ to the following differential equation (assuming the optimal behavior τ^* is found):

$$\frac{\partial V(w,t)}{\partial w} - \frac{\mu(w,t)}{g(w,t)}V(w,t) = -\frac{F(w,t)}{g(w,t)},$$

Let $p(w,t) = -\frac{\mu(w,t)}{g(w,t)}$ and $q(w,t) = -\frac{F(w,t)}{g(w,t)}$, then we have a general expression of first order differential equation

$$\frac{\partial V(w,t)}{\partial w} + p(w,t)V(w,t) = q\big(w,t,\tau^*(w)\big)$$

The completed solution to the first order differential equation is:

$$V(w,t) = e^{-P(w,t)}\left(\int e^{P(w,t)}q(w,t)dw + c\right), \qquad g(w,t) \neq 0$$

where $c \in \mathbb{R}$ and $P(w,t) = \int p(w,t)dw$. ∎

But the optimal foraging strategy $\tau^*(w)$ is still unknown. How can we find that? We can partly solve the problem by using the theorem below. The solution for the optimization problem in the "myopic" strategy is explained in the next chapter.

Theorem:

Assume steady state and growth $g(w,t) = \big(1-\psi(w)\big)E_{energy}(w,t)$ and fecundity $F(w,t) = \psi(w)E_{energy}(w,t)$, where ψ is the allocating function that allocates the positive available energy E_{energy}

to the reproduction.

Then the "myopic" strategy

$$\tau^*(w) = \underset{\tau(w)\in[0,1]}{\operatorname{argmax}} \left\{\frac{E_{energy}(w,t)}{\mu(w,t)}\right\}$$

solves the Hamilton-Jacobi-Bellman equation (HJB), hence is also the "life-history".

Equation (Reproduction value by following the "myopic" strategy): $V(w,t) = \max_{\tau(w)\in[0,1]} \left\{\frac{E_{energy}(w,t)}{\mu(w,t)}\right\}$	**Unit:** $V = mass = [g]$

Proof:

As mentioned the steady state of the HBJ equation can be reformulated to the "life-history" strategy. When the growth is describes as $g = (1-\psi)E_{energy}$ and the fecundity $F = \psi E_{energy}$ under the assumption of positive available energy $E_{energy} > 0$, then the maximum in the this strategy can modify to

$$\tau^*(w) = \underset{\tau(w)\in[0,1]}{\operatorname{argmax}} \{V(w,t)\} = \underset{\tau(w)\in[0,1]}{\operatorname{argmax}} \left\{\frac{Q(w,t)}{\mu(w,t)}\right\}$$

where $Q(w,t) = \phi(w,t)E_{energy}(w,t)$ and $\phi(w,t) = \psi(w) + \frac{\partial V(w,t)}{\partial w}\big(1-\psi(w)\big)$.

The reproductive value is maximized when $\frac{\partial V(w,t)}{\partial \tau(w)} = 0$, i.e.

$$\frac{\partial V(w,t)}{\partial \tau(w)} = \frac{\partial\left(\frac{Q(w,t)}{\mu(w,t)}\right)}{\partial \tau(w)} = \frac{\frac{\partial Q(w,t)}{\partial \tau(w)}\mu(w,t) - Q(w,t)\frac{\partial \mu(w,t)}{\partial \tau(w)}}{\big(\mu(w,t)\big)^2} = 0$$

The first differential in the numerator is derived to

$$\begin{aligned}\frac{\partial Q(w,t)}{\partial \tau(w)} &= \frac{\partial\left(\phi(w,t)E_{energy}(w,t)\right)}{\partial \tau(w)} \\ &= \frac{\partial \phi(w,t)}{\partial \tau(w)}E_{energy}(w,t) + \phi(w,t)\frac{\partial E_{energy}(w,t)}{\partial \tau(w)}\end{aligned}$$

The allocating function ψ is independent of the behavior τ and the differentiation rule says $\frac{\partial}{\partial x}\left(\frac{\partial f}{\partial y}\right) = \frac{\partial}{\partial y}\left(\frac{\partial f}{\partial x}\right)$, hence

$$\begin{aligned}\frac{\partial \phi(w,t)}{\partial \tau(w)} &= \frac{\partial\left(\psi(w) + \frac{\partial V(w,t)}{\partial w}\big(1-\psi(w)\big)\right)}{\partial \tau(w)} \\ &= \big(1-\psi(w)\big)\frac{\partial}{\partial \tau(w)}\left(\frac{\partial V(w,t)}{\partial w}\right)\end{aligned}$$

$$
\begin{aligned}
&= \big(1-\psi(w)\big)\frac{\partial}{\partial w}\left(\frac{\partial V(w,t)}{\partial \tau(w)}\right)\\
&= 0
\end{aligned}
$$

In other words we obtain

$$\frac{\partial Q(w,t)}{\partial \tau(w)} = \phi(w,t)\frac{\partial E_{energy}(w,t)}{\partial \tau(w)}$$

Thus back to the beginning

$$
\begin{aligned}
\frac{\partial V(w,t)}{\partial \tau(w)} &= \frac{\frac{\partial Q(w,t)}{\partial \tau(w)}\mu(w,t) - Q(w,t)\frac{\partial \mu(w,t)}{\partial \tau(w)}}{\big(\mu(w,t)\big)^2}\\
&= \frac{\phi(w,t)\frac{\partial E_{energy}(w,t)}{\partial \tau(w)}\mu(w,t) - \phi(w,t)E_{energy}(w,t)\frac{\partial \mu(w,t)}{\partial \tau(w)}}{\big(\mu(w,t)\big)^2}\\
&= \frac{\frac{\partial E_{energy}(w,t)}{\partial \tau(w)}\mu(w,t) - E_{energy}(w,t)\frac{\partial \mu(w,t)}{\partial \tau(w)}}{\big(\mu(w,t)\big)^2}\\
&= \frac{\partial\left(\frac{E_{energy}(w,t)}{\mu(w,t)}\right)}{\partial \tau(w)}\\
&= 0
\end{aligned}
$$

Which can also be solved by the "myopic" strategy:

$$\tau^*(w) = \underset{\tau(w)\in[0,1]}{\operatorname{argmax}}\left\{\frac{E_{energy}(w,t)}{\mu(w,t)}\right\}$$

By the maximum term in the reproductive value we can conclude that the optimal behavior $\tau^*(w)$ from the "myopic" strategy solves for the steady state HJB equation under the assumption of growth $g = (1-\psi)E_{energy}$ and fecundity $F = \psi E_{energy}$ ■

In this section we have proven that the myopic strategy is an excellent alternative solution to find the "life-history" optimal foraging strategy for the individual at the asymptotic weight. The "myopic" strategy has an advantage over the "life-history" strategy due to the "myopic" strategy is based on the short term optimization and can be solved analytically and therefore only requires low computer power.
As mentioned before the next chapter explains more about the strategies.

2.1.18. Others

This section is a brief note. It is noted that the reproduction value by following the "life-history" strategy is in principle fully consistent with the reproduction value by following the "myopic"-strategy, if $\phi(w,t) = 1$. In other words the reproduction value is increasing constantly by a unit $\frac{\partial V(w,t)}{\partial w} = 1$. We are saying in principle fully consistent and not just fully consistent, because the fecundity and growth expression described in this chapter is the reason for an optimization problem as there is still a difference between the "myopic" strategy and "life-history" strategy even when $\frac{\partial V(w,t)}{\partial w} = 1$. More about this is explained in the next chapter.

2.1.19. Parameters

In this section we summarized all parameters which are used in the model.

Individual physiology				
$\boldsymbol{\alpha}$	Assimilation efficiency	0.60	$-$	
$\boldsymbol{n}$	Exponent of max. intake	3/4	$-$	
$\boldsymbol{h}$	Factor for max. intake	85.0	$mass^{1-n} \cdot time^{-1}$	$[g^{1-n} \cdot year^{-1}]$
$\boldsymbol{p}$	Exponent of standard metabolism	3/4	$-$	
$\boldsymbol{k_s}$	Factor for standard metabolism	10.0	$mass^{1-p} \cdot time^{-1}$	$[g^{1-p} \cdot year^{-1}]$
$\boldsymbol{\mu_0}$	Background mortality factor	0.84	$mass^{1-n} \cdot time^{-1}$	$[g^{1-n} \cdot year^{-1}]$
$\boldsymbol{\eta}$	Size at maturation rel. to asymptotic weight W	0.25	$-$	
$\boldsymbol{\xi}$	Fraction of energy reserves	0.10	$-$	
$\boldsymbol{f_0}$	Initial feeding level	0.60	$-$	
$\boldsymbol{f_c}$	Critical feeding level	0.20	$-$	
$\boldsymbol{\epsilon}$	Efficiency of offspring production	0.10	$-$	
$\boldsymbol{\kappa}$	Factor for maximum recruitment	50.00	$-$	
$\boldsymbol{u}$	Width of maturation transition	10.00	$-$	
$\boldsymbol{w_0}$	Offspring weight	0.0005	$mass$	$[g]$
Individual foraging				
$\boldsymbol{\beta}$	Preferred predator-prey weight ratio	100	$-$	
$\boldsymbol{\sigma}$	Width of selection function	1.30	$-$	
$\boldsymbol{\gamma}$	Factor for search volume	*	$mass^{-q} \cdot vol \cdot (time \cdot \#)^{-1}$	$[g^{-q} \cdot m^3 \cdot (year \cdot \#)^{-1}]$
$\boldsymbol{q}$	Exponent of search volume	0.8	$-$	
Primary production				
$\boldsymbol{\kappa_r}$	Resource spectrum carrying capacity	0.005	$\# \cdot mass^{\lambda-1} \cdot vol^{-1}$	$[\# \cdot g^{\lambda-1} \cdot m^{-3}]$
$\boldsymbol{r_0}$	Growth rate of resource spectrum	4.00	$mass^{1-p} \cdot time^{-1}$	$[g^{1-p} \cdot year^{-1}]$
$\boldsymbol{\lambda}$	Exponent of resource spectrum	2-n+q	$-$	
$\boldsymbol{w_{cut}}$	Upper weight limit of resource spectrum	100	$mass$	$[g]$

$\star \quad \gamma_{foraning\ arena} = \frac{f_0 h \beta^{2-\lambda}}{(1-f_0)\sqrt{2\pi}\kappa_r \sigma} \approx 8080.7235$ and $\gamma_{refuge} = 0.$

3. Method

In this chapter we are discussing the optimization problem in the strategy "myopic", where in the first section we briefly explained why the usage of the "myopic" strategy was preferred to the "life-history" strategy in order to find the optimal behavior, and which method is the best to solve "myopic" strategy. The second section shows that the optimized behavior in the "myopic" strategy can be set up analytically using the growth and fecundity expression described in the previous chapter. But this section uncovers also the limits/problems that the solution has. The third section study what will happen with the feeding level when the analytical optimized behavior from the "myopic" strategy is used. In this section it is also proven that the density at a given weight vanishes if the feeding level at this weight is dropped under the critical level.

3.1. Which method is best to find the optimal behavior?

Let τ be a behavior. In the previous chapter it is shown that the optimal behavior τ^* can be found by following the "life-history" strategy under the assumption steady state in the system (Since we optimized the behavior only when the system is in steady state, hence we can in principle remove the symbol t, but of practical clarity we keep the symbol):

$$V(w,t) = \max_{\tau(w)\in[0,1]} \left\{ \frac{g(w,t)\dfrac{\partial V(w,t)}{\partial w} + F(w,t)}{\mu(w,t)} \right\}$$

where V is the fitness (reproductive value), and g, F and μ are the growth, fecundity and mortality of individuals with the weight w at the time t respectively. But there is a problem. We don't know the explicit expression of $\frac{\partial V(w,t)}{\partial w}$. There is several methods which can solve the problem. One of the popular methods is the so-called dynamic programming. There is a very broad variety for the definition of the dynamic programming, but the most general definition is formulated by (Bertsekas, 2005), where the dynamic programming expresses the evolution of some variables, under which the influence of decisions is made at discrete instances of time. To this we use the so-called upwind method (see **appendix A.1** for more details about the discrete scheme).

One possible way to use the upwind method to find the optimal behavior is to solve it backwards (Clark & Mangel, 1988). When the individual at the asymptotic weight W cannot grow any more, $g(W,t) = 0$ for all time t and behavior τ, then all its energy is always allocated to reproduction, i.e. $\psi(W) = 1$, hence it always maximizes its present reproductive value.

$$V(W,t) = \max_{\tau(W)\in[0,1]} \left\{ \frac{E_{energy}(\mathrm{W},t)}{\mu(\mathrm{W},t)} \right\}$$

Then the "life-history" strategy is totally equal to the "myopic" strategy at asymptotic weight. Thereby we can use backwards solving. But the calculation schemes have one serious draw back – it is computationally intensive (Sainmont, Andersen, Thygesen, Fiksen, & Visser, 2013; Bellman R. E., 1957), which is why we do not focus on that.

This is where the “myopic” strategy enters into the picture. The upwind method in combination with the “myopic” strategy is a nice solution. We have shown in the previous chapter that the “myopic” strategy can be used as an alternative formulation of the “life-history” strategy under the assumption of growth $g = (1 - \psi)E_{energy}$ and fecundity $F = \psi E_{energy}$, where ψ is the allocating function that allocates the available energy E_{energy} to the reproduction. The “myopic” strategy has the advantage that it can be solved analytically, which is a great plus with respect to the computationally intensive.

In the discussion chapter it was also discussed about why the “myopic” strategy will run better in a random environment than the “life-history” strategy. In short it can be said that the future becomes less predictable when the randomly variables are included. This is why we prefer to use the “myopic” strategy to find the optimal behavior rather than the “life-history” strategy.

But the “myopic” strategy has a drawback. If individuals are short of gained energy, then they are in principle dying and according to the “life-history” it does not matter which behavior they have, while in the “myopic” strategy it does matter, which can raise the question whether the behavior is a rational decision. More about this is explained in the next section.

3.2. The optimal “myopic” behavior and its limit

In this section focus will be on the “myopic” decision based on the formulation:

$$V(w,t) = \max_{\tau(w)\in[0,1]} \left\{ \frac{E_{energy}(w,t)}{\mu(w,t)} \right\}$$

where it is assumed that all individuals always try to maximize the gain of the available energy per the risk (the total mortality) by using the optimal foraging strategy $\tau^*(w)$. The individuals must choose a real number τ between 0 (never in the foraging arena) and 1 (lives only in the foraging arena), and the decision-making is based on the local maximum. When $\frac{dV(w,t)}{d\tau} = 0$, the local maximum of the fitness is obtained which means the fitness is local optimized. By using this equation we can find the optimal behavior in the “myopic” strategy.

There is one thing we have to bear in mind before beginning with the optimizing process. If there is no surplus energy ($E_{energy} < 0$), the individuals will not be able to grow ($g = 0$) or fertile ($F = 0$), which means they according to the “life-history” strategy have a zero reproductive value.

$$V(w,t) = \max_{\tau(w)\in[0,1]} \left\{ \frac{g(w,t)\dfrac{\partial V(w,t)}{\partial w} + F(w,t)}{\mu(w,t)} \right\} \xrightarrow{E_{energy}<0} V(w,t) = 0$$

The choice of τ according to the “life-history” strategy has no influence on the optimization of the fitness, if the available energy is zero or negative. When the available energy is negative, the individuals are not able to carry on their genes to the next generations, thus their fitness is zero. It is not time to get the evolution (optimized behavior) to work, because the individuals extinct before the next stage in evolution. But by a pure logical/rational thinking the individuals will - if they can neither grow nor reproduce - prefer to optimize their behavior such that the habitat is chosen based on the lowest total mortality. They will try to puff off their death. But the optimizing process cannot make that if based only on the “life-history” strategy. The problem in the “life-history” strategy is in a way projected onto the “myopic” strategy. If the available energy is negative, then the “myopic” will automatically optimize the behavior in such a way that the risk is maximized (see why in the figure below). Let’s take an example like the figure below. The individual can only choose the two different behavior τ_1 and τ_2, where the consequence for the first behavior is $E_{energy,1} = -1$ and $\mu_1 = 0.1$ while for the second is $E_{energy,2} = -0.1$ and $\mu_2 = 1$. If using the “myopic” strategy then the fish will automatically choose τ_2, because $-0.1 = \frac{E_{energy,2}}{\mu_2} > \frac{E_{energy,1}}{\mu_1} = -10$. But since the energy is negative they neither grow nor reproduce, so does it really pay to choose τ_2 instead of τ_1? Should minimization of the shortage of the energy per mortality (τ_2) be more attractive compared to minimization of the mortality (τ_1)? The higher mortality, the faster they die out due to no reproduction. Our model is built up in such a way that there are no consequence if the mortality is still the same even the available energy becomes more and more negative. Thus the “minimize risk” strategy τ_1 is an attractive behavior in case of negative energy.

