Tuning the Diet of North-East Arctic Cod in the Barents Sea – An Exploration with the end-to-end Model ATLANTIS

Anne Jähkel

Thesis submitted for the degree Master of Science (M. Sc.)

Joint Nordic Master Programme in Marine Ecosystems and Climate
Specialization in Physical Oceanography

Spring 2013

Tuning the Diet of North-East Arctic Cod in the Barents Sea – An Exploration with the end-to-end Model ATLANTIS

Anne Jähkel

In Coorperation with the Institute of Marine Research (IMR)

Submitted to the University of Bergen

Advisors:
Ken Drinkwater, Cecilie Hansen, Mette Skern-Mauritzen

Formal Contact:
Svein Sundby

Abstract

This thesis explores the feeding relationships of Atlantic cod (*Gadus morhua*) on its major prey species within the Barents Sea using the newly developed Atlantis model for the region. Atlantis is an end-to-end model designed to explore the response of the ecosystem under different biological, environmental and fisheries scenarios. However, before one can develop such scenarios, the model needs to be tuned through a diet matrix that should reflect the observed diets of the major species in the system. Generating a realistic diet composition is achieved by adjusting indices linked to the strength of the predation for each prey species. The major work carried out within the thesis has been on the tuning of the cod diet. Five different model runs with different diet indices are presented and evaluated by comparing the results with the cod diet documented in the joint Russian-Norwegian (PINRO-IMR) stomach content database. Emphasis in the thesis was placed upon the prey species, capelin (*Mallotus villosus*) and polar cod (*Boreogadus saida*). A diet matrix was achieved that was able to reproduce, within an order of magnitude, the natural consumption with regards to relative amounts in terms of number of individuals and biomass of the different prey species. Higher predation pressure was found to reduce prey abundance as expected, and a negative correlation was found between cod and capelin, and also with polar cod but the relationship was much weaker than for capelin. The abundance of polar cod correlated with the amount of capelin consumed, i.e. high predation of cod on capelin results in increasing polar cod abundance. Individual weight of cod was observed to decline when there was high abundance of cod suggesting evidence of density dependent processes. Although the relative rankings of prey species consumed based on numbers of individuals and biomass generally matched the database, the absolute values did not with the model underestimating the total consumption. Suggestions for improvements in the tuning process are provided such as tuning more parameters, for example, growth and consumption rates and resolving temporal as well as geographic distributions to better determine the overlap between predators and prey. Finally, possible future research using the Atlantis model is presented.

Acknowledgements

I wish to deeply thank Ken Drinkwater, Cecilie Hansen, and Mette Skern-Mauritzen. Their guidance helped me to sharpen my scientific skills in all possible directions. I very much appreciate offering the chance to work with them and establishing a thesis within the Atlantis project, even though back in December 2011 Ken had a completely different idea of the topic when we first met and suggested to carefully consider chosing the “Atlantis” thesis. For all the encouragement, the vitally critical ideas, and the sharing of his knowledge, I would like to thank Ken. I hereby also would like to thank Svein Sundby for introducing me to Ken. For endless hours of “quizzing” at any(!) time, I sincerely thank Cecilie, who made it possible to get Atlantis running and staying on the right track, even if there were ten more runs to do in no time or a capelin was once again weighing the same as a seal. Thanks for keeping the enormously good mood and patience during all the time. Whenever there was no clear structure of the work left and confusion arouse with obscure output of the model, Mette was at hand with precise thoughts and suggestions on how to proceed. Thanks, Mette! I thank Rasmus Skern for “transfer services”. I would also like to thank several people at the Geophysical Institute and IMR for inspiring conversation and help with databases. Thanks to Corinna Schrum, Svein Sundby, Harald Gjøsæter, Daniel Howell, Bjarte Bogstad, Sigurd Tjelmeland, Geir Odd Johansen, and not least Jan Erik Stiansen. Kudos, my dear referees Jana and Tom! I thank Per Eide for sharing the wonderful picture on my front page. However, credit goes even back further, to Jonas Blühtgen Sølvsteen encouraging my application to the MARECLIM programme. I would like to thank all my fellow MARECLIM student Balamuralli, who shared the feelings of the last months and minutes (we still need to have that ice cream!), but of course also Martin, Karstein, Maria, Rocío, Elise, and Camilla! Thanks for the good times we have had together (and are going to have). And I am ineffably grateful for the care of my parents, Stine, and Theo – for always being with me even though being thousands of kilometers aways. Without your life savers I could have never survived throughout these two years! I also would like to send my thanks to the rest of my family and friends that accompanied me all along and supplying me with postcards from all over the world! Dear “Alrek” crew: ... thanks for all the fish!

Bergen, June 3, 2013
Anne Jähkel

Contents

List of Figures

Front Page: Photo, kind permission of Per Eide

List of Tables

1 – Introduction

1.1 Statement of Purpose

The end-to-end model Atlantis has been applied successfully to several ecosystems, both in terms of capturing natural processes and simulating their interactions with fisheries (Fulton, 2010; Fulton *et al.*, 2011). The management advice in relation to the model results has been suggested to enhance stabilization of these ecosystems under a beneficial fishery (Horne *et al.*, 2010; Brand *et al.*, 2007; Fulton *et al.*, 2007).

The Barents Sea ecosystem is of high interest for research on ecological and economic aspects (Gjøsæter, 1995; Olsen *et al.*, 2007; Jakobsen & Ozhigin, 2011). The biogeographic boundary of the boreal and Arctic regime traversing this arctic shelf sea provides a profound basis for research with respect to possible impacts on the system under changing climate conditions. As a consequence, the necessity for a comprehensive management of the fish stocks follows (Howell & Bogstad, 2010). The Atlantis model could broaden the long-term analysis of the Barents Sea area through exploring ecosystem and fisheries scenarios under changing climate and fishing intensities, either separately or in combination.

At present, several models explore the trophic interactions or the impact of fisheries on different species in the Barents Sea and the Nordic Seas. These comprise more physically-based models including lower trophic levels, such as the NORWegian ECOlogical Model (NORWECOM, Skogen *et al.* (1995)), species specific approaches to an individual based modeling (IBM, Huse *et al.* (2004)), and several multi-species modeling approaches. One example of the latter includes interactions of capelin and cod, which has been applied to the management of the capelin stock since 1998 (Gjøsæter *et al.*, 2002). Trophic interactions between different fish stocks and marine mammals with addition of the human dimension were resolved in the ECOPATH with ECOSIM model, which was intended to capture the ecosystem and also assists in fisheries management (Blanchard *et al.*, 2002; Lindstrøm *et al.*, 2009). However, in Plagányi (2007) the GADGET model showed the greatest potential of contribution to practical fisheries management advice to date. Such a model has been applied to the Barents Sea by Howell & Bogstad (2010), successfully producing historical stock dynamics and testing different harvesting and environmental scenarios. Notwithstanding, the model requires only parts of the ecosystem.