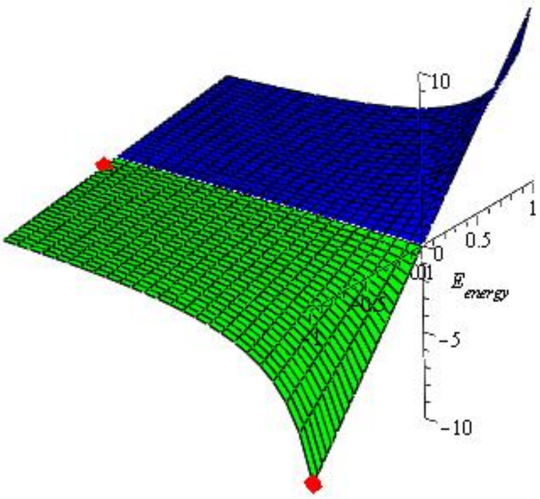


Figure 3.1 The plot of the “myopic” strategy $\frac{E_{energy}}{\mu}$ as a function of the available energy E_{energy} (1st axis) and the total mortality μ (2nd axis). The green area marks $\frac{E_{energy}}{\mu} < 0$, while the blue marks $\frac{E_{energy}}{\mu} > 0$. The red points marks the two different behavior τ_1 and τ_2, which the consequence for the first behavior is $E_{energy,1} = -1$ and $\mu_1 = 0.1$ while for the second is $E_{energy,2} = -0.1$ and $\mu_2 = 1$

Hence we must in principle add the so-called “minimized risk” condition in the “life-history” strategy:

$$\tau^*(w) = \begin{cases} \underset{\tau(w)\in[0,1]}{\operatorname{argmax}} \left\{ \dfrac{g(w,t)\dfrac{\partial V(w,t)}{\partial w} + F(w,t)}{\mu(w,t)} \right\}, & E_{energy}(w,t) > 0 \\ \underset{\tau(w)\in[0,1]}{\operatorname{argmin}} \{\mu(w,t)\}, & E_{energy}(w,t) \le 0 \end{cases}$$

and the “myopic” strategy:

$$\tau^*(w) = \begin{cases} \underset{\tau(w)\in[0,1]}{\operatorname{argmax}} \left\{ \dfrac{E_{energy}(w,t)}{\mu(w,t)} \right\}, & E_{energy}(w,t) > 0 \\ \underset{\tau(w)\in[0,1]}{\operatorname{argmin}} \{\mu(w,t)\}, & E_{energy}(w,t) \le 0 \end{cases}$$

The available energy drops below zero if the feeding level f is below the critical feeding level $f_c = \frac{E_{meta}}{\alpha C_{max}}$ (more about the critical feeding is described in the next section), thus the strategy is simplified to

$$\tau^*(w) = \begin{cases} \underset{\tau(w)\in[0,1]}{\operatorname{argmax}} \left\{ \frac{E_{energy}(w,t)}{\mu(w,t)} \right\}, & f(w,t) > f_c(w) \\ \underset{\tau(w)\in[0,1]}{\operatorname{argmin}} \{\mu(w,t)\}, & f(w,t) \le f_c(w) \end{cases}$$

Let us take a closer look at the "myopic" strategy. There are three possible solutions that satisfy the local maximum (or the local minimum):

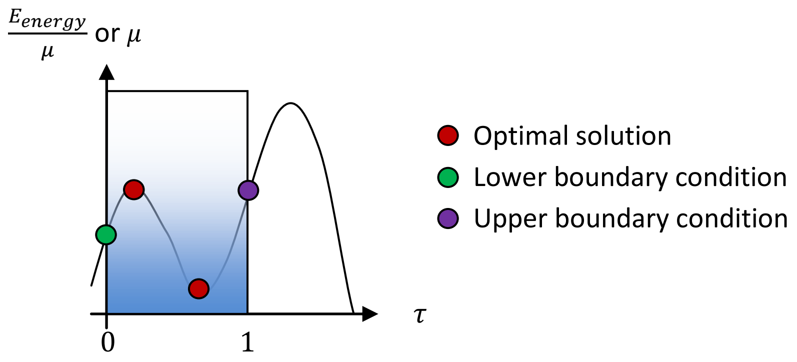


Figure 3.2 A simple illustration of the local optimum in a given interval

Possible solution no. 1 (optimal solution):	Possible solution no. 2 (lower boundary condition):	Possible solution no. 3 (upper boundary condition):
$\frac{\partial\left(\frac{E_{energy}(w,t)}{\mu(w,t)}\right)}{\partial\tau_1^*(w)} = 0$ Or $\frac{\partial\left(\mu(w,t)\right)}{\partial\tau_1^*(w)} = 0$ Condition: $\tau_1^*(w) \in [0,1]$	$\tau_2^*(w) = 0$	$\tau_3^*(w) = 1$

The first possible solution catches the local maximum (and maybe also minimum depending on the actual case), while the last two possible solution are the boundary condition that ensures the maximum is founded even if a local maximum doesn't exists in the interval, e.g. if $\frac{E_{energy}}{\mu} = \tau$ or $\frac{E_{energy}}{\mu} = 1 - \tau$.

More explicit details about the derivation of the first possible solution are described in **appendix A.2** and **appendix A.3**. In the appendices the explicit expression of the solution is found; it can be either none solution, one solution or two solutions dependent on the actual case. Under the assumption of no food and no predation in the refuge, $E_r = 0$ and $\mu_{p,r} = 0$ and $\tau^* \in [0,1]$, the solution principle must be

$$\tau^*_{f>f_c,\mu_{p,r}=0,\mu_{p,f}=\mu_{p,r},E_f\neq E_r}(w) = 1$$

or

$$\tau^*_{f>f_c,\mu_{p,r}=0,\mu_{p,f}\neq\mu_{p,r},E_f=E_r}(w) = 0$$

or

$$\tau^*_{f>f_c,E_r=0,\mu_{p,r}=0,\mu_{p,f}\neq\mu_{p,r},E_f\neq E_r,f_c=1}(w) = \frac{1}{2}\left(\frac{C_{max}(w)}{E_f(w,t)} + \frac{\mu_b(w)}{\mu_{p,f}(w,t)}\right)$$

or

$$\tau^*_{f>f_c,E_r=0,\mu_{p,r}=0,\mu_{p,f}\neq\mu_{p,r},E_f\neq E_r,f_c\neq 1}(w) = \frac{f_c(w) \pm \sqrt{f_c(w) + \left(1 - f_c(w)\right)\frac{\mu_b(w)}{\mu_{p,f}(w,t)}\frac{E_f(w,t)}{C_{max}(w)}}}{1 - f_c(w)} \cdot \frac{C_{max}(w)}{E_f(w,t)}$$

Or

$$\tau^*_{f\leq f_c,E_r=0,\mu_{p,r}=0,E_f\neq E_r,\mu_{p,f}\neq\mu_{p,r}}(w) = \frac{C_{max}(w)}{E_f(w,t)}\left(-1 + \sqrt{\frac{\alpha}{\xi w}\cdot\frac{E_f(w,t)}{\mu_{p,f}(w,t)}}\right)$$

The third behavior $\tau^*_{f>f_c,E_r=0,\mu_{p,r}=0,\mu_{p,f}\neq\mu_{p,r},E_f\neq E_r,f_c=1}$ is not the most interesting behavior, because the "myopic" strategy must in principle be used only when the feeding level is above the critical feeding level $f > f_c$. The problem is that the feeding level $f = \frac{E}{E+C_{max}}$ can never equal 1 unless the size of the stomach is zero which is physically impossible. Therefore we may in principle ignore the solution. As we will also see in the next section that if the feeding level is dropping under the critical feeding level $f < f_c$, then the density at this weight w is going to vanish under the assumption of the total mortality $\mu > 0$. Examining the model using the critical feeding level $f_c = 1$ is therefore not the most interesting way to study the optimal behavior.

We can also ignore the "minimized risk" condition in the "myopic" strategy including the last behavior $\tau^*_{f\leq f_c,E_r=0,\mu_{p,r}=0,E_f\neq E_r,\mu_{p,f}\neq\mu_{p,r}}$, because the condition has a serious drawback. The optimal behavior cannot be derived in the "minimized risk" condition if the encountered food or the predation mortality is identical for both habitats, i.e. no solution if $E_f = E_r$ or $\mu_{p,f} = \mu_{p,r}$ (the reason why can be found in the **appendix A.3**).

And now seen from the view of the evolution theory the "minimized risk" condition is not the most interesting behavior to study, because the species are doomed to die according to the survival of the fitness, so using the "minimized risk" condition just means that they put off their death warrant. This condition does not need our focus. We can assume that the fish are neither full rational nor have the essential intelligent to be able to adjust their strategy according to the available energy being positive or negative. They are assumed to have just enough intelligence to use one and only one strategy which is the “myopic” strategy without the “minimized risk” condition.

As a result of the optimization process it is simplify assumed that all individuals will follow the “myopic” strategy even if negative energy occurs, which brings us back to the beginning of this section.

$$\tau^*(w) = \underset{\tau(w)\in[0,1]}{\operatorname{argmax}} \left\{ \frac{E_{energy}(w,t)}{\mu(w,t)} \right\}$$

So back stands the five possible solutions (or in reality three solutions: $\tau^* = 0, \tau^* = 1$ and $\tau^*_{f>f_c,E_r=0,\mu_{p,r}=0,\mu_{p,f}\neq\mu_{p,r},E_f\neq E_r,f_c\neq 1}$). The last solution is interesting, because this is the only one solution that have an optimal foraging strategy which different from species to species depending on their background mortality. If there is no baseline mortality (background mortality) then this solution will also be independent of species.

$$\lim_{\mu_b\to 0} \tau^*_{E_r=0,\mu_{p,r}=0,\mu_{p,f}\neq\mu_{p,r},E_f\neq E_r,f_c\neq 1}(w) = \frac{f_c(w) \pm \sqrt{f_c(w)}}{1-f_c(w)} \cdot \frac{C_{max}(w)}{E_f(w,t)}$$

The behavior can only be a positive value between 0 and 1, then

$$\tau^*_{E_r=0,\mu_{p,r}=0,\mu_{p,f}\neq\mu_{p,r},E_f\neq E_r,f_c\neq 1}(w) = \frac{f_c(w) + \sqrt{f_c(w)}}{1-f_c(w)} \cdot \frac{C_{max}(w)}{E_f(w,t)}$$

The conclusion in this section is that the optimal behavior under the assumption of no food and no predation in the refuge is either $\tau^* = 0, \tau^* = 1$ or $\tau^* = \frac{f_c \pm \sqrt{f_c + (1-f_c)\frac{\mu_b}{\mu_{p,f}}\frac{E_f}{C_{max}}}}{1-f_c} \cdot \frac{C_{max}}{E_f}$.

3.3. The optimal and critical feeding level

We have shown that the myopic strategy solves the Hamilton-Jacobi-Bellman equation (HJB) under the three following assumptions: steady-state, growth $g = (1-\psi)E_{energy}$ and fecundity $F = \psi E_{energy}$. Now it is interesting to know what will be the critical feeding level and what happens with the feeding level when the optimal behavior τ^* is used.

Theorem:

Let the growth $g = (1-\psi)E_{energy}$ and the fecundity $F = \psi E_{energy}$, where ψ is the allocating function that allocates the non-negative available energy of the individuals E_{energy} to the reproduction.

The energy is defined as $E_{energy} = \alpha f C_{max} - E_{meta}$, hence the critical feeding level f_c is

$$f_c(w) = \frac{E_{meta}(w)}{\alpha C_{max}(w)}$$

where E_{meta} is the structural maintenance (standard metabolism) and C_{max} is the maximum intake and the ingested food is assimilated by an efficiency α.

If the feeding level is dropping under the critical feeding level, then the fitness V (reproductive value) is zero and the density N at this weight w is going to vanish under the assumption of the total mortality $\mu > 0$.

Proof:

When the intake is insufficiently to cover the respiration ($E_{energy} < 0$), the growth is halted and the fecundity is changed to infertile, hence the fitness $V = 0$. Therefore it is important to underline that the critical level

$$E_{energy}(w, t) > 0$$

The available energy is early formulated as the structural maintenance E_{meta} (standard metabolism) subtracted from the consumed energy E_{cf}, i.e. $E_{energy} = E_{cf} - E_{meta}$. The consumed energy has been derived by the expression $E_{cf} = \alpha f C_{max}$, where the ingested food $f C_{max}$ is assimilated by an efficiency α. If the feeding level is isolated by the inequality expression above we get the so-called critical feeding level

$$f_c(w) = f(w, t) > \frac{E_{meta}(w)}{\alpha C_{max}(w)}$$

If the feeding level is dropping under the critical feeding level, then the system has no growth at the weight w, i.e. $g(w, t) = 0$, hence the PDE of the model

$$\frac{\partial N(w, t)}{\partial t} + \frac{\partial g(w, t) N(w, t)}{\partial w} = -\mu(w, t) N(w, t)$$

is reduced to

$$\begin{aligned} \frac{\partial N(w, t)}{\partial t} &= -\mu(w, t) N(w, t) \\ \int_{N(w, t_0, \tau(w))}^{N(w, t, \tau(w))} \frac{1}{N(w, t)} dN(w, t) &= -\int_{t_0}^{t} \mu(w, \tilde{t}) d\tilde{t} \\ \ln\left(\frac{N(w, t)}{N(w, t_0)}\right) &= -\int_{t_0}^{t} \mu(w, \tilde{t}) d\tilde{t} \\ \frac{N(w, t)}{N(w, t_0)} &= \mathrm{e}^{-\int_{t_0}^{t} \mu(w, \tilde{t}) d\tilde{t}} \end{aligned}$$

The total mortality of the individuals is always positive $\mu > 0$ (non-zero value which due to the background mortality can not be zero), thus we see

$$\begin{gathered} \int_{t_0}^{t} \mu(w, \tilde{t}) d\tilde{t} > 0 \\ \mathrm{e}^{-\int_{t_0}^{t} \mu(w, \tilde{t}) d\tilde{t}} < 1 \end{gathered}$$

Hence it is shown that

$$\frac{N(w, t)}{N(w, t_0)} < 1$$

The inequality means that if there is no growth at this weight w, then the density at this weight is going to be vanished. Furthermore the starvation mortality kicks in when the feeding level is dropping under the critical level, which makes the situation harder to survive ■

With knowledge of the critical feeding we continue to the next theorem (Andersen, pers.com.) that defines the optimal feeding level.

Theorem:

Let the fitness V (reproductive value) with the optimal behavior $\tau^*(w)$ be determined by the "myopic" strategy

$$V\big(w,t,\tau^*(w)\big) = \max_{\tau(w)\in[0,1]} \left\{ \frac{E_{energy}(w,t)}{\mu(w,t)} \right\}, \qquad f(w,t) > f_c(w)$$

Where E_{energy} is the non-negative available energy of the individuals and μ is the non-zero total mortality of the individuals, both defined in the previous chapter.

If there is no food and no predation in the refuge (i.e. $E_r = 0$ and $\mu_{p,r} = 0$), then the optimal feeding level equals the square root of the critical feeding level $f^* \to \sqrt{f_c(w)}$, as the background mortality is going towards zero, $\mu_b(w,t) \to 0$.

Proof:

From the previous section we know that the solution to the "myopic" strategy in the refuge under the assumption of positive available energy and no food and no predation is either

$$\tau^*(w) = 1$$

or

$$\tau^*(w) = 0$$

or

$$\tau^*_{E_r=0,\mu_{p,r}=0,\mu_{p,f}\neq\mu_{p,r},E_f\neq E_r,f_c\neq 1}(w) = \frac{f_c(w) \pm \sqrt{f_c(w) + \big(1-f_c(w)\big)\dfrac{\mu_b(w)}{\mu_{p,f}(w,t)}\dfrac{E_f(w,t)}{C_{max}(w)}}}{1-f_c(w)} \cdot \frac{C_{max}(w)}{E_f(w,t)}$$

where $f_c(w)$ is the critical feeding level.

Entering the optimal behaviors into the feeding level $f = \frac{\tau(E_f - E_r)+E_r}{\tau(E_f-E_r)+E_r+C_{max}}$ you obtain the optimal feeding level

$$f_{\tau^*=1}(w,t) = \frac{E_f(w,t)}{E_f(w,t) + C_{max}(w)}$$

or

$$f_{\tau^*=0}(w,t) = 0$$

or

$$f_{\tau^*_{E_r=0,\mu_{p,r}=0,\mu_{p,f}\neq\mu_{p,r},E_f\neq E_r,f_c\neq 1}}(w,t) = \frac{f_c(w) \pm \sqrt{f_c(w) + \left(1 - f_c(w)\right)\frac{\mu_b(w,t)}{\mu_{p,f}(w,t)}\frac{E_f(w,t)}{C_{max}(w)}}}{1 \pm \sqrt{f_c(w) + \left(1 - f_c(w)\right)\frac{\mu_b(w,t)}{\mu_{p,f}(w,t)}\frac{E_f(w,t)}{C_{max}(w)}}}$$

The optimal feeding level under the assumption of no baseline mortality (zero background mortality, $\mu_b = 0$) can be found to be

$$\lim_{\mu_b \to 0} f(w,t) = \frac{f_c(w) \pm \sqrt{f_c(w)}}{1 \pm \sqrt{f_c(w)}} = \pm\sqrt{f_c(w)}$$

The feeding level can only be positive, thus

$$f^* = \sqrt{f_c(w)} \ \blacksquare$$

In short we have shown that the optimal behavior is active if the feeding level is $\sqrt{f_c(w)}$ with the assumption of no food and no predation in the refuge and no background mortality.

4. Results

This chapter treats the "resident" strategy, initially obtained using dynamic programming, to mutants with a slightly different strategy. If the mutants' strategy results in a higher fitness, the mutant strategy will replace the guess. This procedure is repeated until no mutant strategy is able to invade the resident strategy. Comparing the resident strategy and the mutant strategy provides an idea of how the foraging behavior in the ecosystem is evolved during the generations, i.e. an answer to the question of how the fitness and the adaptive behavior differs in the result.

4.1. Resident strategy

In this first section it is discussed how the fish actually optimizes their strategy, i.e. when is the mutant strategy able to replace the resident strategy. In this discussion it is assumed that all fish have genes and intelligence enough to figure out what is the best strategy and that the evolutionary dynamics is much slower than the ecosystem dynamics, i.e. the fish is able to change their strategy when the ecosystem dynamic is calmed down. The two assumptions are used to simplify the model.

Some very difficult questions exists, e.g. do the fish have intelligence enough to "figure out" what is the best to do? Have their ancestors been in similar situations enough times that a gene may be responsible to give the optimal response to the variation in the environment? Or do they respond sub-optimal because their genes are not tuned to the situation?

But we need not answer them, because this project is written from the mathematical and not biological point of view. We only show interest in the steady state solutions that eventually occurs. Evaluating the transients to steady-state may/may not be ecologically relevant. When the system is in steady state, it is reasonable to assume that the fish responds favorably, otherwise other fish would have outperformed them. But when resigning ourselves to the transients used for calculation, only we are also free to choose the transient dynamics that provide the easiest calculation. And the easiest calculation strategy is to assume that the fish do not change strategy while ecosystem dynamics calms down. This corresponds to a strategy of $\tau(w)$ being hard-coded in the genes, as the evolutionary dynamics is much slower than the ecosystem dynamics.