This study is part of a diverse project that for the first time after the development of the model aims at implementing Atlantis for a high-latitude Northern Hemisphere ecosystem. Special features regarding sea ice or large seasonal variation in light conditions shape the challenges of the approach. Calibrating the model to an initial state that is comparable with historical record constitutes the first step towards a functioning model. This covers consideration for all trophic levels of the ecosystem, from phytoplankton to polar bears. In accordance to the determinism that is involved, the importance of tuning the model cannot be denied.

Major attention for implementing the ecological characteristics of the ecosystem within the model is given to the trophic interactions. Realistic feeding relationships (who eats whom and how much) are needed to capture the ecosystem dynamics within Atlantis. Abiotic factors such as the nutrient supply to the lower trophic levels determine the production levels for the food web, however the Barents Sea capelin and Northeast Arctic cod strongly determine the structure of the ecosystem as the dominant fish populations in the region. Their pivotal roles in the Barents Sea ecosystem have been reviewed in previous research, e.g. Hjermann *et al.* (2010); Dolgov (2009); Wassmann *et al.* (2006). Cod is one of the top predators of the system, while capelin, which control the energy transfer from the lower to the higher trophic levels as they feed on phytoplankton, are the major prey for many fish, seabirds, and even some marine mammals (Gjøsæter & Båmstedt, 1998; Carscadden & Vilhjálmsson, 2002). Additionally, polar cod is included in this study for reasons of its position in the food web predominantly in the colder northern region of the Barents Sea (Orlova *et al.*, 2009). Under future climate conditions the overlap of polar cod, capelin, and cod is of large interest for their feeding relations. A shift in the distribution of the species northwards may change the composition of the cod diet.

Cod is omnivorous. Therefore, the prey field includes most of the other important species in the Barents Sea, but capelin is the major component. Intensive tuning of the cod diet is justified, for example because it determines a broad range of trophic interactions. Special focus on the examination of the prey species capelin, as well as polar cod, defines the scope for this study. Thereby, the inclusion of the most important species interactions and those species with the most complete datasets are ensured.

One approach to tune the species interactions within Atlantis is through the diet matrix. Here the strength of the predator-prey linkage is parameterized. The joint PINRO-IMR stomach content database for cod (Mehl & Sunnanå, 1991; Mehl & Yaragina, 1992; ICES, 2012a) with record since 1984 have been used as the major diet reference for this thesis. At present, the Atlantis model for the Barents Sea is still under development. Therefore, one fixed version of the code and the parameterization was considered throughout the thesis to secure comparability of the results.

The aim of this thesis is to establish a diet matrix for cod within the current model that is realistic with regard to representing the historical consumption data. The tuning will consider all species resolved in the stomach database. However, it will exclusively utilize information that was averaged for the entire cod population. For the approach in this thesis no age specific tuning of the diet is undertaken. Major focus will be given to capelin and polar cod in the analysis to examine whether Atlantis, at this stage, can capture natural characteristics of the predator-prey interactions. The exploration of the required changes to achieve the desired predation by cod will help to understand the sensitivity of the model to diet matrix tuning. Not least, the study provides information on the appropriateness of this tuning exercise in the light of application to other species and future diet tuning.

The rest of this chapter covers background information on the Barents Sea oceanography, ecosystem, and fisheries. The Atlantis model is presented within the second chapter, including a description on the parameterization of three investigated fish species (capelin, cod, and polar cod) followed by the methods for tuning the cod diet. Chapter 3 presents the results of all model runs starting with the initial set-up, the comparison of the tuning runs, analysis of the cod-capelin-polar cod interactions in the model, as well as additional information from early runs from the tuning work not fully presented in the thesis. The combination of model results and survey data is presented in the discussion (Chapter 4) along with ideas for improving the tuning procedure and potential future research. A summary of the conclusions is given in Chapter 5.

1.2 The Barents Sea

1.2.1 Oceanography and Climate

Adjacent to the Arctic Ocean in the north and the Northern Atlantic in the southwest, the Barents Sea is an important flow-through area of the large-scale current system between the Arctic and subarctic (Wassmann *et al.*, 2006). Off the northern coast of Norway and Russia (Fig. 1.1), this shelf sea extends to 80°N and is enclosed by Spitsbergen, and Franz Josef Land in the north, and Novaya Zemlya in the east (Loeng & Drinkwater, 2007). As the largest of the pan-arctic shelf seas covering 1.6 x 10^6 km^2 (Ozhigin *et al.*, 2011) the Barents Sea is 230 m deep on average, with a maximum depth of about 500 m (Hunt *et al.*, 2012). The area is divided into two major regimes based upon the dominating water masses: a southern Atlantic, i.e. boreal (Ekman, 1953), and a northern Arctic regime. In the study by Loeng (1991) the water masses generally are characterized as the high-salinity (> 35), warm (3.5 – 6.5°C) Atlantic water (AW) and the low-salinity (34.4 – 34.8), cold (< 0°C) Arctic water (ArW). The third major water mass is defined by the inflowing Norwegian Coastal Current (NCC). Coastal water varies seasonally as well as interannually in temperature (similar to AW) and salinity (average < 34.7). The latter depends on, for example, the freshwater runoff from the large rivers (Sætre, 2007).

Atmospherically, an Arctic high pressure system dominates in winter resulting in cold climate and up to 60% of the Barents Sea covered with ice (Loeng, 1979). However, the southwestern area is permanently ice free. In summer, the Arctic low pressure system causes

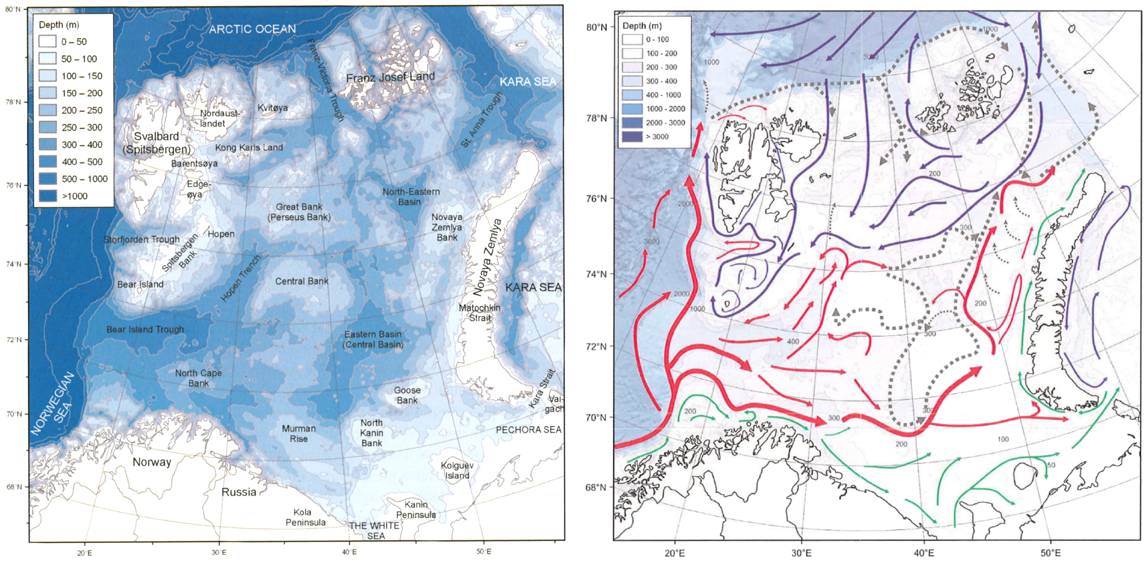


Figure 1.1: The Barents Sea: Bathymetry (left) and current system of the shelf sea (right). Arrows indicate: red – warm Atlantic Waters (AW), blue – cold Arctic Waters (ArW), blue dotted – sub-surface flow, and green – Coastal Waters. Maps from Ozhigin *et al.* (2011).