4.1.1. Static model

(static encountered food + static predation mortality)

To locate the mechanism behind the adaptive foraging behavior in the model (i.e. when the fish actually optimizes their strategy) under the given standard parameters described in **chapter 2.1.19** the simplification of the model is used, i.e. the static encountered food and the static predation mortality has been used (see more about these in **chapter 2.1.4** & **2.1.12.2**). The static model means an assumption of no food and no predation in the refuge, i.e. zero volumetric search rates in the refuge $V_r(w) = 0$ for all individual weights w. Furthermore the model is stimulated with these conditions: the encountered food and the predation mortality should both be defined as a given fixed function in the foraging arena (static). All fish are assumed to encounter the amount of the food in the foraging arena corresponding exactly to their maximum intake, i.e. $E_f(w) = C_{max}(w) = hw^n$, where h is the maximum intake factor (consequence the feeding level can not exceed ½). The fixed total mortality is defined in this case as $\mu_{total}(w) = \mu_p(w) +$

$\mu_b(w)$. μ_p is the predation mortality given by ahw^{n-1} in the foraging arena (for $n < 1$ the predation mortality is inversely proportional to the weight) and 0 in the refuge, and μ_b is the background mortality given by $\mu_0 W^{n-1}$ in both habitats. a is the predation factor, μ_0 is the background mortality factor and W is the asymptotic weight (for $n < 1$ the background mortality is inversely proportional to the asymptotic weight). In the next chapter the dynamic encountered food and predation mortality is used.

All stimulated figures in this section are run for a species with the asymptotic weight $W = 100$.
The first figure below (**Figure 4.1**) illustrates the feeding level as a function of the individual weight and the encountered food in the foraging arena. The green surfaces are the resulting feeding level of the optimized behavior when using a low predation mortality factor, e.g. $a = 0.025$. The yellow and red surfaces refers to a medium or high predation mortality factor respectively, e.g. $a = 0.1$ and $a = \infty$. The colored surface is the maximum feeding level, i.e. $\tau(w) = 1$ for all weight w. One way to achieve the maximum feeding level is when the foraging arena is assumed risk free $a = 0$. The three different color lines are the critical behavior where the optimized strategy is entering (see more about this in **Figure 4.3**). The figure shows that when there is enough food, the fish regardless of individual weight tends to have the same feeding level, especially if the risk is extremely high. The lightweight fish are much easier to be saturated compared to heavyweight fish due to the small stomach. The feeding level is inversely proportional to the stomach C_{max} due to the expression $f = E/(E + C_{max})$, and since the exponent n in the expression of the stomach $C_{max}(w) = hw^n$ is defined as a positive value, the stomach is proportional to the weight, hence the feeding level is inversely proportional to the weight. In short it requires a large amount of food before the heavyweight becomes saturated.

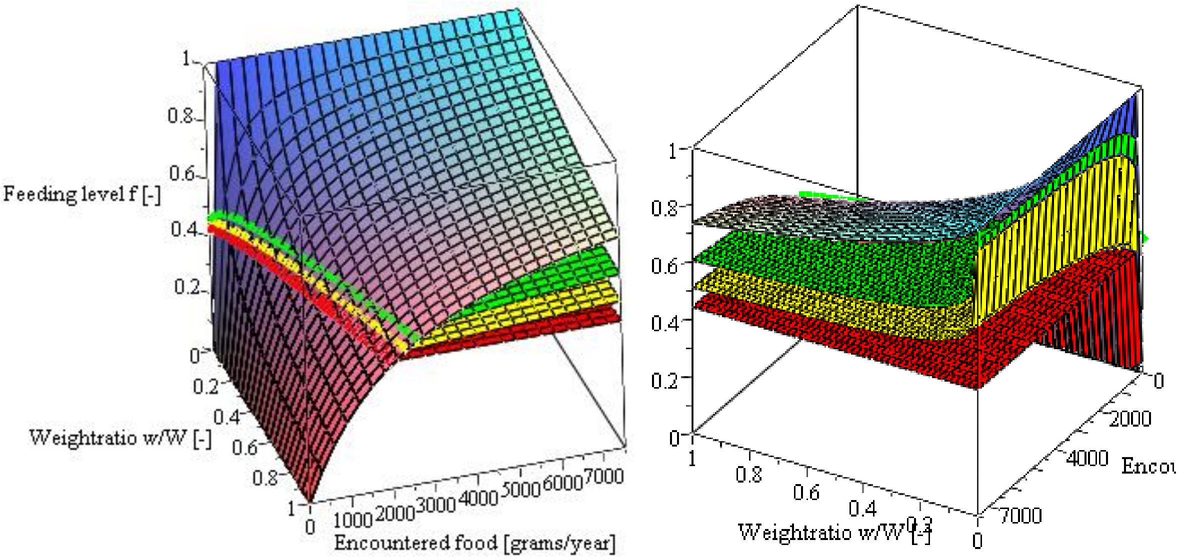


FIGURE 4.1 Feeding level as a function of the weight and the encountered food in the foraging arena seen from two different viewpoints. The maximum feeding level (i.e. $\tau = 1$, colored surface), the optimized feeding level (green surface if predation mortality factor is low, a = 0.025, yellow surface if medium a = 0.1 and red surface if extremely high a = ∞) and the critical behavior (three lines, where the individual is changed behavior from $\tau = 1$ to $0 \leq \tau < 1$). The maximum feeding level is achieved when the predation mortality factor is zero, a = 0.

The second interesting result of the figure is that the fish start to be cautious when there is enough of food. They don't want to run the 'unnecessary' risk of eating more. But due to no food in the refuge, they are still willing to spend an amount of time in the foraging arena even if the risk is infinity/extremely large. The extremely large risk surface tells us what their “minimum” feeding level is. They have to be in the foraging arena to gather energy to the growth and reproduction, otherwise they will die. They do not move into the foraging arena unless there food in the foraging arena.

The next figure (**Figure 4.2**) illustrates how the encountered food in the foraging arena and the individual weight affects the foraging strategy. The blue line marks the strategy shift from $\tau = 1$ (always in foraging arena) to $0 \leq \tau < 1$ (sometimes in the foraging arena and sometimes in the refuge). The yellow line is an example of the optimized behavior, where in this case the assumption of the fish is always to find and eat an amount of the food corresponding to their maximum intake (i.e. $E_f(w) = C_{max}(w) = hw^n$), is used. The figure concludes that the higher predation factor a, the lesser time the fish will spend in the foraging arena, and that the larger fish spends more time in the foraging arena comparing to the smaller fish. The reason for this behavior is that as the larger fish have a larger stomach they have to eat more to become saturated, and the food only exists in the foraging arena.

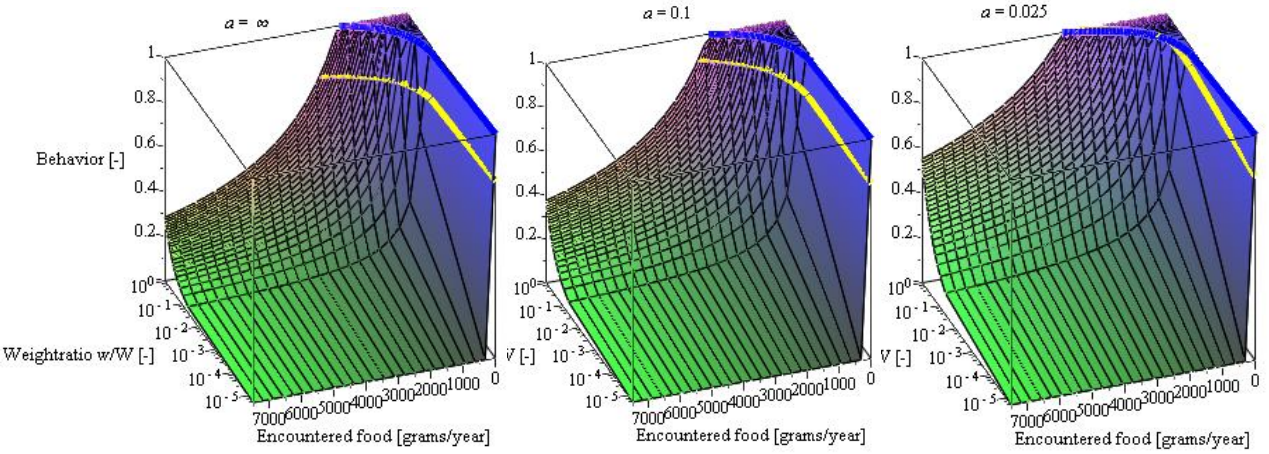


FIGURE 4.2 The behavior (strategy) as a function of the weight and the encountered food in the foraging arena with three different predation mortality factor (Left figure: a = ∞. Middle figure: a = 0.1. Right figure: a = 0.025). The blue line marks the line in which the behavior changes from $\tau = 1$ to $\tau < 1$. The yellow line marks the behavior if the encounter food is equal to the stomach, i.e. $E_f = C_{max}$.

When the model is run with the fixed encountered food $E_f(w) = C_{max}(w)$ and infinity big risk or is run risk free, the optimized behavior is the same for all individual weight (using the standard parameters):

$$\lim_{a \to \infty} \tau_{E_f = C_{max}}(w) \approx 0.7947$$
$$\lim_{a \to 0} \tau_{E_f = C_{max}}(w) = 1$$

In case of an extremely risk or in case of an risk free environment all individuals are using the same foraging strategy to achieve the acceptable feeding level which again is the same for all individuals.

The consequence of the predation factor a is illustrated better in the next figure. The left figure illustrates the behavior as a function of the predation factor and the weight ratio, while the right figure demonstrates the behavior of the individual at the asymptotic weight as a function of the weight ratio.

Both figures is simulated with the assumption $E_f(w) = C_{max}(w)$.

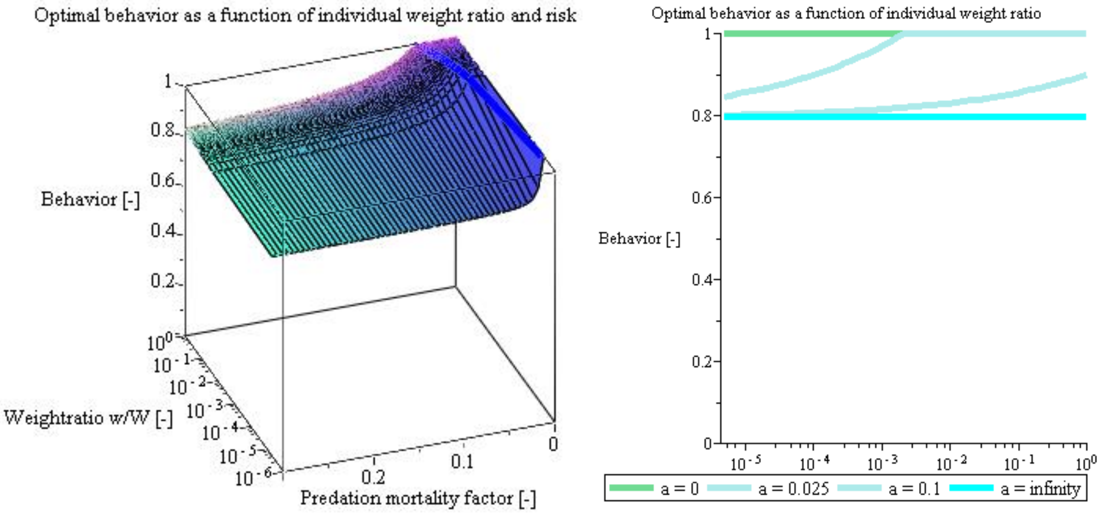


FIGURE 4.3 (left) The optimized behavior as a function of the individual weight ratio and predation mortality factor. (right) the optimized behavior of the individual at the asymptotic weight. The assumption the encountered food is equal to the stomach of the individuals $E_f = C_{max}$ is used in both figures.

By the figures in this section we can conclude in short that even if the predation risk is infinity big, all fish still have to spend much of their time in the foraging arena. The fish will spend less time in the foraging arena, if the encountered food is larger, or vice versa.

The next figure (**Figure 4.4**) illustrates the connection between the feeding level and the behavior for the individuals at the asymptotic weight. The figure tells how much the encountered food is need before the individual begin to change their behavior. The conclusion is that the higher the risk, the smaller the amount of food is needed before behavior begins to change. But the figure also shows that a minimum level exists regarding how low a feeding level they can survive. All individuals spend their time in the foraging arena regardless the risk until a certain feeding level is reached. Basically all individuals do not need a feeding level above $\sqrt{f_c}$, where f_c is the critical feeding level, because everything above this level is ‘unnecessary’ risk with the infinity big risk in the foraging arena. When the risk decreases, everything above the level becomes less ‘unnecessary’ and can be considered as a bonus instead.

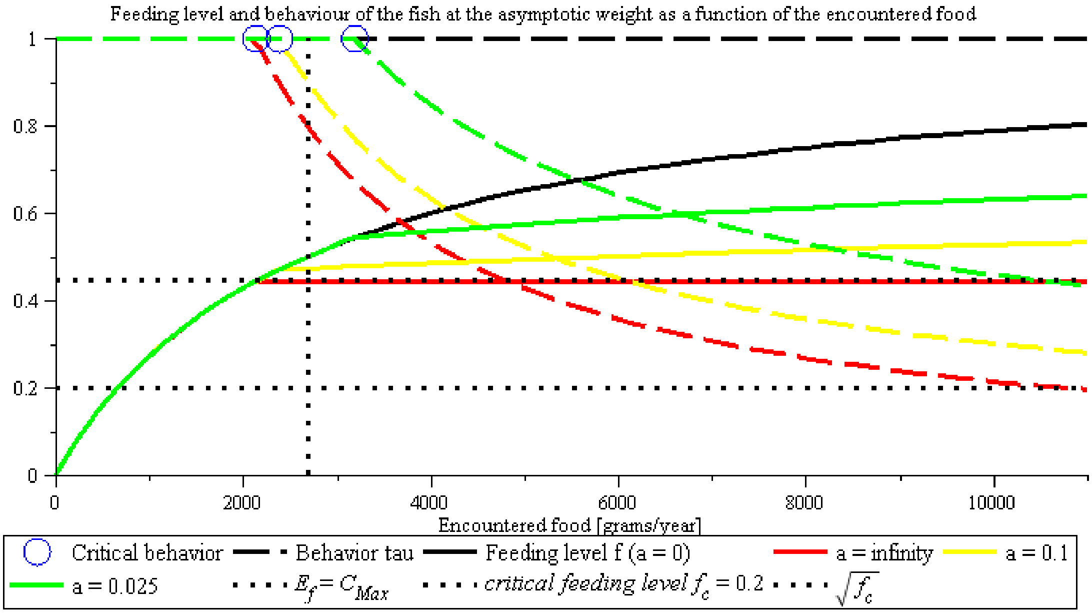


FIGURE 4.4 The feeding level and the behavior of the individuals at the asymptotic weight $W = 100g$ as a function of the encountered food in the foraging arena when using four different predation factors.

4.2. Examples of the optimized behavior

In this section we try to look at some examples that can illustrate what will happens with the population if the optimized strategy is included? And does the optimized strategy really lead to a better chance of survival? The first figure in this section is stimulated with the asymptotic weight $W = 100$ g and the standard parameters given in **chapter 2.19**. The top graph in the figure is the behavior as a function of the weight ratio (individual weight per its asymptotic weight W), the second graph is the feeding level as a function of the weight ratio, the third graph is the biomass as a function of the weight ratio, and so the growth as a function of the weight ratio, the next two graph is the mortality and survival probability – also both as a function of the weight ratio. The bottom graph is the recruitment as a function of the time. The bottom graph ensures that we can see whether the population of the species is growing, decreasing or stabilizing. The result shows a clear difference between the included (green) and the non-included (blue) adaptive behavior. The result also shows that the population is very sensitive with respect to the choice of the adaptive behavior. A small change in the behavior leads to a big change in the population (e.g. in this case the biomass is changed from the average about $10^{-2}\ \#/m^3$ to $10^{4}\ \#/m^3$). The adaptive behavior brings down the feeding level, growth and mortality in exchange of promoting biomass and changing the survival chance and not least the recruitment, where the recruitment decreases with time in the non-included adaptive behavior, while the recruitment of the non-included adaptive behavior increases with time. It is an important difference because it determines whether the species is dying or not.

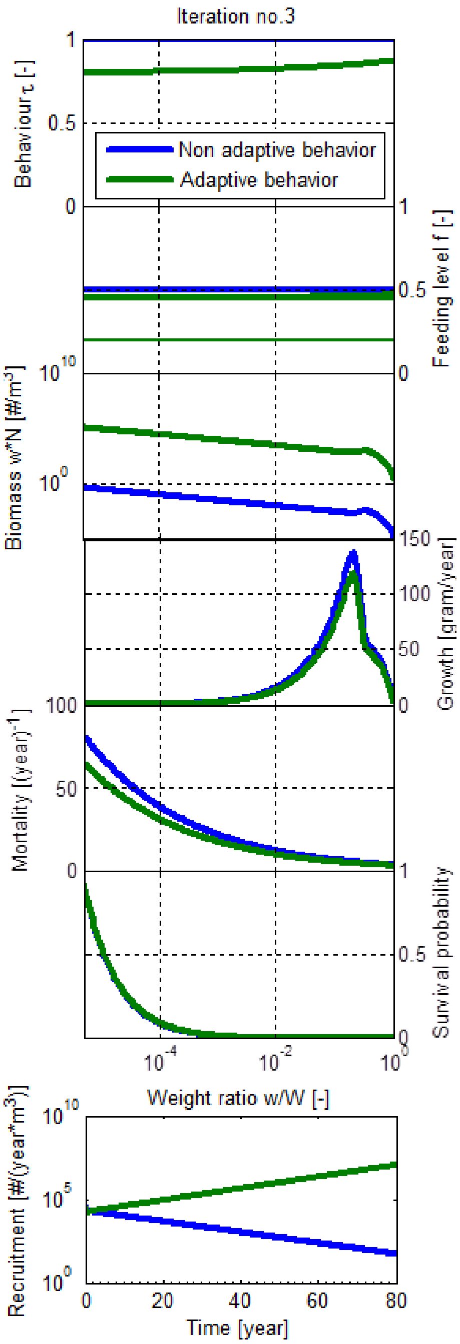


Figure 4.5. The model by using the **last time step optimizing** process with the **static encountered food and the static predation mortality** (predation mortality factor a = 0.142). With (green) and without (blue) adaptive behavior. Result tells the adaptive have a colossal influence on the population. Adaptive behavior bring down the feeding level, growth, mortality but in exchange for promoting the recruitment, biomass and survival chance. The adaptive behavior prevents the species dies out.