warmer climate. From the 1970s on, but most obvious during the last 20 years, the Atlantic inflow for the Barents Sea has increased (Skagseth *et al.*, 2008; Carmack *et al.*, 2006). As a consequence thereof, the sea-ice cover has reduced with a new measured record minimum in September 2012 (Zhang *et al.*, 2013). This involves a more dominant boreal ocean climate. Some authors suggest that the Barents Sea system has undergone an "Atlantification" (Wassmann *et al.*, 2004). Likewise, ACIA (2005) and IPCC (2007) state that temperatures increased constantly over the last 50 years for the Arctic, on average 2 – 3°C. The long-term temperature record of the Kola section has been used in several studies to show the negative correlation of temperature and ice edge location (Vinje, 2001). The prognostication of an ice-free Arctic in summer before the middle of this century has been suggested by Wang & Overland (2009), notwithstanding the possibility of cooling until 2030 as suggested by Klyashtorin & Lyubushin (2007) owing to multi-decadal oscillation patterns.

1.2.2 Ecosystem

The structure of the Barents Sea ecosystem is described by Wassmann *et al.* (2006) and if hereafter not cited separately, information refers to this article.

One third of the primary production (PP) in the entire arctic region occurs in the Barents Sea alone. The overall PP principally depends on the strength of the Atlantic water inflow. Furthermore, interannual variations in PP are also tied to changes in solar radiation impacting day length, air temperature, and sea-ice cover. The so called ice-edge effect describes how the retreating marginal ice zone (MIZ) in spring facilitates an early stratified ocean and provides a productive euphotic zone (Sakshaug & Skjoldal, 1989). Almost 50% of the PP occurs in this period until late April, building up an enormous food source for zooplankton. Particularly in the MIZ, the benthic-pelagic coupling is effective and an efficient microbial loop is likewise coupled to the grazing food web. The energy transfer via high fatty acids from lower to the top trophic levels (fish, mammals) happens between May and July through the herbivorous zooplankton, e.g. copepods and krill. This maximum in plankton production is followed by a peak in stock biomass of the carnivores in August and September.

A large variety of phytoplankton species fuels the basis of the food chain in the Barents Sea ecosystem. More than 200 species have been identified, though the most abundant are diatoms, dino- and silicoflagellates, coccolithophorides, monads, and ice algae. The benthic community benefits from the high PP export through sinking, especially if zooplankton grazing is low because of a mismatch in time with the bloom. The strong benthic-pelagic coupling guarantees a highly efficient recycling chain in the Barents Sea. Amphipods and especially copepods dominate the zooplankton community and both krill and shrimp are further main contributors at this trophic level. In addition to the *in situ* plankton, copepods are advected into the Barents Sea both from the Norwegian Sea and the Arctic Ocean. The *Calanus* genus serves as substantial prey for many of the more than 200 fish species in the Barents Sea (Stiansen & Fillin, 2006).

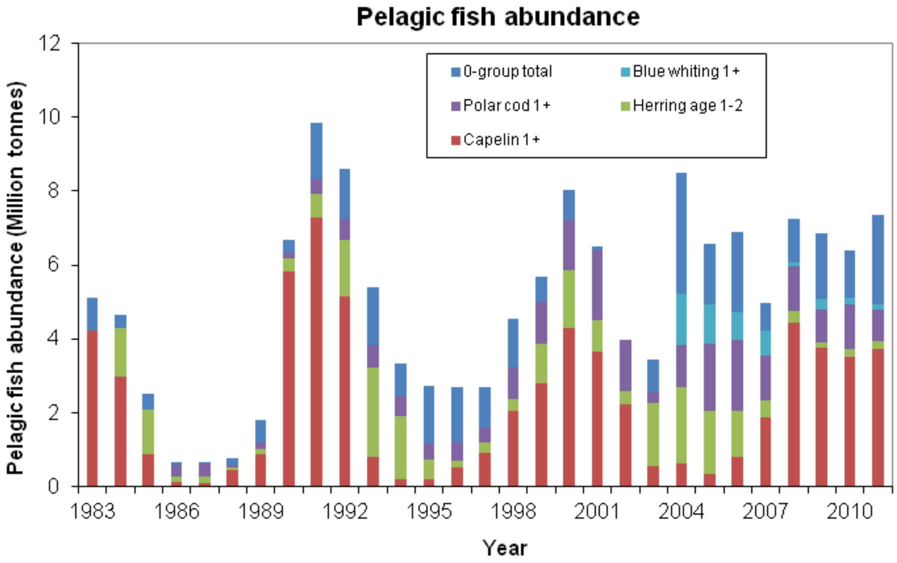


Figure 1.2: Biomass of pelagic fish stock in Barents Sea between 1983 and 2011. From ICES (2012a).

The Barents Sea capelin is recognized as the keystone species of the system (Hjermann *et al.*, 2010). This capelin stock is the largest in the world (ICES, 2012a). From the 1980s on, three major collapses of the capelin stock profoundly influenced the ecosystem, both top-down and bottom-up effects (Howell & Bogstad, 2010; Gjøsæter *et al.*, 2009; Tjelmeland & Bogstad, 1998). Besides capelin, the Norwegian spring-spawning herring and polar cod are the most abundant pelagics in the Barents Sea. The herring are not permanent residents in the Barents Sea, but the immature individuals spend 3 – 4 years within these nursery grounds (compared to only 1 – 2 years in the Norwegian fjords). Furthermore, fish of the *Sebastes* genus and blue whiting (first recorded in 2003) are important for the pelagic system (Dolgov *et al.*, 2010). The historical record of the stock biomass for these species shows that polar cod increased, especially after 2000 (Fig. 1.2). The figure also includes the 0-group fish, since the Barents Sea is an important nursery area for many species. The juveniles constitute a significant and increasing part of the pelagic biomass.

In addition to nutrients and zooplankton, fish larvae enter the Barents Sea with the AW inflow (Ingvaldsen *et al.*, 2004). This advection of larvae and young juveniles can result in the 0-group fish overlapping with predators, which in some years causes recruitment failure (Eriksen *et al.*, 2009). Climatic conditions can also lead to variability in fish populations, e.g. Stenseth *et al.* (2002), and in combination with the close feeding relationships, reviewed in Bogstad *et al.* (2000), greatly influence the structure of the ecosystem.

The top predators are Northeast Arctic cod, harp seal, and minke whale. Bogstad *et al.* (2000) compared the consumption-biomass ratios, hence the relative consumption for the different species in the Barents Sea. The relative consumption by cod equaled those for harp seals and minke whales combined. This is also true for the sum of relative consumption by all other piscivore fish in the Barents Sea. Therefore, cod is considered the top predator in the Barents Sea.

The marine mammal community in the Barents Sea includes the all-year residents harp, ringed, and bearded seals, and the baleen whales, humpback, minke, and fin whale, which are summer residents. Polar bears, as well as numerous colonies of sea birds, complete the Barents Sea food web. Common bird species are guillimots (common and Brünnich's), Little Auk, as well as black-legged kittiwake, and the puffin (Gjøsæter *et al.*, 2009).

Top Predator – Northeast Arctic Cod Dolgov (2009) suggested the outstanding position of the Atlantic cod (*Gadus morhua*, Linnaeus, 1758) as the dominant predator in the Barents Sea ecosystem as a cause of its stock recovery compared to cod stocks in other regions of the North Atlantic Ocean. Widely distributed in the Barents Sea, especially during feeding in summer, the major concentrations of cod are around the area of Svalbard and the southeast, off the coast of Novaya Zemlya. Earlier, the cod was also abundant near the

Polar Front (PF). However recently, most cod are found in the northeast Barents Sea up to 82°30' N, which is a a record high northern limit of occurrence (Eriksen, 2012). The northward shift of the entire life cycle distribution of the stock (spawning, nursery, feeding grounds) is associated with a temperature increase during the last decades (Drinkwater, 2005; Sundby & Nakken, 2008). Additionally, the former authors state generally higher growth of the cod in warm years and the ACIA (2005) indicates mortality declines with higher AW inflow (warmer ocean temperatures).

The temperature tolerance of cod covers -0.5 to 10°C (pers. comm. Bj. Bogstad), which is a remarkable range that partly explains the wide cod distribution. Vertically in the water column this relates to depths of 100 – 400 m where about 80% of the population are found (Eriksen, 2012). The maximum age reached by cod is 30 years. Likewise, with regards to the size (up to 169 cm) and weight (up to 55 kg) cod easily defends its top position besides mammals in the ecosystem (Wienerroither *et al.*, 2011). The diet of cod consists of zooplankton, crustaceans, and fish.

Spawning season of the cod starts in February. Therefore, in the first three months of the year the mature individuals (maturity at age 8 – 10) migrate out of the Barents Sea southwards to the spawning grounds. These lie along the Norwegian Coast mainly between 67°30' and 70°N, especially in the Lofoten region (Nakken, 2008; ICES, 2012a).

Keystone species – Barents Sea Capelin The planktivore Barents Sea capelin (*Mallotus villosus*, Müller 1776) reach a (rare) maximum length of 20 cm at oldest ages (Wienerroither *et al.*, 2011). Lipid-rich krill is a major, in some years up to 100%, food source for larger capelin, but the general diet consists of copepods, mostly *C. finmarchicus* and seasonally *C. hyperboreus*. Capelin is opportunistic, but selects prey in relation to size and maturity, i.e. larger capelin eat larger/mature individual zooplankton (Gjøsæter, 2009).

The major feeding area during summer is the northern Barents Sea along the highly productive zones, the MIZ (Wienerroither *et al.*, 2011). The PF, as has been shown recently, is thought to be of less importance as a feeding area because of PP except during the spring bloom (Erga *et al.*, 2012 (in press). In response to warmer temperatures (Stenevik & Sundby, 2007) and the declining ice-cover, capelin have migrated even farther north than 80°N and an arctic amphipod, *Themisto libellula*, becomes more important as a diet component (Eriksen, 2012). During overwintering in the southern areas only larger individuals continue feeding (Gjøsæter, 2009).

Maturity of capelin depends on length rather than age and is reached at ca. 14 cm, typically no later than three years of age(Gjøsæter & Båmstedt, 1998). Capelin is a short-lived species reaching scarcely more than five years of age since capelin are semelparous.

This partly explains the strong fluctuations of the stock size. Moreover, the fluctuations relate to the coupling of the capelin life history to physical as well as predation factors.

The spawning season typically starts in early March and lasts for 2 – 3 weeks (Aglen *et al.*, 2012). Nevertheless, capelin may spawn between March and September in accordance with their fitness. Also, the migrational pattern determines the spawning time, e.g. individuals that arrive the spawning grounds off the northern Norwegian coast from the east spawn last (Sakshaug *et al.*, 2009). Depending on whether the eggs are spawned more easterly or westerly, larvae drift either to the central Barents or to the Svalbard archipelago. Because of higher temperatures and larger amounts of food, western capelin generally were better-off than their eastern relatives as shown from otolith analyses (Sakshaug *et al.*, 2009).

Pelagic Competitor of Capelin – Polar Cod Polar cod (*Boreogadus saida*, Günther 1862) is the most abundant fish in the Arctic and assumed to comprise two populations in the Barents Sea, a southeastern one off the Russian coast and a northwestern Svalbard group (Nakken, 2008). In cold years, both populations overlap spatially and form a continuous distribution over the entire Barents Sea area, mainly north of the PF. Polar cod is pelagic for the adult stages but also strongly connected to the ice (sympagic), especially for spawning and during early life stages. This bears a significant difference to the large Northeast Arctic cod. Because of antifreeze glycopeptides and the aglomerular kidneys, polar cod may encounter waters near the freezing point of sea water at about -1.9°C (Devries, 1982; Christiansen *et al.*, 1996). Moreover, the polar cod is small with an average adult size of only 30 cm in length (Craig *et al.*, 1981; Eriksen, 2012).

Similar to capelin and other pelagics, polar cod migrates north for feeding with the ice retreat in spring. Moreover, they have been known to migrate out of the Barents Sea. Until the end of summer, polar cod stay in cold waters at a depth of 300 – 400 m (Nakken, 2008). Overwintering depths are shallower and can reach the surface in waters up to 5°C. Polar cod generally spawn once but at a maximum twice in their life time after maturing at the age of four or reaching 15 cm. The average maximum age of polar cod is five years and thus, the species is rather short-lived like capelin (Hop *et al.*, 1997). Spawning commonly takes place in winter underneath the ice in the White Sea.

The diet of polar cod is dominated by amphipods as well as copepods. Polar cod use the sympagic habitat for feeding on ice-associated fauna (Søreide *et al.*, 2006). Whereas, the juveniles can prey directly upon ice algae, large individual polar cod may contain fish in their stomachs (Eriksen, 2012). Polar cod is a major prey for many birds (up to 60% of diet), white whales in summer, and several seal species, mainly before their spawning season. Owing to a wider range of distribution of most species in the Barents Sea over the last years, polar cod as a prey increasingly contribute to the diet weight of other fish that now also prey in the northern areas (Eriksen, 2012). In the Arctic food web, where capelin is not present, polar cod is the most important species in terms of energy transfer to the higher trophic levels.