The consequence of the behavior on the different species is experimented in the next two figures (**Figure 4.6** & **Figure 4.8**) (the model is still stimulated for the single-species stated). The figures are simulated with different values of the predation mortality factor a. Figure (**Figure 4.6**) for medium risk factor $a = 0.14$ while so risk free factor $a = 0$ is display in (**Figure 4.8**). Both figures are calculated through 4 times of iteration (or 3 times excl. the initialized iteration). The iteration ensures that the optimized solution is convergent. 4 times of iterations is usual enough. Every iteration has four graphs; the first graph is the behavior as a function of the weight ratio (The ratio makes it possible for us to compare the results across species), the second graph is the feeding level, the third graph is the biomass, and the last graph is the recruitment. All stimulations are initialized with the behavior $\tau(w) = ½$ for all weight w. Every graph has four different species, i.e. four different asymptotic weights. The asymptotic weights are all chosen partly random. The largest species has $W = 100$ g, while the second largest is $W = 50$ g, the third $W = 25$ g and finally $W = 12.5$ g

The first graph in the first iteration in **Figure 4.6** shows that all individual and species are initialized with the behavior $\tau = ½$. The consequence of the behavior is that the feeding level is about 1/3. They do not gain energy enough to reproduce in such amount that they can cope with the predation factor is $a = 0.14$. For this factor the optimized behavior is calculated to be about $\tau \approx 0.8$, i.e. a higher value for the matured individuals and lower value for the new offspring individuals. The optimized behavior makes it possible for all individuals to gain more energy for reproduction, but unluckily the predation mortality factor (hence also total mortality) is still too high for some species to survive. The recruitment of the two smallest species (green and blue in the third graphs in the 2nd, 3rd and 4th iteration) falls as the time passes. Some species die faster than they can reproduce new offspring, so the two smallest species are doomed to death. The species with the larger asymptotic weight perform better than the species with small asymptotic weight due to their lower background mortality compared to the small species. The three last iterations in figure are the same, which means that the optimal behavior is converged.

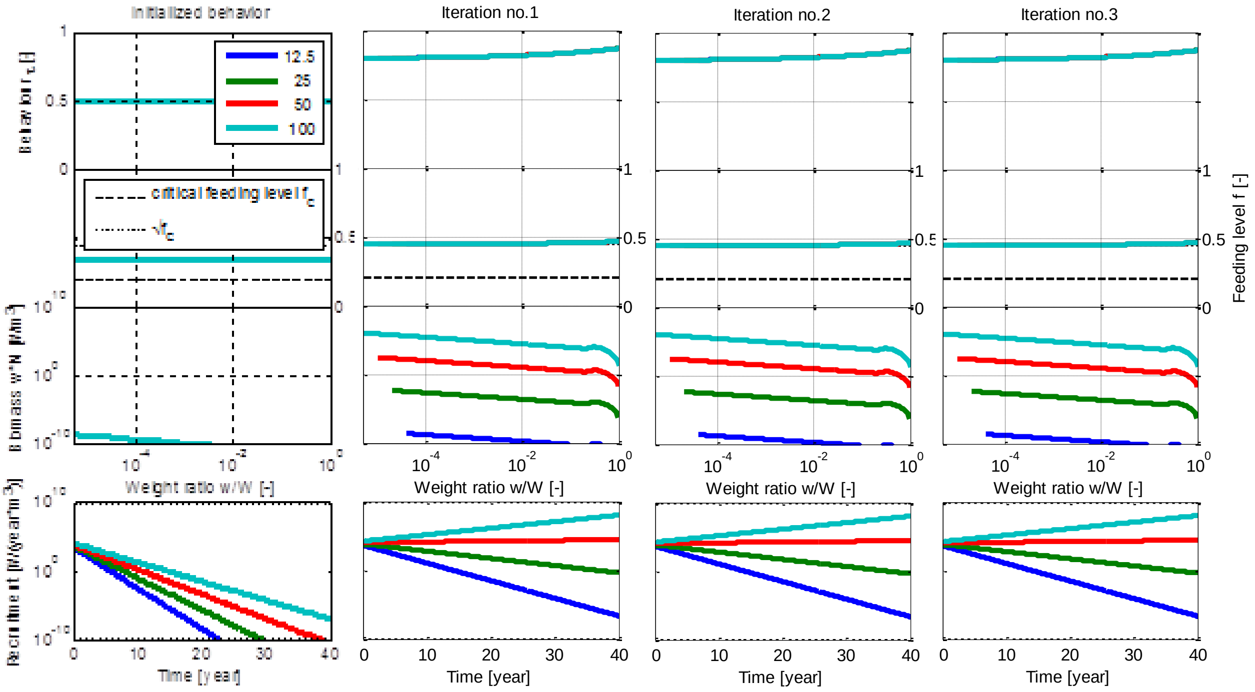
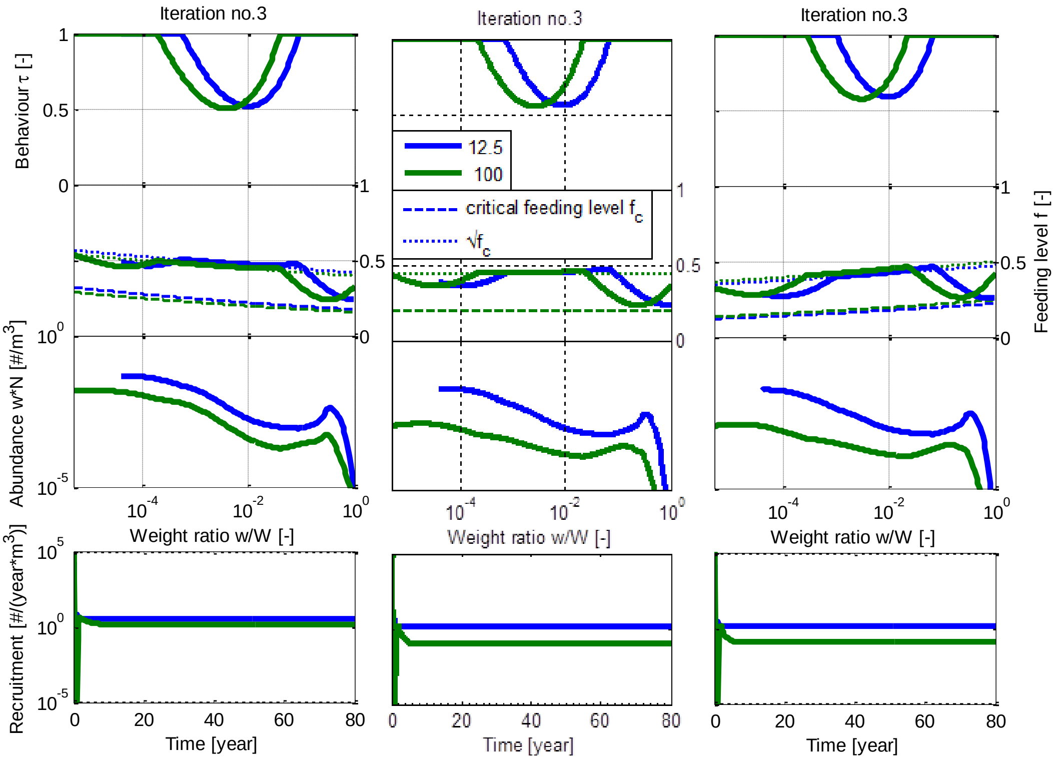


FIGURE 4.6 **Last time step optimizing** iteration of the behavior (top) and its consequence on the biomass (middle) and recruitment (bottom) of the different species (i.e. species different asymptotic weight – color) when using **static encountered food** and **the static predation mortality** with the predation factor $\boldsymbol{a = 0.14}$.

In the **Figure 4.6** both the optimal and the critical feeding level is plotted. It is a bit hard to see the details in the figure, then a more legible experiment with the critical feeding level can be given by a dynamic model like the next figure (**Figure 4.7**). The plot displays three different cases. The critical feeding level f_c depends on the metabolism activity $E_{meta} = k_s w^p$, the size of stomach $C_{max} = hw^n$ and the assimilation efficiency α. Since the efficiency and the maximum intake factor h and the metabolism factor k_s are just scaling constants, the feeding level will scale up or down depending on the factors. Therefore we concentrate only on the experiment of the exponents p and n. Two different species $W = 100$ g and $W = 12.5$ g is sufficient in this case to show a legible result.



(0.75) n > p (0.70) (0.75) n = p (0.75) (0.70) n < p (0.75)

FIGURE 4.7 **Last time step optimizing** the behavior (top) and its consequence on the biomass (middle) and recruitment (bottom) of the different species (i.e. species different asymptotic weight – color) when using **dynamic cannibalistic encountered food**, **the cannibalistic predation mortality** with predation factor $a = 0.0425$ and **dynamic resource spectrum** with $w_{cut} = 100$.

Here we see that the optimal behavior is active when the feeding level is about the optimal level $\sqrt{f_c}$ and the large species seems to start early optimizing their behavior, but only because $\frac{w}{W_2} < \frac{w}{W_1}$. As long as the feeding level is in between $\sqrt{f_c}$ and f_c the optimal behavior will be $\tau = 1$. By the figure you can see that the feeding level near maturation weight $w/W \ = 1$ is close to dropping below the critical feeding level. This is why the biomass in this area is weakly decreased.

What happens if there is no predation in the foraging arena, i.e. $a = 0$? When there is no predation in the foraging arena all species can not see an advantage of staying in the refuge, therefore they all move in the foraging arena. The consequence is logically that the biomass explodes, but an interesting thing happens here. In the next figure (**Figure 4.8**) we will see what happens if no predation takes place in the foraging arena.

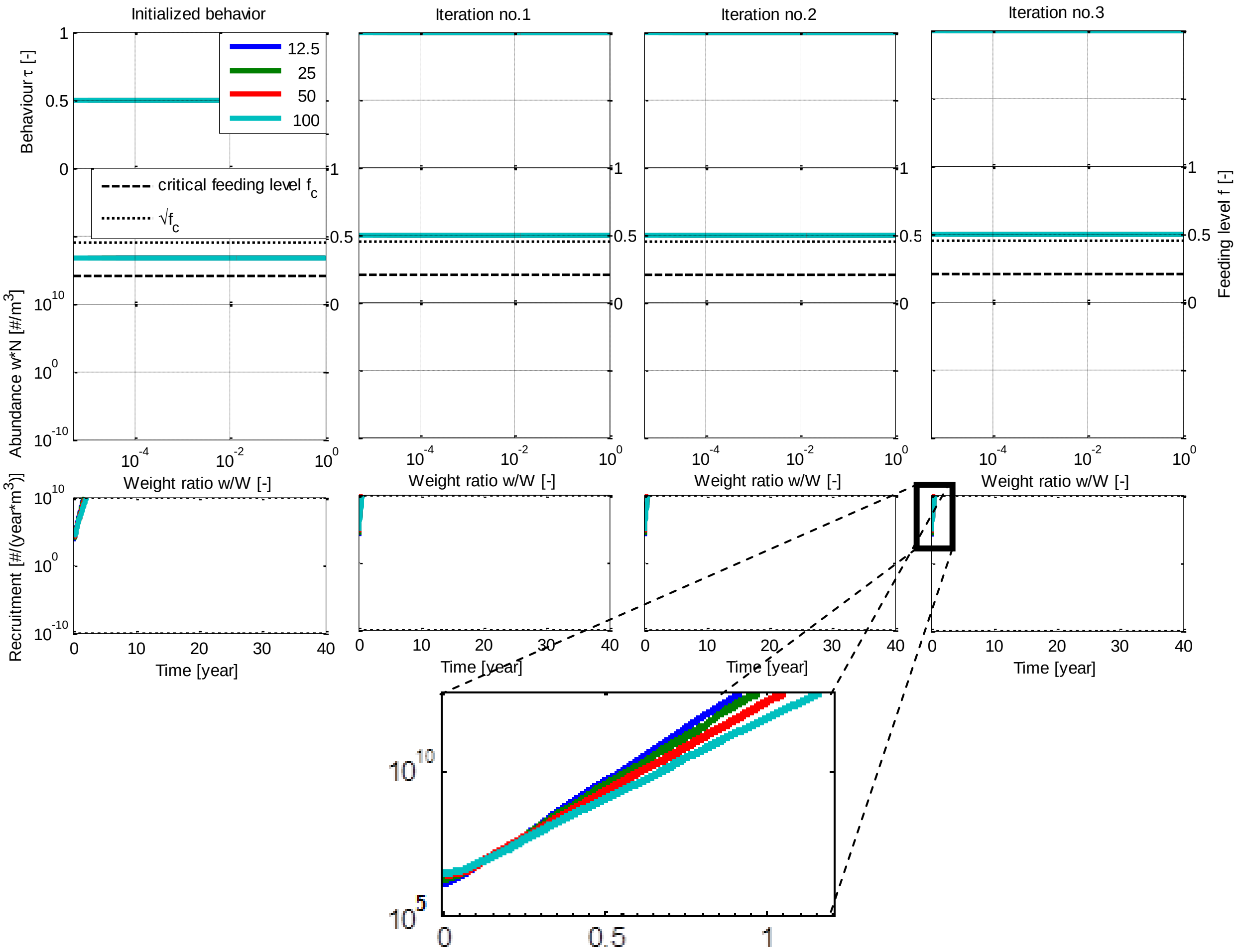


FIGURE 4.8 **Last time step optimizing** iteration of the behavior (top) and its consequence on the biomass (middle) and recruitment (bottom) of the different species (i.e. species different asymptotic weight – color) when using **static encountered food**, **the static predation mortality** with predation factor $a = 0.00$.

In the recruitment graph in **Figure 4.8** it is shown that the smallest slope of the recruitments is among the largest species $W = 100$ g (turquoise), which means the largest species perform less good compared to the other smaller species if predation mortality is not included in the model. The pressure of predation is larger among the small species compared to the large species, because the resource spectrum can grow to $w_{cut} = 100$ g, which is equal to the maturation weight of the largest species. Therefore the smallest species has the biggest gain by no predation. The feeding level shows that there is more than enough food items, which means that starvation mortality is not kicked in, hence there is only one mortality source left; the background mortality. The main question here is thus, how can the gain be higher than the background mortality, being higher among the small species compared to larger species, as the background mortality seems to have no big influence on the recruitment. A possible explanation is the early fecundity among the small species and the lately fecundity among the large species (see in the section about fecundity chapter 2.1.11) has given an advantage for the small species.

4.3. Cannibalism

Cannibalism is commonly known among fish. According to (Smith & Reay, 1991) cannibalism has been classified into seven different types, depending on life-history stage, age difference between cannibal and prey and so on. Our model is built such that cannibalism is stimulated as simple as possible. Do species eat their own species or not? In the size-structured model the potential for cannibalism is a consequence of the assumption that the prey selection is due to relative prey size only. Cannibalism is central to the single-species state. Compared to the non-cannibalistic single-species state that only has the resource spectrum as food, the cannibalistic single-species have better food opportunities as they can gain food from the resource spectrum and they can eat their own species. Furthermore, cannibalism is often more pronounced in a single-species state compared to co-existence states (Hartvig & Andersen, 2013). The co-existence states means that more than one species can coexist in one community. We look only at single-species state. The question is: does the adaptive behavior change the relation between cannibalism and the overall fitness?

That question is what this chapter is trying to answer. This chapter examines the model with an adaptive behavior and cannibalism. The examinations will give us an idea of how the adaptive behavior plays a role for cannibalism among fish in the ecosystem and how cannibalism plays a role for the adaptive behavior. These investigations will uncover a central part in the understanding of the adaptive foraging behavior.

A main different from the past section is that the dynamic encountered food is now included in the model. The dynamic encountered food expression means that the species is now density dependence. When the ecosystem is in a non-cannibalistic single-species state, i.e. the species eat only the resource spectrum, the species tends to be sensitive with respect to the density of the resource spectrum. The sensitivity will be damped by either setting a fixed (static) resource spectrum $N_R = \kappa_r w^{-\lambda}$ or by adding cannibalism into the system. Here κ_r is the carrying capacity of the resource spectrum, and λ is the exponent of the resource spectrum expressed as $\lambda = 2 - n + q$, and finally where n is the exponent of the maximum intake and q is the exponent of the search volume rate.

The sensitivity will be damped when adding the static resource spectrum. Using the dynamic encountered food with the same static predation mortality from the previous chapter, the species will increase in number as the resource spectrum in the foraging arena will never run out. There is food enough to all individuals. Thus we need a large predation mortality factor in this case. Running a simulation using the dynamic encountered food with the fixed resource spectrum, will not allow us to see a worthwhile change compared to using the static encountered food. This is caused the fixed resource spectrum which generates a very stable dynamic encountered food situation, in other word the dynamic encountered food is forced to behave as a “fixed” encountered food intensity. The species will have nearly the same optimized behavior, feeding level and biomass. Therefore they will be more interesting in using the dynamic resource. The stimulated effects of using the dynamic resource will be more realistic if dynamic predation mortality is also added. Since the system is now more sensitive with respect to density dependence, the predation mortality factor is set back to the same level as before in the previous section, i.e. $a = 0.0425$. Otherwise the species will begin to die out due to starvation.