Food Web Interactions

Trophic interactions rely on spatial and temporal overlap of species, which can be modified by climate variability. As the environmental factors in the Barents Sea are continuously fluctuating, interactions in the ecosystem are highly dynamic. Bottom-up control in the Barents Sea is a clear climate signal. This means that the lowest trophic levels are impacted by climate and this signal is transported upwards through the food web. One example of the control on the lower trophic levels is the advection of copepods from the Norwegian Sea into the Barents depending on the NAC. Furthermore, the primary production, which is connected to the ice edge, has continuously shifted northwards during the last decades owing to the retreat of the MIZ (Wassmann *et al.*, 2004). Consequently, the overall biomass distribution of the system also tends to move northwards.

On the other end, top-down forcing is established principally through fishing the major predators, which in turn can affect all trophic levels down to mesozooplankton (Yaragina & Dolgov, 2009). The same authors, though, describe the wasp-waist control as most pronounced in the Barents Sea since the pelagic fish at the intermediate trophic level regulate the energy flux to the top predators by grazing on the zooplankton. The dynamics of the capelin stock in the sub-Arctic and polar cod in the Arctic regime (Fig. 1.3) determine the trophic structure (Anon., 2009).

The capelin stock biomass has exhibited tremendous fluctuations in recent decades. Gjøsæter *et al.* (2009) describe the three major collapses that occurred from the beginning 1980s on. The first collapse happened between 1985 and 1989 when the capelin biomass declined from several million tonnes to below one million. During these years (1987 – 1990) the capelin fisheries were banned. The second and third lows in abundance lasted from 1993 – 1997 and 2003 – 2007, respectively. The most severe changes occurred during the first collapse. During the second and third collapse other forage fish were present in higher abundance mitigating food shortage. Nonetheless, the cod condition changed. Since other prey, such as the preferred zooplankton during these periods, are less digestible and nutritious, cod loses in total length and takes longer to mature (Wassmann *et al.*, 2006). The hepasomatic index (HSI), an indicator of fish condition, decreased and hence, the total egg production per unit spawning stock biomass (SSB) declined. So even though the effect of the capelin collapse lead to an increase in zooplankton abundance (similar for shrimp), these were no substitute for capelin as prey for cod, which is the most lipid-rich food available in the sub-Arctic part of the Barents Sea. Polar cod in the northern regions might have been a proper substitute with an even larger energy content ($7\,\mathrm{kJ\,g^{-1}}$) than capelin ($5\,\mathrm{kJ\,g^{-1}}$) (Hop & Gjøsæter, in press; Hedeholm *et al.*, 2011)). However, the spatial overlap of cod and polar cod only increased recently. Therefore, at the times of the capelin collapses, Atlantic cod switched to younger cod. Cannibalism was most common during the second collapse because of the increased overlap of mature and immature individuals. Sea birds and harp seals were severely impacted by the first collapse (Tjelmeland & Bogstad, 1998).

Conclusions for the causes of the capelin collapses are drawn by Howell & Bogstad (2010). First, several studies suggest that high herring abundance and related strong predation on the capelin larvae by herring caused capelin recruitment failure, e.g. Huse & Toresen (2000); Hallfredsson & Pedersen (2009); Gjøsæter *et al.* (2009). The second collapse showed that herring abundance was sufficient but not a necessary criteria for a capelin collapse (Hamre, 1994; Johansen *et al.*, 2002; Hallfredsson & Pedersen, 2007). The 0-group cod as well as other fish, e.g. haddock, prey on capelin larvae and impact their recruitment alike. The high fishing pressure that recurred after the first collapse increased the potential for the second decline of the capelin stock (Howell & Bogstad, 2010).

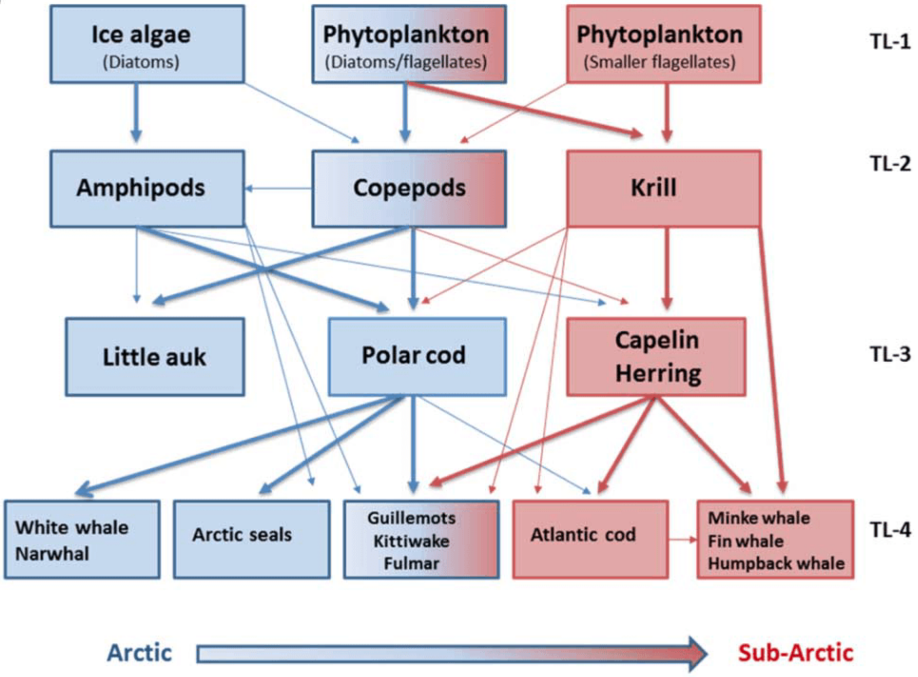


Figure 1.3: Capelin and polar cod in the food web of the Barents Sea (Sub-Arctic and Arctic regime, respectively). Arrow thickness relates to strength of the links in terms of energy flow. A potential shift in the system from Arctic (blue) to sub-Arctic (red) is expected. From Hop & Gjøsæter (in press).

Currently, the capelin stock is increasing and in general, most of the fish stocks in the Barents Sea are at their highest levels for the last decades (ICES, 2012a). Additionally, the northward shift in distribution, especially for cod and capelin, causes intensified competition (Anon., 2009). For example, baleen whales face reduced availability of zooplankton because of the increasing overlap between the plankton and capelin. However, as observed earlier by Piatt & Methven (1992) the whales might efficiently switch to predation on capelin. Likewise, capelin is suggested to overtake the position of polar cod in higher latitudinal areas as the sub-Arctic regime proceeds north (Hop & Gjøsæter, in press).

The Diet of the Cod

Yaragina *et al.* (2011) give three major reasons for the dominant role of cod in the Barents Sea, namely the high abundance (largest cod stock in the world, Anon. (2011)), long migrations (approximately 2000 km), as well as the omnivorous and opportunistic feeding behavior (Pálson, 1994; Wassmann *et al.*, 2006). As mentioned above, the cod diet reflects the state of the ecosystem in the Barents Sea. The total amount consumed by the cod depends largely on the cod stock size and the abundance of the prey species. The annual consumption varied between 2.3 and 6.1 million tonnes (calculations IMR, Institute of Marine Research in Bergen, Norway) for the period 1984–2008 (Dolgov *et al.*, 2011).

From the joint PINRO-IMR stomach content database (methods described by Mehl & Yaragina (1992)) cod consumption can be followed over the past 30 years. The feeding preferences differ for juvenile and adult cod. Whereas the young cod prey predominantly on macrozooplankton, the larger individuals prey on everything that is available, although with some size selection. More than 200 species have been recorded and 25 are dominant species in the cod stomachs. The main diet components are capelin and crustaceans, which are to a major extend shrimp, copepods, and krill. The consumed capelin biomass equals approximately 1.2 million tonnes per year(Dolgov *et al.*, 2011). Minor diet components are polar cod, herring, haddock, redfish, long rough dab, and blue whiting (maximum 5 – 20% of the diet). As mentioned above, in years of low prey abundance cod is cannibalistic. Halibut is exclusively important for the old age classes of cod.

The composition of the diet is variable throughout the year, depending on where the cod resides and which prey are available. Dolgov *et al.* (2011) summarized the following: in early February until March, capelin that migrates south to the Norwegian coast for spawning is a dominant part of the diet. Krill is important in spring and summer-time, whereas polar cod becomes present later during the year and especially in autumn, when the cod is distributed widest, including also in the northernmost parts of the Barents Sea. Likewise, annual variability can be observed (Fig. 1.4). In years of low capelin abundance, as in 1985 – 1989 (Fig. 1.2), the diet proportion of capelin went down to less than 5%, whereas shrimp and amphipods became more important components.

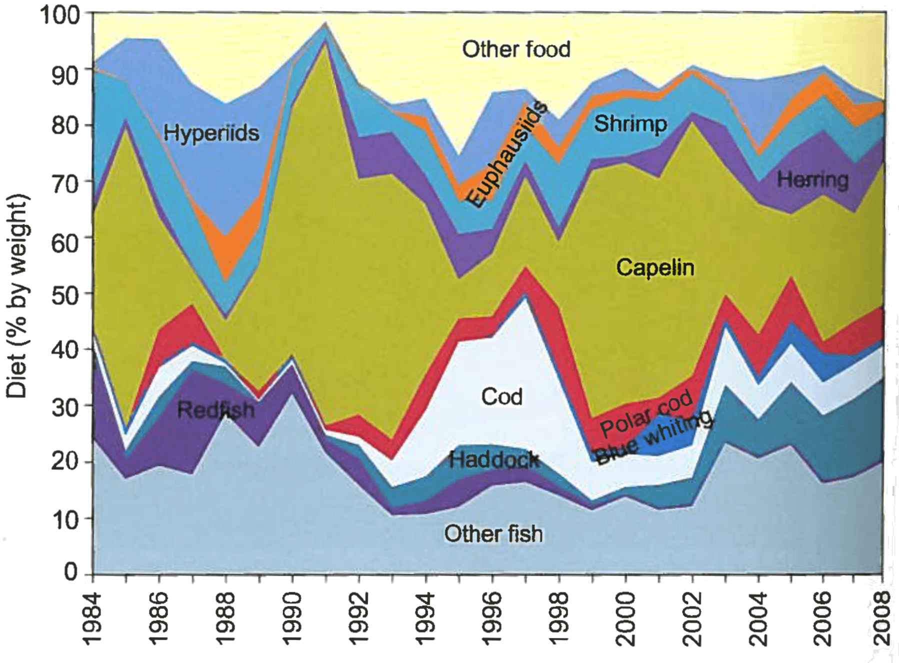


Figure 1.4: Diet proportions for cod between 1984 and 2008. From Yaragina *et al.* (2011).

1.2.3 Fisheries

The ACIA (2005) states that the largest fisheries in the Barents Sea are for capelin, cod, shrimp, seals, and whales. These fisheries belong exclusively to Norway and Russia, which is an advantage for managing the stocks when compared to the complicated situation in EU waters with many more interest groups. In 2001, Norway ranked as the largest fish exporter in the world with four billion US dollars income mainly through salmon followed by white fish. Because of the recovery of the Northeast Arctic cod in the Barents Sea, the cod fishery is almost back at the level of their heyday prior to the 1970s before the stock declined substantially. A total catch of 720 thousand tonnes was recently reported (ICES, 2012a). The capelin fishery has been limited by quotas, e.g. in 2009 with a catch of 306 thousand tonnes to keep the stock at a sustainable level. This is not comparable to 1977, for example, where 3 million tonnes of capelin were caught in the Barents Sea (Wienerroither *et al.*, 2011). The only period when polar cod fisheries were high (roughly 350 thousand tonnes) was during the late 1960s owing to the poor demersal fish stock at that time (Anon., 2009). Since 1973, Norway has not been fishing polar cod at all, and Russian fisheries are low (less than 50 thousand tonnes).

The cod management wants to exclude the juvenile part of the stock from fisheries ("3 - years harvest control Rule") and therefore includes regulations on minimum catch size, mesh size of fishing gear, maximum bycatch of juvenile cod, closure of areas with high density of juveniles, and seasonal as well as area restrictions (ICES, 2012a). Since the late 1970s the Joint Russian-Norwegian Fisheries Commission regulates the cod fisheries after the Total Allowable Catch (TAC) recommendations by ICES (Yaragina *et al.*, 2011).

The capelin stock has been monitored since 1973 by the IMR and first catch regulations imposed the next year. The three declines in capelin strongly affected the more important commercial species such as cod and required a change in management of the stock. The data on stock size (mature/immature) from the autumn acoustic survey (Gjøsæter *et al.*, 1998) in combination with research results on the food web interactions of capelin, e.g. Bogstad & Gjøsæter (2001); Gjøsæter *et al.* (2009); Godiksen *et al.* (2006); Hjermann *et al.* (2010); Ushakov & Prozorkevich (2002), have lead to a precautionary approach for capelin management since 1998 that is intended to enhance stable stock conditions. Regulations for TAC have been set to retain a minimum of 200 000 t SSB given by a 95% probability. However, the third collapse occurred in the early 2000s afterwards. The regulations are still imperfect and a minimum spawning stock of 1 million tonnes should be guaranteed according to (Gjøsæter *et al.*, 2011). In conclusion, the development away from a single species management towards a more complex model proceeded during the last decades (e.g. review in Gjøsæter *et al.* (2002)), but still none of the management strategies tested so far prevented collapses of the stock (Howell & Bogstad, 2010)

The ecosystem approach (EA) is widely accepted to be the key plan in future fisheries management (United Nations, 2005; Ridgeway & Maquieira, 2006; Browman & Stergiou, 2004, 2005). In the long run, an EA for the Barents Sea could ensure a management of all important stocks together. Eide (2008), for example, showed that for the area the temperature increase is rather small and suggested that despite all climatic changes the management strategy had a stronger impact on the fish stock. The cod biomass fluctuates independently of management plans in the study of Eide (2008). The understanding of the trophic interactions and finding of indicators for environmental fluctuations needs to be further implemented. The Atlantis model provides possibilities to do so and to explore the long-term ecological dynamics of the system under different fishing scenarios.