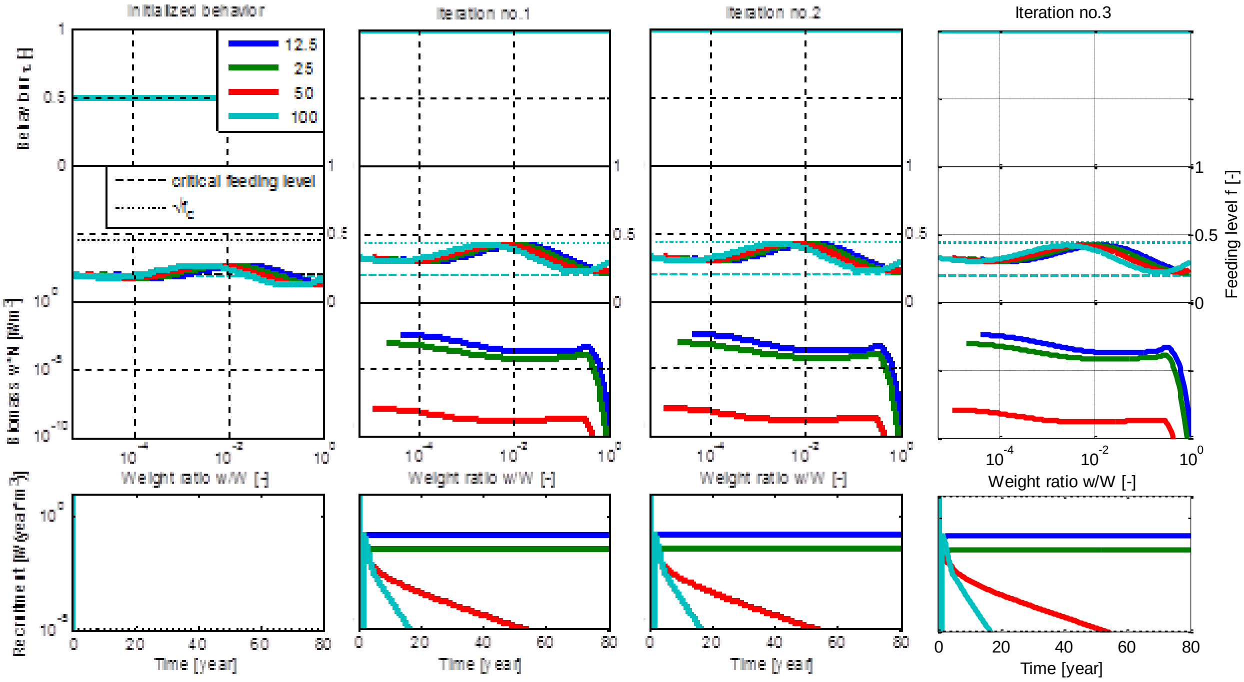


FIGURE 4.9 Last time step optimizing iteration of the behavior (top row) and its consequence on the feeding level (2nd row) and the biomass (3rd row) and the recruitment (bottom row) of the different single-stated species (i.e. species different asymptotic weight – color) when using dynamic cannibalistic encountered food, dynamic resource spectrum with $w_{cut} = 100g$ and cannibalistic predation mortality with the predation factor $a = 0.0425$.

The figure above (**Figure 4.9**) shows that the feeding level is between f_c and $\sqrt{f_c}$. It is why the optimized behavior is $\tau(w) = 1$ for all individual weights, which indicates that all fish are fighting about the food in the foraging arena. There is simply not food enough. Some of the largest species do not make it particularly well. We have to increase the carrying capacity κ_r, in order for the fish to obtain the optimal feeding level $\sqrt{f_c}$ (see **Figure 4.10**), hence the fish can begin to be more cautious by spending less time in the foraging arena. In the 1st iteration (or 2nd iteration if the initialized iteration is counted) an optimization is made which do not seem good, hence another try has been made to optimize. The new optimization converges and we find the same results in the 2nd and 3rd iteration. The peak in the feeding level above level $\sqrt{f_c}$ in the 1st iteration is cut off in the 2nd iteration. The recruitment graphs show that all four species are stabilized and has achieved the so-called steady-state.

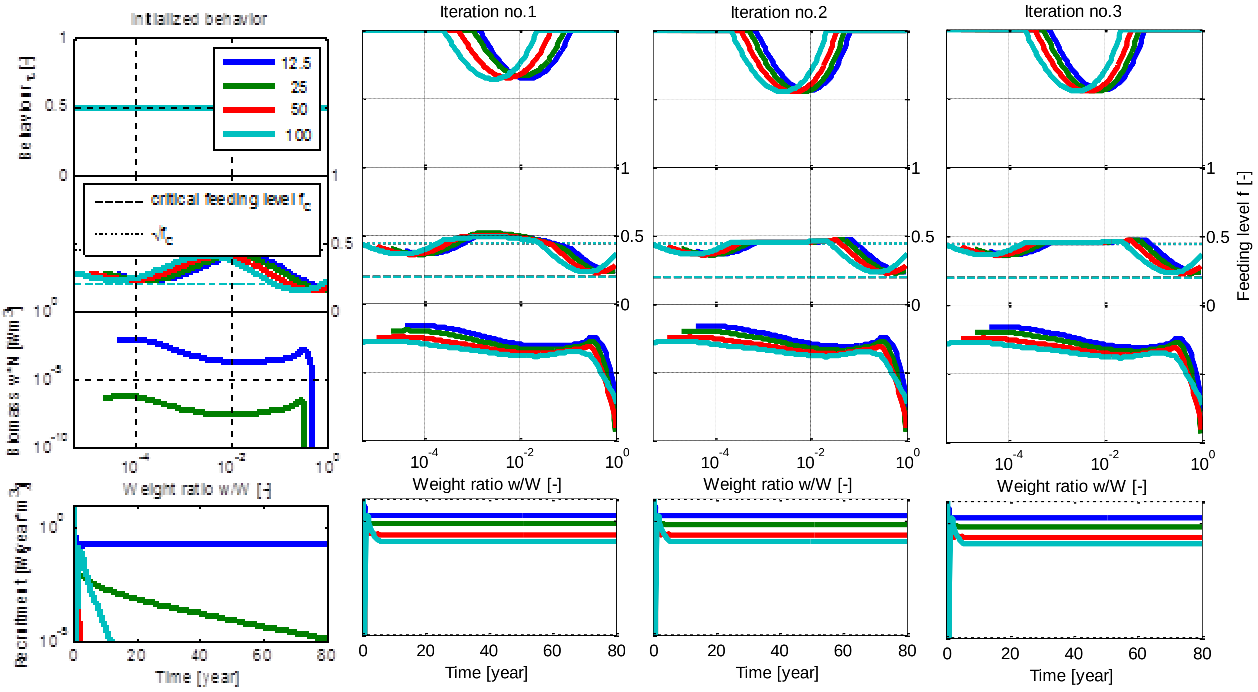


FIGURE 4.10 **Last time step optimizing** iteration of the behavior (top row) and its consequence on the feeding level (2nd row) and the biomass (3rd row) and the recruitment (bottom row) of the different single-stated species (i.e. species different asymptotic weight – color) when using **dynamic cannibalistic encountered food**, **dynamic resource spectrum** with $w_{cut} = 100$ g and the carrying capacity $2\kappa_r$ and **the cannibalistic predation mortality** with the predation factor $a = 0.0425$.

4.3.1. Cannibalism's influence on the oscillation in the system

There is one more feature in the result, which we have not spoken about. It is the so-called oscillation or the prey-predator cycle. The system can hit an oscillating situation, where the density of the fish begins to increase due to a positive food option. But then the prey spectrum is beginning to shrink as a consequence of too many predators. As the density of the preys is decreased the predators are also decreasing. With the decreasing density of the predators the preys begin to expand again. With the abundance of the resource, the fish begin also to expand again. And the cycle runs again. An stimulated example is illustrated in the recruitment in the figure below (**Figure 4.11**), where showing both cannibalistic state (right) and non-cannibalistic state (left). The non-cannibalistic figure (left) shows that the adaptive behavior does not give advantages only. It has also got a disadvantage. The included adaptive behavior (green) improves very little the biomass but in the other hand the ecosystem gets more sensitive (bigger amplitude in the oscillation) compared the non-adaptive behavior (blue). The cannibalism seems to damp the oscillating effect. We can also interpret the figure as if we have added (green) and removed (blue) the option of the individual to come into the refuge. The removing of a habitat improves the risk to "destabilize" the ecosystem or make it more sensitive. This situation and how we can use this interpretation is discussed in more details in the discussion chapter (**chapter 5**).

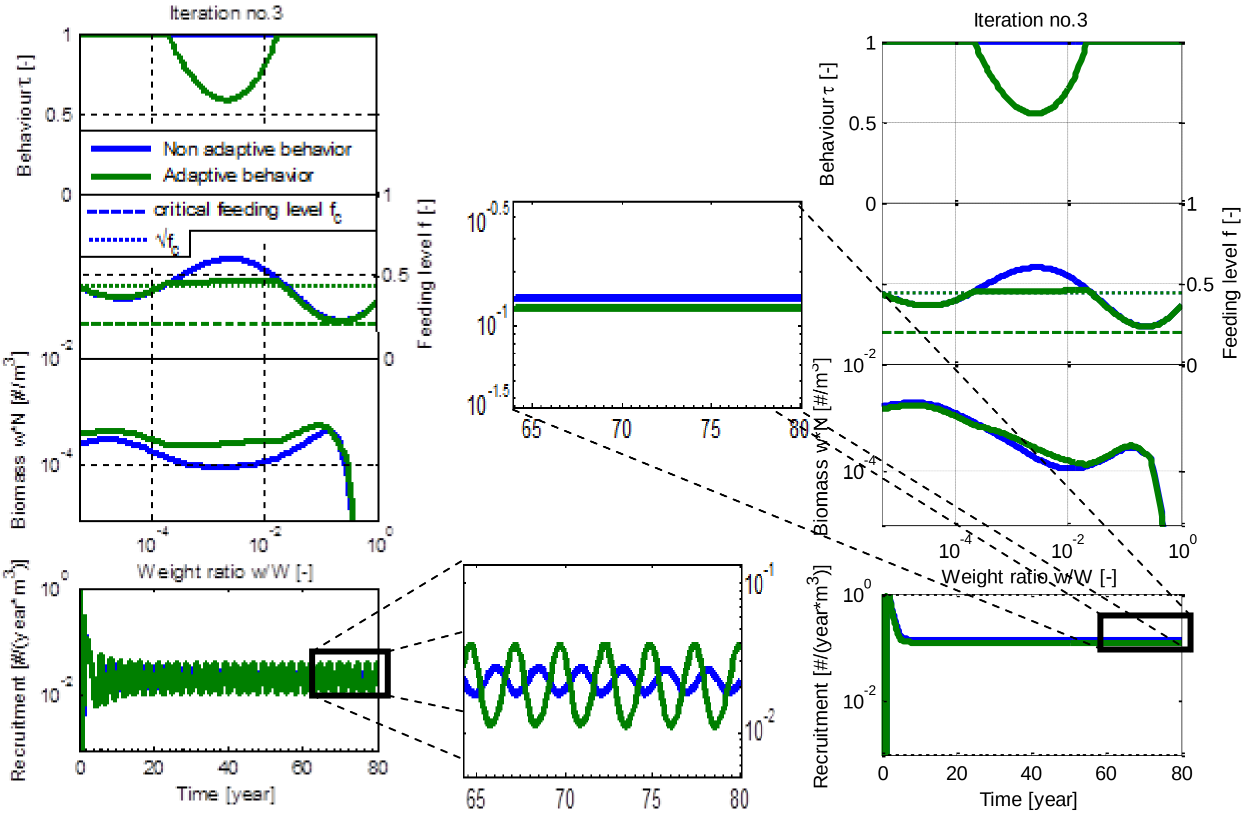


Figure 4.11 **Last time step optimizing** with (green) and without (blue) adaptive behavior (top graph) and its consequence on the feeding level (2nd top graph) and the biomass (3rd top graph) and the recruitment (last graph) of the one single-stated species $W = 100$ g **with cannibalism (right)** and **without cannibalism (left)** when using **dynamic encountered food**, the predation mortality with the factor $a = 0.0425$ and **dynamic resource spectrum** with $w_{cut} = 100$ g and the carrying capacity $2\kappa_r$.

The oscillation becomes very more evident, if the model is run in the non-cannibalistic state, because the non-cannibalistic single-species' food comes only from the resource spectrum. All have to compete for food, the food items running out quickly. The cannibalism allows more flexibility in food resources which is why it is less sensitive for to oscillation. The algorithm of the optimization process uses data from the last time step under the assumption that the system is in steady state at the last time step. Thus the algorithm is very sensitive, if it is in face of oscillations at the last time step.

The oscillation becomes very more evident in the next two figures (**Figure 4.12-13**), when the model is run with an upper bound for the resource spectrum set to a low weight, $w_{cut} = 0.5g$. The low bound puts a greater strain on the density dependence (oscillation), especially the non-cannibalistic species. In the figure we can see that a small change in period deferment of the oscillation generates a large change in the optimal behavior. As long as there is an oscillation in the system we can not be sure that the iteration of behavior will be convergent. Thereby we can conclude that the current optimization process is not excellent/suitable to solve the non-steady state Hamilton-Jacobi-Bellman equation.

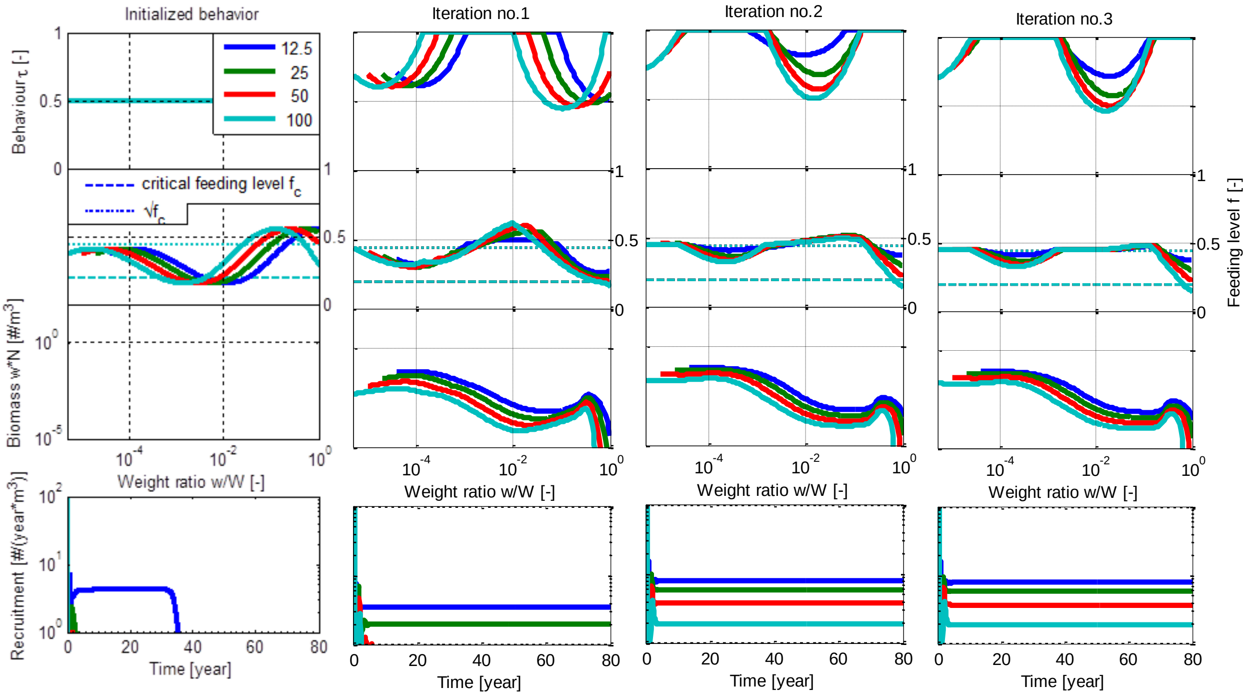


FIGURE 4.12 **Last time step optimizing** iteration of the adaptive behavior (top row), its consequence on the feeding level (2nd row), the biomass (3rd row) and the recruitment (bottom row) of the different single-stated species (i.e. species different asymptotic weight – color) when using **dynamic cannibalistic encountered food** and **dynamic resource spectrum** with $w_{cut} = 0.5$ g and the carrying capacity $2\kappa_r$ and **cannibalistic mortality** with the predation factor $a = 0.0425$.

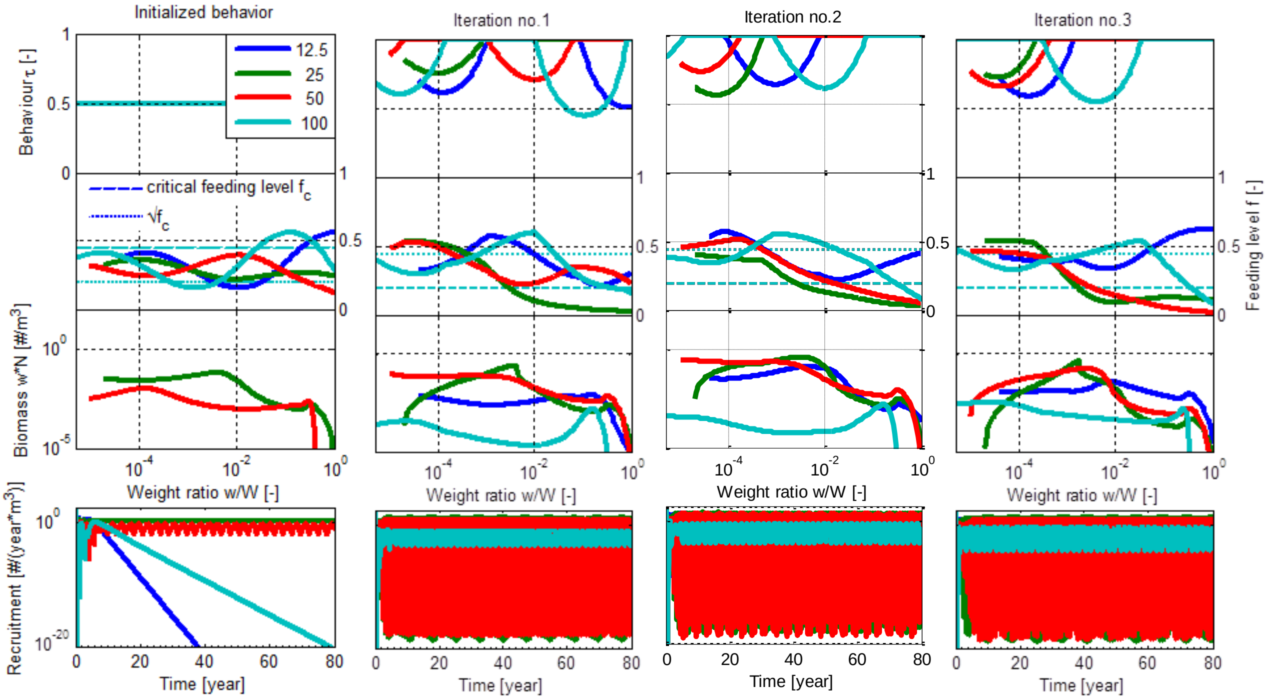


FIGURE 4.13 **Last time step optimizing** iteration of the adaptive behavior (top row), its consequence on the feeding level (2nd row), the biomass (3rd row) and the recruitment (bottom row) of the different single-stated species (i.e. species different asymptotic weight – color) when using **dynamic non-cannibalistic encountered food**, **dynamic resource spectrum** with $w_{cut} = 0.5$ g and the carrying capacity $2\kappa_r$ and **non-cannibalistic mortality** with the predation factor $a = 0.0425$.

4.3.2. A possible solution to the oscillation problem

A possible to solve the oscillating problem is to use the average data of the encountered food in foraging arena E_f and predation mortality in foraging arena μ_f over time, e.g. the last 20 year, instead of use the data at the last time step. The result of using the average technique is that the most of the behaviors seems to be convergent after several numbers of iterations (see **Figure 4.14**). An interesting feature of the figure is that a species with asymptotic weight $W = 50$ g (red line) seems unlike other species to change whole time between the two different optimal stated (the same behavior in iteration no 5, no 7, and other odd number iteration and the same behavior in iteration no 6, no 8 and other even number iteration). But since the most of the optimal behaviors are convergence, we can by the figure temporary conclude that the average technique is a reasonable technique to solve the oscillating problem (It does not mean that the problem is solved, because the system is still in an oscillating stated).

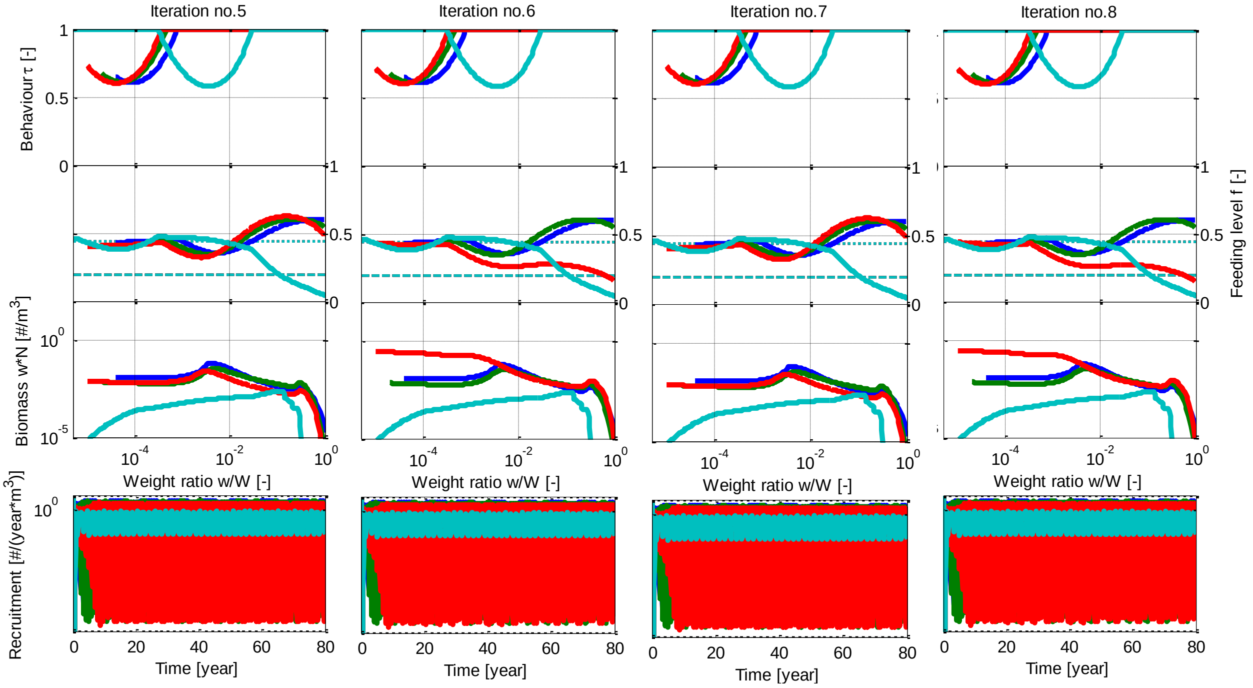


FIGURE 4.14 **Average optimizing** iteration of the adaptive behavior (top row), its consequence on the feeding level (2nd row), the biomass (3rd row) and the recruitment (bottom row) of the different single-stated species (i.e. species different asymptotic weight – color) when using **dynamic non-cannibalistic encountered food**, **dynamic resource spectrum** with $w_{cut} = 0.5$ g and the carrying capacity $2\kappa_r$ and **non-cannibalistic mortality** with the predation factor $a = 0.0425$.

5. Discussion

In this chapter the main results of the work in this thesis are discussed along with suggestions for future research. The discussion is divided into four parts. The first deals with the methods used to find the optimal behavior and which pros and cons they have, while the second part discusses how well the model represents the natural systems and how we can improve the model. The third part and the final part goes into a small discussion about the numerical setup.

5.1. Pros and cons in the method

In the used model the fitness is defined as the reproductive value based upon three key components; growth, mortality and fecundity. The growth function determines how large a part of the available energy should be allocated to the somatic growth, while the fecundity determines the remaining available energy allocated to reproduction. How much available energy the individuals obtain depends on the actual food intake. If the intake is insufficiently to cover the structural maintenance (standard metabolism) then growth and reproduction is halted.
The mortality is defined by the three main sources; the first source is the ageing mortality (also called background mortality) which ensures that the large individuals also dies and depends only on the size of the asymptotic weight; the second source is predation mortality that is determined the individuals choice of behavior, while the third and last source is the starvation mortality. If the starvation mortality as shown in **appendix A.2** is formulated as the available energy inversely proportionality to weight multiplied efficiency (see **chapter 2.12.3**), then the starvation mortality does not played any substantial role in the choice of the optimal behavior.

There is one more key component that also plays an important role in the optimization procedures described above. This fourth key component is the usage of the assumption that the system is in steady state when the optimization procedures start. The assumption results in some drawbacks by the optimization procedures. We have chosen to simplify the model by assuming that the evolutionary dynamics is much slower than the ecosystem dynamics, i.e. the individual is only able to optimize their strategy when the ecosystem dynamic is calmed down. In other words the reproductive value should be independent of time $\partial V/\partial t = 0$ (steady state).

But what will happen if the fish do actually optimize while the population is not in steady state? We have not focused on that in the thesis. There are some cases in this thesis in which the optimized behavior is found using a method and assumption of the system being in steady state, even through the system is in fact non-steady state, e.g. the oscillation in the system occur as shown in the **chapter 4.3**. Therefore it is a deficiency in the discussion on how we can solve the HJB equation in the non-steady state, especially if the oscillating state occurs. Why is it important to find a method that can be used to solve the non-steady problem? In real life no one will just wait to die by not making a change in the optimization of their behavior before the system is in the steady state. When one species know they are going to die out, they get into a desperately situation where they will be willing to do anything in order not to die out, e.g. try to change their behavior. But what about the oscillating state? Does an optimal behavior exists which can solve the stated oscillating system better than the behavior found by the steady state method?

According to the law of conservation the “energy” in the system is preserved, even if the system is oscillating. Just like in steady state. A possible better method which can solve the oscillating stated system better than the current method is an algorithm that can automatically take the average of the oscillating system. We have only done it in manually (**Figure 4.14**), but as you will find in the discussions throughout the next pages there are many aspects of real life environment which is still missing for the models to be complete.

There is one more thing we have to discuss details. As mentioned earlier in a short discussion in the chapter about the method where we raised the question (Sainmont, Andersen, Thygesen, Fiksen, & Visser, 2013), if the fish are assumed to have perfect state information; it is assumed in our model that the fish know the perfect information needed to make the ”life-history” / “myopic” decision. The perfect information exists only in the ideal world. In real life there will always be randomly environments influencing the decision. In a random environment the advantage of accounting for the future declines simply because the future becomes less predictable. In other word we can therefore expect that the ”myopic” strategy improves in random environments while the “life-history” strategy declines in random environments. And we have shown in this thesis that the “myopic” can replace the “life-history” strategy, thus we can expect that the method described in this thesis will work reasonable in the real life.

But the “myopic” strategy has a drawback. If individuals are short of energy, they will in principle be dying, and thus according to the “life-history” it does not matter which behavior they have. But in the “myopic” it does matter, and we can discuss whether the behavior decided in the “myopic” strategy is rational. We have chosen to ignore this aspect in our model by assuming that the fish follows only one strategy, i.e. no “minimized risk” condition in “myopic” strategy. It raises a question: is it really rational of us to ignore the condition? Should we not develop the “life-history” such that it can take the negative energy into account?

5.2. Improvement of the model

Since the model is built up to represent a natural system, we can discuss how well the model actually does that. There is many another factors which can have major effect on the results of the model, e.g. temperature effects on physiological such as metabolic rates and energetic costs of behavior. The metabolic rate is the energy flux required to start chemical reactions in an organism. The higher the temperature, the faster the chemical reactions. The increasing temperature boosts the metabolic rate, hence more ingested energy is required to survive, but the temperature increases also the growth (Gillooly, Charnov, West, Savage, & Brown, 2002). In other words the dynamic in the ecosystem becomes speeds up as the temperature increases.

Temperature in the surface of sea is mainly warmer compared to the bottom of the sea (Dowsett, Robinson, & Foley, 2009). We can speculate that if the growth rate per metabolic rate increases as the temperature is increasing, then the optimal behavior (especially the offspring, since they allocate most of their energy to growth) is to spend more time in the surface of sea (foraging arena). But if the growth rate per metabolic rate decreases as the temperature is increasing, then the optimal behavior is to spend less time in the surface of sea.

The second possible major factor can be the different feeding pattern through life-story. The feeding pattern of the offspring, juveniles and adults are not the same. The offspring eat most of the resource, while the adult eat most the other smaller species and sometimes also own species as adult have a larger tendency to cannibalism compared to offspring and juveniles (Hartvig, 2011).

There is one more trait that could be implemented in the model. It is the so-called the ‘generalist vs. specialist’. The specialization is saying to reduce resource competition (Zablotski, 2013) via niche partitioning. I have not taken the trait into account in the model. The current model has only proven why the behavior is not always the same throughout the whole lifetime of the fish and which great influence the behavior has on the growth, mortality and reproduction (i.e. survival rate and fitness). But what does specialization mean exactly? In short we can define specialization as a trade-off between the improved ability to eat the preferred prey (gain) and reduced ability to eat the less preferred prey (cost) (Zablotski, 2013). The specialists have like generalists some advantages and disadvantages. A specialist may concentrate on find preferred food, it will be able to obtain most of its nutritional requirements, but it may have a hard time finding its favored food. A generalist may be surrounded by many different edible foods, but they may not be that good for the organisms, or it may take a long time to process the food. A conflict of interest therefore exists. Which strategy is the best? The trait is not included in the current model, because it will make the model much more complex than presented here, which we have no time to deal with.

According to articles (Walker, Hill, Kaplan, & McHillan, 2002; Raine & Chittka, 2008) the adults/fast-learning should have an excellent hunting ability to find and kill the preferred prey, while the offspring/slow-learning have poor ability to find and kill the preferred prey. We can speculate that the age-/learning-dependent hunting ability hold also for the pelagic fish.

A second trait could be included too. As mentioned before the search volume factor is very difficult to assess, and we know that many other factors exists which have an influence on the search volume factor. We have made use of the assumption that all individuals in the model are cruising predator, since most of the pelagic species do actually search for food. But in the natural system there exist many other predation techniques, e.g. a sit-and-wait (ambush strategy) predator can have a lower search volume factor, but then also the advantage of a lower metabolism. By this way the different foraging strategy can have an effect on the predation mortality. Thus predation techniques (e.g. ambush, voyage, toxic, fast run and so on) must be implemented as a part of further development of the model.

But not only predation techniques must be implemented. There are also defense techniques like schooling, hiding, toxic-immunity and endurance run. In the current model predation mortality only depends on the predators search volume and not upon the defense strategy of the prey. The defense technique costs for reduced mortality is to increase structural maintenance requirements so that less energy is available for growth, reproduction and activity. Some defense techniques can be useful, but can also be such a serious disadvantage that it increases mortality. Let us now take an example: the shell. The shell protects the turtles against predators, but if the shell is too thick, the turtles will be dived and drowned in the sea due to the shell being too heavy. But all in all the reduced mortality due to a certain defense technique can be implemented by utilizing the so-called food web framework so that predators become more weakly coupled to defense techniques.

There is also a major factor that could be implemented in the model, daily/seasonal environment. The fish eat the zooplankton, and zooplankton is in fact depending on the existence of phytoplankton. In the oceans, annual blooms occur during the early spring in middle to high latitudes, especially in subpolar regions, and daily blooms occur during the early day. In such localities phytoplankton do not flourish during the winter or night because of the short duration and low intensity of sunlight, and because they are preyed upon by grazing zooplankton (Encyclopaedia Britannica Online Academic Edition). It has also been seen that a trade-off exists between feeding at the surface during the winter/night and avoiding the attention of visual predators by migrating to depth during the summer/day and maintaining a sufficient feeding on the phytoplankton during winter/night-time (Sainmont, Andersen, Thygesen, Fiksen, & Visser, 2013). We can implement the daily/seasonal environment by adjusting the search rate such that it is depending on the intensity of sunlight that varies over seasons/days.

When the seasonal environment is included in the model there is so one more possible trait that has to be included in the model and this is the different spawning periods. Most aquatic animals, apart from aquatic mammals, are reproduced through a process of spawning. The process of spawning typically involves females releasing eggs into the water. Egg's survival chance is very depending on the environment, e.g. temperature and predators, which is why most fish have different strategies that can improve the survival chance, e.g. spawn at different times during the year and/or have very different spawning habitats.

The search rate is not the only influence on variation in the sunlight during day or year. Sunlight also influences the temperature of the water. The more sunlight, the warmer the water becomes. The temperature usually has a direct effect on the habitat's internal ecology system, e.g. the coral. When the coral dies out, most of the small fish loses their refuge. Though some large active swimmers like white shark (Goldman, 1997) and tuna (Carey & Lawson, 1973) can hold higher core temperature, most pelagic fish are ectothermic (cold-blooded) allowing their body temperatures only to vary with ambient temperature (Wikipedia, the free encyclopedia, 2013), which means that the temperature can also have a direct physical effect on the fish, e.g. metabolic rates and energetic costs of behavior as mentioned before.

In the natural system there is several species (i.e. different asymptotic weight) that are living together, but our model is only built up as a single-species stated. The model can easy be developed further to the several-species stated. By this way we can uncovered whether the mechanisms behind the adaptive behavior in the single-species state still holds in the several-species state, and whether the conclusion of the mechanism behind the co-existence made by (Pedersen M. , 2006) still holds if the adaptive behavior is included.

The habitats in the model are built in such way that there is no limit of density. You can place infinity many fish in the foraging arena and refuge. In real life there is a constraint on how much can be placed in a given habitat. It will be interest to know how the carrying capacity of a given habitat will change the behavior. Which size of weight has the first priority, i.e. will the offspring or adults be first in line for a place in a favorable habitat? This competition is called interference competition (Andersen, pers. comm.) and can for example occur directly between individuals via aggression. The aggression is expected to increase the mortality among the physically weak species/individuals.

The model is based on the assumption that the most marine fish species of commercial importance are gonochoristic, i.e. their sexes are separate. But the model is also based on the assumption that the reproductive efficiency can be defined as a constant, which can be a serious problem when including the gonochoristic sexual. The efficiency must be dependent on the density. Let's take an extremely example. There are only two individual fish in the earth; the one fish (female) are living in the Atlantic Sea, while the second fish (male) are living in the Pacific Sea. They can only reproduce offspring if they find each other. What is the probability of they will find each other before they die of old age? They have a chance to find each other if their volumetric search rate is large enough, otherwise they have no chance. In other word the reproductive efficiency decreases if they are too few (low density) and increases if they are not too many (high density). If they are too many, there will be no places to offspring, hence the reproductive efficiency is not optimal.

There is also a debatable assumption in the definition of the reproduction. We have assumed in the model that the fish are iteroparous, i.e. they spawn more than once during their lives. But there exists some exceptions to this rule, e.g. Pacific salmonids, capelin, and eels (Murua & Saborido-Rey, 2003). Our model can't really be used to describe these species.

Finally individuals of a given weight size are assumed identical in the model. This is clearly not the case in natural systems since individual differences are present. In short randomly variables should be implemented, e.g. offspring weight must be variables, or a random normal distribution growth curve should be used. No one can give birth to babies at same weight every time, and no one can follow the same growth curve in the real life. Coincidences or the so-called individual diversity are a fundamental principle at the laws of nature. The individual diversity makes the model very realistic but on the other hand also makes it extremely complex.
As mentioned in the first section in this chapter the advantage of accounting for the future declines in a random environment simply because the future becomes less predictable, thus the "myopic" strategy improves in random environments compared to the "life-history" strategy. By included the random variables we can maybe make a detailed investigate about the robustness of the behavior. Assuming a very robust behavior has a very small average reproductive value, while the non-robust behavior has a very high average reproductive value. Which behavior must be chosen?

5.3. Numerical setup

The model here is stimulated by using the semi-implicit upwind scheme. It takes a considerable time to simulate. An implementation in a more computationally efficient programming language can naturally speed up computation further, but an implementation as discussed in the report by (Pedersen M. , 2006) of the QUICK scheme along with the techniques used by (Zijlema, 1996) instead of the semi-implicit upwind scheme can expect to speed up simulations further and reduce the numerical diffusion since fewer grid points and smaller Δt can be used. However it is noted in the report (Pedersen M. , 2006) that numerical diffusion in the semi-implicit upwind scheme was concluded not to play any qualitative role for the results of simulations. My model is built up on this conclusion. If this conclusion is wrong, then the results in my report could be misleading. I have not time enough pick to up the desired competition in order to check whether the conclusion is correct, thus I must assume that the conclusion is correct, hence assume that the results in my report are not misleading.

6. Conclusion

In this thesis we have developed a size-structured model of a marine ecosystem that takes the adaptive behavior into account. The model is simple because we need only one trait, asymptotic weight, to characterize the species. To understand the mechanism behind the adaptive behavior and its influence on the population and avoiding further complicated analysis the model is stimulated only in single-species state. Individuals get food intake from size-dependent predation through a normal-distribution size-selection function, and a background spectrum which is contained by the (zoo)plankton and includes suitable food items for the smallest individuals. The main part of the model is based on the so-called dynamic energetic budget (DEB), which is covered by the bioenergetic model allocating gained energy from food intake into somatic growth, structural maintenance and not least reproduction. The case studied here is a zooplanktivorous forage fish in a water column. We defined the water column as two habitats: a foraging arena in the surface where there is food available but where there is also risk of predation, and a refuge at depth where there is little or no food but also much smaller risk from visual predators. The decision an individual faces is how much time during a day should be spend on the foraging arena. This decision is the adaptive behavior we are trying to study. The model is stimulated in different cases/increasing complicated stages, e.g. fixed and dynamic resource spectrum, fixed and dynamic encountered food, fixed and dynamic mortality, with and without cannibalism. From the food intake and the environment the mortality and reproduction of the individuals are calculated. Note that all parameters used in the model are taken from the literature. All the experiments are made trying to answer the three main questions:

What is the optimal habitat and how does it change during the lifetime of an organism (ontogeny)?