2 – Methods

2.1 The ATLANTIS Model

The Atlantis model was developed by Elizabeth Fulton (2001) as a tool for fisheries management evaluation in Australia (Fulton *et al.*, 2004). Atlantis has also been applied to different coastal areas worldwide such as the California Current (Horne *et al.*, 2010) and the Gulf of Maine (Link *et al.*, 2010), and is under construction for European waters, for example the North Sea (ICES, 2012b). The version of the model used in this study covers the Nordic Seas and the Barents Sea (hereafter called NoBa Atlantis).

Atlantis belongs to the type of models also known as whole-of-system models (Fulton, 2010). These intend to explore the marine ecosystem in a way to capture the entire food web (including the human dimension) in combination with the abiotic environment, integrate the physical and biological processes at different scales, and provide dynamic coupling (two-way) between the components (Travers *et al.*, 2007). The same authors state such an holistic approach to ecosystem modelling as end-to-end modelling. Atlantis examines additional driving factors besides the natural system, i.e. the socio-economic conditions. The model is built upon submodules of the physics, biology and fisheries and uses output from other models and/or field and laboratory data. Ideally, Atlantis provides a comprehensive overview of the existing knowledge on the investigated ecosystem, e.g. spatial distribution of stocks and energy flow through the system (Hansen, 2010a).

The spatial resolution of Atlantis is a coarse three dimensional division into polygons (in the following called boxes). Many of the parameters are defined for the entire system, but some, such as distribution, are spatially dependent. In order to remain as biologically homogeneous as possible within each box, the boxes should match the major hydrodynamic (water masses, mesoscale activity), geographical (bathymetry), and biological (benthos population, fish stocks) features. Trophic resolution occurs at a functional group level, i.e. assemblages of species with similar ecological characteristics (diet, longevity, size, habitat, predators, migration), which are considered as units for parametrization. Functional groups may, however, also consist of a single species. This is valid for dominant species, like humpback whales, or the ones holding a key position in the ecosystem, such as capelin for the Barents Sea. Likewise, species of economical interest may be parameterized as a single group. The groupings of vertebrates use an explicit age-structured formulation. Invertebrates, on the contrary, are represented as biomass pools (in the following called pooled species). For the Barents Sea, two groups were divided into juveniles and adults, i.e. shrimp and squid. Some groups that cannot be classified as species are still treated as groups within the model, for example the detritus.

Movement between the boxes is realized by either advective transfer (currents, planktonic biomass) or directed movements (vertebrates) and in addition, density-dependent/ forage-dependent movement may be applied (currently not for NoBa Atlantis). The flexible parameterization allows many options. However, all initial conditions, e.g. biomass, growth, stock-recruitment parameters, depend on the quality of field and laboratory observations. Often, data may be incomplete or experimental work assumes conditions not observed in the wild (Kaplan *et al.*, 2010). Therefore, the strength of Atlantis is not to define exact quotas for policy makers, but lies within the exploration of different environmental and fishing scenarios, of which the results may be used to provide the best management strategies among tested scenarios (Fulton *et al.*, 2007).

2.1.1 NoBa Atlantis

The Barents Sea is an important area for fisheries in Norway and Russia, especially for cod, capelin, and haddock. Until now, the majority of the management strategies depend on single stock assessment. A basic multi-species management also exists for capelin fisheries (Gjøsæter *et al.*, 2002). Further models are used to investigate the multi-species interactions of the Barents ecosystem in combination with fisheries (Howell & Bogstad, 2010; Tjelmeland & Bogstad, 1998). Nevertheless, only for the capelin stock management is the model

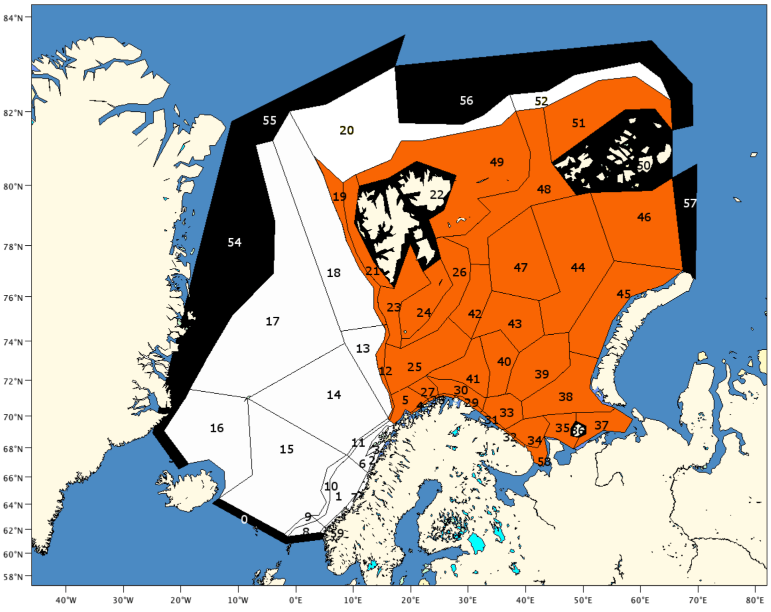


Figure 2.1: Overview of the Model Area for NoBa Atlantis with Boxes 0 - 59: Orange boxes indicate area of Barents Sea, black are boundary boxes, white boxes comprise the rest of NoBa Atlantis grid. Boxes 20 and 52 could be included in climate change scenarios. (Snapshot box set-up out of DIVE)

implemented in the harvesting strategy. Atlantis is another approach to ecosystem-based management. Given the usefulness of Atlantis in other regions (Fulton, 2010) and the ability to explore different ecosystems and fishing scenarios, the Institute of Marine Research (IMR) in Bergen decided to build an Atlantis model for the Barents Sea, the development of which was undertaken by C. Hansen.

The development started as part of the MENUII–project and is currently covered by the @ECO–project. The Nordic Seas were included in the model owing to their close connection to the Barents Sea, both physically and biologically. The idea was to use NoBa Atlantis to investigate a number of climate and fisheries scenarios, initially concentrating on the important commercial groups, then examine possible vulnerable species and groups, and eventually the ecosystem.

The model grid consists of 60 boxes, which cover an area of about $4 \cdot 10^6$ km^2 (Fig. 2.1). Vertically, each box has a given number of depth layers depending on the individual mean depth of the box. The maximum number of layers is seven, plus one sediment layer. Each of these has a predefined depth: 0-50 (layer 1), 50-150 (layer 2), 150-250 (layer 3), 250-375 (layer 4), 375-500 (layer 5), 500-1000 (layer 6), 1000-1250 (layer 7). If a box has a mean depth deeper than 1250 m, the deepest layer extends down to the bottom.

The model is forced by the ocean climate, including temperature, salinity, and volume fluxes over all boundaries between the boxes (ice thickness and concentration will be included in future), in addition to precipitation and evaporation. These physical conditions are output from a set-up of the Regional Ocean Model System ROMS, with a horizontal resolution of 20 km (Shchepetkin & McWilliams, 2005; Haidvogel *et al.*, 2008), while the primary production is derived from the NORWegian ECOlogical Model NORWECOM (Skogen *et al.*, 1995; Skogen & Søiland, 1998).