The optimal habitat has been demonstrated in this thesis, where we have chosen to focus primarily on the cases with assumed no predation and no food in the refuge. Thereby it is found that the optimal habitat approaches the feeding level $\sqrt{f_c}$, where f_c is the critical feeding level, as background mortality goes towards zero. The background mortality is assumed constant and independent of the individual's weight but it does depend on species' asymptotic weight. This mortality ensures the largest individuals in the model indeed are occurred of mortality. It is the one of three main sources of mortality. The two others are predation mortality and starvation mortality.

It is shown that if the feeding level is below the critical feeding level some individuals with a given behavior vanish/die (due to insufficient food supply to cover the structural maintenance, they neither grow nor reproduce), but when the feeding level is above $\sqrt{f_c}$, they have most likely too much food depending on the background mortality. If the feeding level is in between $\sqrt{f_c}$ and f_c, then they spent whole of their time in the foraging arena due to insufficient food supply (but enough to cover the structural maintenance then they are still living).

If the predation mortality is identical in both habitats but no identical encountered food, then the optimal behavior is logical to spend all of their time in the habitat which has the most food, i.e. the foraging arena. But if the predation mortality differs in the habitats while they have identical encountered food, then the optimal behavior is logically to spend time in the refuge, because it is the most safely habitats.

The expression of the optimal behavior becomes more complex if the habitats have both different predation mortality and different encountered food. But the analytical expression of the optimal behavior is found. This behavior is the most interesting, because it gives a nice picture of how the behavior changes during the lifetime of an individual. The results presented in this thesis shows that when dynamic encountered food and dynamic predation mortality is included, the juveniles and the adults seem to have the tend to have a feeding level in between $\sqrt{f_c}$ and f_c, hence must spend all their time in the foraging arena, while the juveniles have the optimal feeding level $\sqrt{f_c}$ thus do not need to do so. Naturally the optimal behavior depends on a row of factors such as the size of the stomach, the amount of the encountered food, the predation mortality, background mortality and not least the critical feeding level. We have formulated the starvation mortality being proportional to energy per individual weight which kicks in only when the energy is negative. The calculation shows that the starvation mortality doesn't play any important role in the decision for the optimal behavior.

How can we find the optimal behavior when we have dynamic processes?

The main principle in finding the optimal behavior is to maximize the fitness. We use the reproductive value as a measurable expression of the fitness. When dynamic processes are involved, the theoretical optimal behavior becomes complex, but we can still find the optimal behavior using some simple assumptions, e.g. that the evolutionary dynamics is much slower than the ecosystem dynamics, i.e. the individual is able to optimize their strategy only when the ecosystem dynamic is calmed down. In other words the system should be in steady state before the individuals optimize their behavior. The steady state makes it possible to find the optimal behavior using the "life-history" strategy, which is based on the three key components; the growth, the fecundity and the mortality. We can in principle solve it using dynamic programming, e.g. the numerical upwind scheme method, and solve it backwards (i.e. find first the optimal behavior at the maturation weight and solve it backwards). But the strategy is still too complex, because the "life-history" strategy needs an explicit expression of the slope of the reproductive value. Therefore we need to use one more assumption. The second assumption is the individuals' surplus of ingested energy after losing to the structural maintenance goes direct to the growth and reproduction. By this assumption there is demonstrated that the "life-history" strategy can be replaced by the "myopic" strategy, which makes it easier to find the optimal behavior, because it can be implemented analytical.

How do the fitness and the adaptive behavior change the result?

If the foraging arena is no longer available to the fish, predation decreases (because all the time is now spent in the relatively safe habitat refuge) but starvation is much larger (because the food supply in this habitat is poor). As a result the total mortality may increase. A similar situation holds if the refuge is removed, starvation decreases (because all the time is now spent in the foraging arena) but predation is very much larger (because the safe in this habitat is poor). As a result the total mortality may also increase. We have shown an example where we remove a habitat (refuge) resulting in the higher total mortality. This illustrates an important point about assessing the consequences of the destruction of part of a fish's habitat. An accurate assessment requires knowledge of not just how often a fish uses a given area but also of the role that the area plays in the fish's life history and furthermore of how the fish's behavior will change when an area can no longer be used. Allowing a wide range of options, the two habitats refuge and foraging arena, has resulted in a better living conditions; higher growth, higher reproduction and lower mortality. We have also shown that the option not only has a consequence for the individuals but also has a consequence for whole species. It is a determining factor whether the species will die out or survive, even if the refuge is not used so often as the foraging arena or vice versa. A similar point applies to arguments about welfare: the importance of an activity cannot be determined from how often it is performed (Dawkins, 1990; Houston & McNamara, 1999).

It is shown that the adaptive behavior has improved a bit of the individuals' fitness, and the small improvement is enough to increase the species' recruitment drastically and it can be the crucial factor in whether the species dies out or not. But the adaptive behavior have the disadvantage that it makes the species more sensitive with respect to the prey-predators cycle (bigger amplitude in oscillation), especially if the species is non-cannibalistic. Cannibalism dampens the oscillating effect. Therefore the adaptive behavior has indirectly increased the important role of cannibalism.

To sum it all up, the "myopic" strategy is equally good as the "life-history" strategy to find the optimal behavior if assuming the available energy is allocated direct to growth and fecundity. And the adaptive behavior brings down the feeding level, growth, mortality but in exchange for promoting the recruitment, biomass and survival chance and prevents the species dies out in some cases.

Glossary

Density dependence
The size of a population that is regulated by the size itself, e.g. through food limit.

Gonochorism
Gonochorism describes the state of having only one of the two distinct sexes in any one individual organism and can only reproduce with the opposite sex.

Iteroparity
Individuals that spawn more than once during their lives. They are unlike the semelparity that reproduce once during their lives.

Pelagic fish
Fish that forage in the entire water column. They are unlike the demersal fish, that spend most of their time in the bottom of the sea, and benthic fish that live only on the bottom of the sea.

Plankton
Plankton is a collective term for the mostly small, single-celled organisms - organisms that float freely in the sea. The group includes very small organisms, but on the other hand, there are quite a huge amount of them in the sea. The group is also the lower part of the marine food chain. Zooplankton are protozoa, small crustaceans (e.g. Krill, copepods) and eggs, sperm and larvae of larger animals.

Acronyms

DEB	Dynamical Energy Budget
PDE	Partial Differential Equation
HJB	Hamilton-Jacobi-Bellman equation
FDM	Finite Differential Method
QUICKER	Quadratic Upwind Interpolation for Convective Kinematics

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A. Appendices

A.1. Numerical setup of PDE

Among one of the most commonly and simply numerical methods to solve an inhomogeneous linear advection problem is the upwind scheme. The simplest upwind scheme possible, that can solve our PDE problem, is the first order upwind scheme given by (n is a superscript and not a power):

$$(1 - explicit) \quad \frac{N_i^{n+1} - N_i^n}{t^{n+1} - t^n} + \frac{g_i^n N_i^n - g_{i-1}^n N_{i-1}^n}{w_i - w_{i-1}} = -\mu_i^n N_i^n \quad g_i^n, g_{i-1}^n > 0$$

$$(2 - explicit) \quad \frac{N_i^{n+1} - N_i^n}{t^{n+1} - t^n} + \frac{g_{i+1}^n N_{i+1}^n - g_i^n N_i^n}{w_{i+1} - w_i} = -\mu_i^n N_i^n \quad g_{i+1}^n, g_i^n < 0$$

For simplicity we use the notations $\Delta t^n = t^{n+1} - t^n$ (time step) and $\Delta w_i = w_i - w_{i-1}$ (weight step). In this case a constant time step and a logarithm weight step is used.

The growth function g_i is non-negative in the interval $[w_0, W]$, where $w_i \in [w_0, W]$ for all i, then we implement only (1).

One problem when using the first-order upwind method is that the scheme introduces numerical diffusion in the solution when it is used with very large gradient step length, e.g. in our case very large time step or very small weight step. The numerical diffusion increases the error in the calculation as time runs.

But due to the deadline of the course and the simplicity of the scheme we have to accept to use the scheme. To minimize the numerical diffusion the implicit method is used instead of the explicit method. The upwind scheme is a one-dimensional case of partial differential equation; so it is stable if the following Courant-Friedrichs-Lewy condition is satisfied (LeVeque, 2007; Wikipedia, the free encyclopedia, 2013):

$$\left| g_i^n \frac{\Delta t^n}{\Delta w_i} \right| \leq K_{max}$$

The condition is a necessary condition for ensuring the numerically scheme to converge while solving the PDE. The essence of the criterion is that Δt^n should be small enough not to allow individuals to skip any mass cell w_i during their growth trajectory. The value of K_{max} depends on the method used to solve the discretized equation. An implicit method is usually less sensitive to numerical instability (Hirsch, 1990) compared to an explicit method so larger values of K_{max} can be tolerance, which is perfect when using very small weight step $\Delta w_i \ll 1$. Therefore we used the implicit method:

$$(1 - implicit) \quad \frac{N_i^{n+1} - N_i^n}{\Delta t^n} + \frac{g_i^n N_i^{n+1} - g_{i-1}^n N_{i-1}^{n+1}}{\Delta w_i} = -\mu_i^n N_i^{n+1} \quad g_i^n, g_{i-1}^n > 0$$

We need to solve it at each time step for N^{n+1} so we rearrange:

$$\underbrace{N_{i-1}^{n+1}\left(-\frac{\Delta t^n}{\Delta w_i} g_{i-1}^n\right)}_{\boldsymbol{A}_i} + N_i^{n+1}\underbrace{\left(1 + \Delta t^n \mu_i^n + \frac{\Delta t^n}{\Delta w_i} g_i^n\right)}_{\boldsymbol{B}_i} = \underbrace{N_i^n}_{\boldsymbol{S}_i}$$

Before a matrix can be set up for the whole system, the boundary condition on the left boundary must be specified, i.e. the least existing weighted fish in the system. The left boundary is determined by the number of offspring the fish population can produced at time n. The flow of offspring is called a recruitment flow $R^n = g(w_0)N(w_0)$. The equation for the first grid point is:

$$(1 - implicit - first\ gridpoint) \quad \frac{N_1^{n+1} - N_1^n}{\Delta t^n} + \frac{g_1^n N_1^{n+1} - R^n}{\Delta w_1} = -\mu_1^n N_1^{n+1} \quad g_1^n > 0$$

Reformulating to:

$$N_1^{n+1}\underbrace{\left(1 + \Delta t^n \mu_1^n + \frac{\Delta t^n}{\Delta w_1} g_1^n\right)}_{\boldsymbol{B}_1} = \underbrace{N_1^n + \frac{\Delta t^n}{\Delta w_1} R^n}_{\boldsymbol{S}_1}$$

Now we can then set it up as a matrix:

$$\begin{bmatrix} \boldsymbol{B}_1 & & & & \\ \boldsymbol{A}_2 & \boldsymbol{B}_2 & & & \\ & \boldsymbol{A}_3 & \ddots & & \\ & & \ddots & \boldsymbol{B}_{N-1} & \\ & & & \boldsymbol{A}_N & \boldsymbol{B}_N \end{bmatrix} \begin{bmatrix} \boldsymbol{N}_1^{n+1} \\ \boldsymbol{N}_2^{n+1} \\ \vdots \\ \boldsymbol{N}_{N-1}^{n+1} \\ \boldsymbol{N}_N^{n+1} \end{bmatrix} = \begin{bmatrix} \boldsymbol{S}_1 \\ \boldsymbol{S}_2 \\ \vdots \\ \boldsymbol{S}_{N-1} \\ \boldsymbol{S}_N \end{bmatrix}$$

The dynamic resource spectrum can also be discretized by using the implicit forward difference.

$$\frac{{N_R}_i^{n+1} - N_i^n}{\Delta t^n} = r_0 w_i^{p-1}\left(\kappa_R w_i^{-\lambda} - {N_R}_i^{n+1}\right) - {\mu_{p,f}}_i^n {N_R}_i^{n+1}$$

Again we need to solve it at each time step for N^{n+1} so we rearrange:

$${N_R}_i^{n+1}\underbrace{\left(1 + \Delta t^n\left(r_0 w_i^{p-1} + {\mu_{p,f}}_i^n\right)\right)}_{\boldsymbol{B_R}_i} = \underbrace{{N_R}_i^n + \Delta t^n r_0 \kappa_R w_i^{p-1-\lambda}}_{\boldsymbol{S_R}_i}$$

Set it up as a matrix:

$$\begin{bmatrix} \boldsymbol{B_R}_1 & & & & \\ & \boldsymbol{B_R}_2 & & & \\ & & \ddots & & \\ & & & \boldsymbol{B_R}_{N-1} & \\ & & & & \boldsymbol{B_R}_N \end{bmatrix} \begin{bmatrix} \boldsymbol{N_R}_1^{n+1} \\ \boldsymbol{N_R}_2^{n+1} \\ \vdots \\ \boldsymbol{N_R}_{N-1}^{n+1} \\ \boldsymbol{N_R}_N^{n+1} \end{bmatrix} = \begin{bmatrix} \boldsymbol{S_R}_1 \\ \boldsymbol{S_R}_2 \\ \vdots \\ \boldsymbol{S_R}_{N-1} \\ \boldsymbol{S_R}_N \end{bmatrix}$$

By the matrix equation we can easy find N^{n+1} for resource spectrum at each time step.

A.2. Derivate the optimal behavior for “myopic” strategy

In this section we focus on the local maximum problem in the “myopic” decision based on the formulation:

$$V(w,t) = \max_{\tau(w)\in[0,1]} \left\{ \frac{E_{energy}(w,t)}{\mu(w,t)} \right\}$$

Here it is assumed that all individuals maximize their gain of energy per risk (mortality). The possible solutions for the local maximum problem is:

$$\frac{\partial \left(\frac{E_{energy}(w,t)}{\mu(w,t)} \right)}{\partial \tau(w)} = 0, \qquad \tau(w) \in [0,1]$$

The derivation can expand to

$$\frac{\frac{\partial E_{energy}(w,t)}{\partial \tau(w)} \cdot \mu(w,t) - E_{energy}(w,t) \cdot \frac{\partial \mu(w,t)}{\partial \tau(w)}}{\left(\mu(w,t)\right)^2} = 0$$

Or more simplify

$$\frac{\partial E_{energy}(w,t)}{\partial \tau(w)} \cdot \mu(w,t) - E_{energy}(w,t) \cdot \frac{\partial \mu(w,t)}{\partial \tau(w)} = 0 \quad (\boldsymbol{A.3.1})$$

Expression of the energy in the individuals:

$$E_{energy}(w,t) = E_{cf}(w,t) - E_{meta}(w)$$

where $E_{meta}(w) = k_s w^p$ is the metabolism and E_{cf} is the consumed energy in the individuals.

Expression of the consumed energy in the individuals:

$$E_{cf}(w,t) = \alpha f(w,t) C_{max}(w)$$

Among the functions in the expression of the energy only the feeding level f is dependent on the strategy τ, then the derivate of the gain of energy with respect to τ gives

$$\frac{\partial E_{energy}(w,t)}{\partial \tau(w)} = \alpha \frac{\partial f(w,t)}{\partial \tau(w)} C_{max}(w)$$

Expression of the feeding level:

$$f\big(w,t,\tau(w)\big) = \frac{E(w,t)}{E(w,t) + C_{max}(w)}$$

The derivate of the feeding level with respect to τ is

$$\frac{\partial f(w,t)}{\partial \tau(w)} = \frac{\frac{\partial E(w,t)}{\partial \tau(w)} \cdot \big(E(w,t) + C_{max}(w)\big) - E(w,t) \cdot \frac{\partial\big(E(w,t) + C_{max}(w)\big)}{\partial \tau(w)}}{\big(E(w,t) + C_{max}(w)\big)^2}$$

Expression of the encountered food items:

$$\begin{aligned} E(w,t) &= \tau(w) E_f(w,t) + \big(1 - \tau(w)\big) E_r(w,t) \\ &= \tau(w)\left(E_f(w,t) - E_r(w,t)\right) + E_r(w,t) \end{aligned}$$

By the expression the derivate of the encountered food with respect to τ becomes

$$\frac{\partial E(w,t)}{\partial \tau(w)} = E_f(w,t) - E_r(w,t), \qquad \frac{\partial\big(E(w,t) + C_{max}(w)\big)}{\partial \tau(w)} = E_f(w,t) - E_r(w,t)$$

Now we substitute back.

$$\frac{\partial f(w,t)}{\partial \tau(w)} = \frac{\left(E_f(w,t) - E_r(w,t)\right) \cdot C_{max}(w)}{\left(\tau(w)\left(E_f(w,t) - E_r(w,t)\right) + E_r(w,t) + C_{max}(w)\right)^2}$$

$$\frac{\partial E_{energy}(w,t)}{\partial \tau(w)} = \alpha \frac{\left(E_f(w,t) - E_r(w,t)\right) \cdot \big(C_{max}(w)\big)^2}{\left(\tau(w)\left(E_f(w,t) - E_r(w,t)\right) + E_r(w,t) + C_{max}(w)\right)^2}$$

Expanding expression of the energy in the individuals:

$$E_{energy}(w,t) = \alpha \frac{\tau(w)\left(E_f(w,t) - E_r(w,t)\right) + E_r(w,t)}{\tau(w)\left(E_f(w,t) - E_r(w,t)\right) + E_r(w,t) + C_{max}(w)} C_{max}(w) - E_{meta}(w)$$

Now we change focus to the total mortality

Expression of the encountered food items:

$$\mu(w,t) = \mu_p(w,t) + \mu_s(w,t) + \mu_b(w)$$

The first term is predation mortality, the second the starvation mortality and the last term the background mortality. Among the terms only the background mortality is independent on the strategy τ, then the derivate of the total mortality gives

$$\frac{\partial \mu(w,t)}{\partial \tau(w)} = \frac{\partial \mu_p(w,t)}{\partial \tau(w)} + \frac{\partial \mu_s(w,t)}{\partial \tau(w)}$$

Expression of the predation mortality:

$$\begin{aligned}\mu_p(w,t) &= \tau(w)\mu_{p,f}(w,t) + \big(1-\tau(w)\big)\mu_{p,r}(w,t)\\ &= \tau(w)\left(\mu_{p,f}(w,t) - \mu_{p,r}(w,t)\right) + \mu_{p,r}(w,t)\end{aligned}$$

The derivate of the predation mortality with respect to τ is

$$\frac{\partial \mu_p(w,t)}{\partial \tau(w)} = \mu_{p,f}(w,t) - \mu_{p,r}(w,t)$$

Expression of the starvation mortality:

$$\mu_s(w,t) = \begin{cases} -\dfrac{E_{energy}(w,t)}{\xi w}, & E_{energy}(w,t) < 0 \\ 0, & otherwise \end{cases}$$

The derivate of the starvation mortality gives

$$\frac{\partial \mu_s(w,t)}{\partial \tau(w)} = \begin{cases} -\dfrac{1}{\xi w}\dfrac{\partial E_{energy}(w,t)}{\partial \tau(w)}, & E_{energy}(w,t) < 0 \\ 0, & otherwise \end{cases}$$

Back to

$$\frac{\partial E_{energy}(w,t)}{\partial \tau(w)} \cdot \mu(w,t) - E_{energy}(w,t) \cdot \frac{\partial \mu(w,t)}{\partial \tau(w)} = 0$$

By this equation we expand the expression of the total mortality μ and its derivate $\frac{\partial \mu}{\partial \tau}$

$$\frac{\partial E_{energy}(w,t)}{\partial \tau(w)} \cdot \left(\mu_p(w,t) + \mu_s(w,t) + \mu_b\right) - E_{energy}(w,t) \cdot \left(\frac{\partial \mu_p(w,t)}{\partial \tau(w)} + \frac{\partial \mu_s(w,t)}{\partial \tau(w)}\right) = 0$$

and use the explicit expression of the starvation mortality then we can eliminate the starvation mortality in the total mortality

$$\frac{\partial E_{energy}(w,t)}{\partial \tau(w)} \cdot \left(\mu_p(w,t) + \mu_b\right) - E_{energy}(w,t,\tau) \cdot \frac{\partial \mu_p(w,t)}{\partial \tau(w)} = 0$$

For both positive and negative $E_{energy}\big(w,t,\tau(w)\big)$. From here we expand the equation to the explicit expression:

$$\begin{aligned}&\alpha \frac{\left(E_f(w,t) - E_r(w,t)\right) \cdot \left(C_{max}(w)\right)^2}{\left(\tau(w)\left(E_f(w,t) - E_r(w,t)\right) + E_r(w,t) + C_{max}(w)\right)^2} \cdot \left(\tau(w)\left(\mu_{p,f}(w,t) - \mu_{p,r}(w,t)\right) + \mu_{p,r}(w,t) + \mu_b\right)\\ &\qquad - \left(\alpha \frac{\tau(w)\left(E_f(w,t) - E_r(w,t)\right) + E_r(w,t)}{\tau(w)\left(E_f(w,t) - E_r(w,t)\right) + E_r(w,t) + C_{max}(w)} C_{max}(w) - E_{meta}(w)\right) \cdot \left(\mu_{p,f}(w,t) - \mu_{p,r}(w,t)\right)\\ &\qquad = 0\end{aligned}$$

By dividing α and $\mu_{p,f}(w,t) - \mu_{p,r}(w,t)$

$$\begin{aligned}\frac{\left(E_f(w,t)-E_r(w,t)\right)\cdot\left(C_{max}(w)\right)^2}{\left(\tau(w)\left(E_f(w,t)-E_r(w,t)\right)+E_r(w,t)+C_{max}(w)\right)^2}\cdot\left(\tau_i(w)+\frac{\mu_{p,r}(w,t)+\mu_b}{\mu_{p,f}(w,t)-\mu_{p,r}(w,t)}\right)\\ -\left(\frac{\tau(w)\left(E_f(w,t)-E_r(w,t)\right)+E_r(w,t)}{\tau(w)\left(E_f(w,t)-E_r(w,t)\right)+E_r(w,t)+C_{max}(w)}C_{max}(w)-\frac{E_{meta}(w)}{\alpha}\right)=0\end{aligned}$$

And so let the term $\frac{\tau(w)\left(E_f(w,t)-E_r(w,t)\right)C_{max}(w)}{\tau(w)\left(E_f(w,t)-E_r(w,t)\right)+E_r(w,t)+C_{max}(w)}$ from the last bracket multiplied into the first bracket

$$\begin{aligned}&\frac{\left(E_f(w,t)-E_r(w,t)\right)\cdot C_{max}(w)}{\left(\tau(w)\left(E_f(w,t)-E_r(w,t)\right)+E_r(w,t)+C_{max}(w)\right)^2}\\ &\cdot\left(C_{max}(w)\left(\tau(w)+\frac{\mu_{p,r}(w,t)+\mu_b}{\mu_{p,f}(w,t)-\mu_{p,r}(w,t)}\right)-\tau(w)\left(\tau(w)\left(E_f(w,t)-E_r(w,t)\right)+E_r(w,t)+C_{max}(w)\right)\right)\\ &-\frac{E_r(w,t)C_{max}(w)}{\tau(w)\left(E_f(w,t)-E_r(w,t)\right)+E_r(w,t)+C_{max}(w)}+\frac{E_{meta}(w)}{\alpha}=0\end{aligned}$$

Remove the two terms $C_{max}(w)\tau(w)$ in the first bracket

$$\begin{aligned}&\frac{\left(E_f(w,t)-E_r(w,t)\right)\cdot C_{max}(w)}{\left(\tau(w)\left(E_f(w,t)-E_r(w,t)\right)+E_r(w,t)+C_{max}(w)\right)^2}\\ &\cdot\left(C_{max}(w)\frac{\mu_{p,r}(w,t)+\mu_b}{\mu_{p,f}(w,t)-\mu_{p,r}(w,t)}-\left(\tau(w)\right)^2\left(E_f(w,t)-E_r(w,t)\right)-\tau(w)E_r(w,t)\right)\\ &-\frac{E_r(w,t)C_{max}(w)}{\tau(w)\left(E_f(w,t)-E_r(w,t)\right)+E_r(w,t)+C_{max}(w)}+\frac{E_{meta}(w)}{\alpha}=0\end{aligned}$$

Eliminate the denominators by multiplying all terms with the first denominator $\left(\tau(w)\left(E_f(w,t)-E_r(w,t)\right)+\right.$ $Erw,t+Cmaxw2$ and thereafter dividing by $Cmaxw$

$$\begin{aligned}&\left(E_f(w,t)-E_r(w,t)\right)\left(C_{max}(w)\frac{\mu_{p,r}(w,t)+\mu_b}{\mu_{p,f}(w,t)-\mu_{p,r}(w,t)}-\left(\tau(w)\right)^2\left(E_f(w,t)-E_r(w,t)\right)-\tau(w)E_r(w,t)\right)\\ &-E_r(w,t)\left(\tau(w)\left(E_f(w,t)-E_r(w,t)\right)+E_r(w,t)+C_{max}(w)\right)\\ &+\frac{E_{meta}(w)}{\alpha C_{max}(w)}\left(\tau(w)\left(E_f(w,t)-E_r(w,t)\right)+E_r(w,t)+C_{max}(w)\right)^2=0\end{aligned}$$

By eliminating all brackets we get a simple homogenous second order polynomial equation.

$$A\left(\tau(w)\right)^2+B\tau(w)+C=0$$

with

$$\begin{aligned}A&=\left(f_c(w)-1\right)\left(E_f(w,t)-E_r(w,t)\right)^2\\ B&=2\left(\left(f_c(w)-1\right)E_r(w,t)+f_c(w)C_{max}(w)\right)\left(E_f(w,t)-E_r(w,t)\right)\end{aligned}$$

$$C = \left(f_c(w) - \frac{E_r(w,t)}{E_r(w,t) + C_{max}(w)}\right)\left(E_r(w,t) + C_{max}(w)\right)^2 + \frac{\mu_{p,r}(w,t) + \mu_b}{\mu_{p,f}(w,t) - \mu_{p,r}(w,t)}\left(E_f(w,t) - E_r(w,t)\right)C_{max}(w)$$

where $f_c(w) = \frac{E_{meta}(w)}{\alpha C_{max}(w)}$ is the critical feeding level and the condition to use the second order polynomial equation is $\mu_{p,f} \neq \mu_{p,r}$ due to the last denominator in the term C. We can make use of the logical thinking to conclude that if the predation mortality in both habitats is identical, $\mu_{p,f} = \mu_{p,r}$, then the individuals should choose the habitat which has the largest encountered food, i.e. E_f or E_r. If $E_f > E_r$, then $\tau = 1$. But if $E_f < E_r$, then $\tau = 0$. It does not give any meaning to have two habitats, if the encountered food and the predation mortality is identical in both habitats $E_f = \mu_r$.

$$\tau^*_{\mu_{p,f}=\mu_{p,r}}(w) = \begin{cases} 1, & E_f(w) > E_r(w) \\ 0, & E_f(w) < E_r(w) \end{cases}$$

Back to the homogenous second order polynomial equation, the solution is

$$\tau^*(w) = \frac{-B \pm \sqrt{D}}{2A}$$

where $D = B^2 - 4AC$. The strategy τ must be a real number (between 0 and 1), then the extra condition is $D \geq 0$. Here we can see that the optimal foraging strategy is different from species to species according to their background mortality, predation mortality and encountered food.

The expression $\tau^*(w) = \frac{-B\pm\sqrt{D}}{2A}$ can only be used if $A \neq 0$, i.e. $E_f \neq E_r$ and $f_c \neq 1$. But if $A = 0$, i.e. $E_f = E_r$ or $f_c = 1$, then we have a simple homogenous first order polynomial equation $B\tau(w) + C = 0$, thus the solution is

$$\tau^*(w) = \frac{C}{B}$$

where $B \neq 0$, i.e. $E_f \neq E_r$ and $f_c \neq \frac{E_r}{E_r + C_{max}}$. The solution can be used only if $A = 0$ and $B \neq 0$, which means that the condition becomes $E_f \neq E_r$, $f_c = 1$ and $C_{max} \neq 0$. The stomach is already defined such that it can not be zero, otherwise it will not give a meaning, hence the condition can simplify to $E_f \neq E_r$ and $f_c = 1$.

If $A = 0$ and $B = 0$, i.e. $E_f = E_r$, then there are in principle no solution. But when the amount of encountered food is the identical for the foraging arena and the refuge, the starvation mortality must be the same in the both habitats. Using logical thinking we can conclude that if the amount of the encountered food in both habitats is identical, $E_f = E_r$, then the individuals should choose the habitat which has the smallest predation mortality, i.e. $\mu_{p,f}$ or $\mu_{p,r}$. If $\mu_{p,f} < \mu_{p,r}$, then $\tau = 1$. But if $\mu_{p,f} > \mu_{p,r}$, then $\tau = 0$. It does give not make sense to have two habitats, if both have the same encountered food $E_f = E_r$ and the predation mortality $\mu_{p,f} = \mu_{p,r}$. In short we can say the optimal behavior in this case is

$$\tau^*_{E_f=E_r}(w) = \begin{cases} 1, & \mu_{p,f}(w) < \mu_{p,r}(w) \\ 0, & \mu_{p,f}(w) > \mu_{p,r}(w) \end{cases}$$

Let us assume now no food and no predation in the refuge $E_r = 0$ and $\mu_{p,r} = 0$, then we have

$$\begin{aligned} A &= (f_c(w) - 1)\left(E_f(w,t)\right)^2 \\ B &= 2f_c(w)C_{max}(w)E_f(w,t) \\ C &= \left(f_c(w) + \frac{\mu_b}{\mu_{p,f}(w,t)}\frac{E_f(w,t)}{C_{max}(w)}\right)C_{max}(w)^2 \end{aligned}$$

The optimal behavior in the second order polynomial equation can simplify to

$$\tau^*_{E_r=0,\mu_{p,r}=0,\mu_{p,f}\neq\mu_{p,r},E_f\neq E_r,f_c\neq 1}(w) = \frac{f_c(w) \pm \sqrt{f_c(w) + (1-f_c)\frac{\mu_b}{\mu_{p,f}(w,t)}\frac{E_f(w,t)}{C_{max}(w)}}}{1-f_c(w)} \cdot \frac{C_{max}(w)}{E_f(w,t)}$$

While the optimal behavior in the first order polynomial equation is

$$\tau^*_{E_r=0,\mu_{p,r}=0,\mu_{p,f}\neq\mu_{p,r},E_f\neq E_r,f_c=1}(w) = \frac{1}{2}\left(\frac{C_{max}(w)}{E_f(w,t)} + \frac{\mu_b}{\mu_{p,f}(w,t)}\right)$$

And because the encountered food and predation mortality can’t be negative, we have

$$\tau^*_{E_r=0,\mu_{p,f}=\mu_{p,r},E_f\neq E_r}(w) = 1$$

and

$$\tau^*_{\mu_{p,r}=0,\mu_{p,f}\neq\mu_{p,r},E_f=E_r}(w) = 0$$

The four possible solutions are all under the condition $\tau(w) \in [0,1]$.

A.3. Derivate the optimal behavior if using the "minimized risk" condition

In this section we focus on the local minimum problem in the "minimized risk" strategy based on the formulation:

$$V(w,t) = \min_{\tau(w)\in[0,1]} \{\mu(w,t)\}, \qquad E_{energy}(w,t) < 0$$

where it is assumed that all individuals have negative available energy E_{energy}, thus neither grow or reproduce. They try then to minimize the risk (mortality). The possible solution for the local minimum problem can be founded by solve the equation

$$\frac{\partial \mu(w,t)}{\partial \tau(w)} = 0$$

The expression of the total mortality is

Expression of the encountered food items:

$$\mu(w,t) = \mu_p(w,t) + \mu_s(w,t) + \mu_b$$

The first term is predation mortality, the second the starvation mortality and the last term the background mortality. Among the terms only the background mortality is independent on the strategy τ, then the derivate of the total mortality gives

$$\frac{\partial \mu(w,t)}{\partial \tau(w)} = \frac{\partial \mu_p(w,t)}{\partial \tau(w)} + \frac{\partial \mu_s(w,t)}{\partial \tau(w)}$$

By using the same method in the previous section we obtain

$$\frac{\partial \mu(w,t)}{\partial \tau(w)} = \mu_{p,f}(w,t) - \mu_{p,r}(w,t) - \frac{1}{\xi w}\frac{\partial E_{energy}(w,t)}{\partial \tau(w)}$$

where $\mu_{p,f}$ and $\mu_{p,r}$ are the predation mortality in the foraging arena and the refuge respectively and ξ is the starvation mortality factor.

$$\frac{\partial E_{energy}(w,t)}{\partial \tau(w)} = \alpha \frac{\left(E_f(w,t) - E_r(w,t)\right)\cdot\left(C_{max}(w)\right)^2}{\left(\tau(w)\left(E_f(w,t) - E_r(w,t)\right) + E_r(w,t) + C_{max}(w)\right)^2}$$

where E_f and E_r are the encountered food in the foraging arena and the refuge respectively and C_{max} is the size of individuals' stomach.

Thus the optimal behavior τ^* in the equation

$$\frac{\partial \mu(w,t,\tau)}{\partial \tau(w)} = \mu_{p,f}(w,t) - \mu_{p,r}(w,t) - \frac{\alpha}{\xi w}\frac{\left(E_f(w,t) - E_r(w,t)\right)\cdot\left(C_{max}(w)\right)^2}{\left(\tau^*(w)\left(E_f(w,t) - E_r(w,t)\right) + E_r(w,t) + C_{max}(w)\right)^2} = 0$$

is isolated to the expression

$$\tau^*_{f\leq f_c, E_f \neq E_r, \mu_{p,f} \neq \mu_{p,r}}(w) = \frac{C_{max}(w)\left(-1 \pm \sqrt{\frac{\alpha}{\xi w} \cdot \frac{E_f(w,t) - E_r(w,t)}{\mu_{p,f}(w,t) - \mu_{p,r}(w,t)}}\right) - E_r(w,t)}{E_f(w,t) - E_r(w,t)}$$

under the condition $E_f \neq E_r$ and $\mu_{p,f} \neq \mu_{p,r}$.

If $\mu_{p,f} = \mu_{p,r}$ or $E_f = E_r$, we can't isolate the optimal behavior. It is a serious drawback by the "minimized risk" strategy.

If no food and no predation is assumed in the refuge $E_r = 0$ and $\mu_{p,r} = 0$, then the optimal behavior is

$$\tau^*_{f\leq f_c, E_r=0, \mu_{p,r}=0, E_f \neq E_r, \mu_{p,f} \neq \mu_{p,r}}(w) = \frac{C_{max}(w)}{E_f(w,t)}\left(-1 \pm \sqrt{\frac{\alpha}{\xi w} \cdot \frac{E_f(w,t)}{\mu_{p,f}(w,t)}}\right)$$

The square root term is always positive due to all variables and parameters in the term are positive. The same holds for the fraction beyond the brackets. The consequence by these properties for the optimal behavior under the condition $\tau \in [0,1]$ is that it is simplified to

$$\tau^*_{f\leq f_c, E_r=0, \mu_{p,r}=0, E_f \neq E_r, \mu_{p,f} \neq \mu_{p,r}}(w) = \frac{C_{max}(w)}{E_f(w,t)}\left(-1 + \sqrt{\frac{\alpha}{\xi w} \cdot \frac{E_f(w,t)}{\mu_{p,f}(w,t)}}\right)$$

A.4. MATLAB code

The MATLAB code of the stimulation made in this thesis is saved in the zip-file. Run a file named "main_test" and choose a number. The number is used to tell MATLAB which stimulated figure in this report you want to look. The file is used to plot the figures 4.5-4.14.

A.1. MAPLE code

The MAPLE code of the stimulation made in this thesis is saved in the zip-file. Run a file named "analytic tau". The file is used to illustrate the figures 4.1-4.4.