The biota is divided into 52 functional groups. All groups are listed with names, acronyms, and included species in Table A.1. A long list of parameters is applied to each of the groups, e.g. spawning time, number of recruits, swimming speed, fraction of mature at age, functions for structural (bone) and reserve (fat) weight, consumption rates, etc. Within the boundary boxes parameters for migrating species, such as whales, are adjusted if they re-enter the model depending on what happens to them outside (for example, changes in the number of individuals owing to reproduction, changes in weight, etc.). Data for the different species come from previous Norwegian projects as FishExChange, NorExchange, Inferno, or BarEcoRe and various publications (Hansen, 2010b). It should be noted that the fisheries submodule is still under development.

2.1.2 Calibration of the Model

Before Atlantis can be used properly, the initial set-up needs calibration and afterwards the tuning work has to be evaluated. Understanding has to be achieved on how comparable the results are to reality and hence applicable for management. In the article by Kaplan *et al.* (2010) the authors give a summary on important steps for the calibration of Atlantis:

» Prevent most species from going extinct.

» Vertebrate growth such that size-at-age is reasonable.

» For species with available historical data, the model should recreate observations of abundance from surveys or assessments.

» For species with no historical data, the model should yield reasonable time series of abundance (within certain limits, e.g. no extinction or population explosion).

» Capture the observed spatial distributions.

Accordingly, the dominant focus of tuning lies in adjusting the parameters to obtain the observed and relative fluctuations in the abundance and biomass of the species. Growth and consumption rates, mortalities, and Beverton Holt parameters for the recruitment are important for determining the basic population dynamics. Tuning of the diets, however, is another substantial part of the calibration process. Even if the stable state of the ecosystem was achieved by calibrating to the points above, the trophic interactions still could be incorrect. For an ecosystem, such as the Barents Sea, the trophic food web is short compared to more temperate regions and thus, the responses are stronger. In order to retrieve a reasonable representation of the dynamics of the ecosystem, the adjustment of diet proportions for each species is pivotal. Additionally, the spatio-temporal distribution has to be modified for defining the interactions. Building upon the previous work of setting up NoBa Atlantis, the cod diet was intended to be calibrated with regard to the third key point above.

2.2 Run Setup

During the work on this thesis several updates of the code as well as changes of the parameters owing to tuning were used before settling on a final version. This is owing to the on-going development of Atlantis, both from the work with implementing NoBa Atlantis and the developers in Australia. The latest and only update of the Atlantis code to be mentioned here is revision 3728. In total, 96 runs were submitted for this thesis. Table A.2 lists 28 selected runs that are mentioned within the thesis, including the five that were selected for analysis. More information on this issue is given in Section 3.3, as well as in Chapter 4. The reason for choosing so few runs is because NoBa Atlantis is a model under development, which is important to note for the entire thesis. All results have to be evaluated in terms of this limitation. At the moment, the results for several species, such as for abundances or weights, are incomparable to absolute values of the historical record. Yet, relative proportions may still be realistic.

Certain limitations for the applied version of the parameter files were that the updates on tuned consumption rates and recruitment options for most of the species by C. Hansen had to be ignored in order to remain consistent. Likewise, the latest update of the code in combination with the parameter files used here caused instabilities for the lower trophic levels, which to investigate the reasons why was beyond the scope of this thesis. Therefore, for the very last runs krill and mesozooplankton were excluded. Even though the results can be improved and in some cases are disputable, this was the only way to retrieve results within the time frame of this thesis. Suggestions for improvement are presented in Chapter 4. Finally, it can be noted that the reproducibility is good seeing that changes between runs with identical set-up are below 1% for the output (not presented in this thesis, pers. comm. C. Hansen). Therefore, one run is considered sufficient for representative results after changing the parameterization.

2.2.1 Parameter Files

The basic set-up for the runs comprised input (definition/parameter/forcing) files for:

» the run set-up,

» the physical properties,

» the functional groups,

» and the biology.

All runs lasted for 9855 days, which is equivalent to 27 years of 365 days each. The computing time used for one single run was between 2 and 3 hours. The general output, including abundance and weight, was determined three times a year, i.e. at day 121 (April), 242 (August), and 365 (December). The mortality rates, though, could only be given for the last day of each year with the current version of the model. This is the reason all of the results, i.e. abundance, weight and mortalities, are only for December but they should at least provide a consistent picture. Furthermore, it has to be noted that the output only represents a snapshot of the chosen time, i.e. day 365 for the results of this thesis.

The physical oceanography, including salinity and temperature data, was fed into the model through a hydrodynamic file following the pattern of the ROMS model for year 1981, but excluded vertical fluxes. Year 1981 was repeated over the entire period of the run. In this way, variation owed to ocean climate was excluded. The solar radiation is calculated by the model, and dummy files were used for precipitation/evaporation. The initialization of all biological parameters was done according to historical data from the early 1980s as well. During the beginning of the 1980s the polar cod population was below 0.5 million tonnes, and thus much lower compared to the other two, capelin (3 - 5 million tonnes) and cod (ca. 1 million tonnes) (ICES, 2012a). Cod and capelin are the major focus of this study, because of their strong predator-prey linkage. In addition, polar cod was investigated more closely owing to the competitive position in the ecosystem with capelin. The realization of the most important characteristics of these three species with regard to the study is summarized in the following Table 2.1, where all parameters are given.

When tuning the diet of cod in Atlantis, it should be kept in mind that capelin is a short-lived species, which in the model has five age groups compared to ten for all other vertebrates and mammals. Capelin die after spawning or at least upon reaching age 5 in the model. The age of maturity is reached after two years. Polar cod has a longer life time than capelin in the model but still one year class per age group. The cod have two year classes per age group and mature later. For the consumption the gape size defines how small/large the prey may be compared to the predator body size. The lower limit of cod is set to a very low number so that the small prey, such as zooplankton, will be included. For the smaller polar cod and capelin a higher value for the lower gape size limit is sufficient. The upper gape size of cod is set so that the prey may reach 75% of the cod body size (Bj. Bogstad, pers. comm. via C. Hansen).

Studying the diet of cod requires the overlap of prey and predators. Only then the entire effect of the tuning can be understood, i.e. who is competing with whom. Therefore, Table 2.1 gives overlapping prey and predator species first and afterwards the remaining different for each species. Distributional overlap is given in Figure 2.2. The horizontal distribution of cod (upper figure, blue squares) is mainly in the central parts of the Barents Sea and overlapping with more than half of the boxes for capelin distribution (yellow shading). Polar cod (red circles) is overlapping with the other two species especially in the southeastern Barents Sea and around Svalbard. For the northernmost boxes polar cod is not overlapping with the others. The set-up of the vertical distribution in the model (lower figure) shows that the best overlap in concentration of the three species lies between 150 and 250 m. The distribution of all species in NoBa Atlantis was set according to maps of average distribution (Jakobsen & Ozhigin, 2011). This explains, for example, why blue whiting, even though not present in the Barents Sea until 2003, is distributed off the northern coast of Norway in Atlantis.

The interaction between species in the Atlantis model is described by a diet matrix, which consists of an index between 0 and 1 that indicates the fraction of prey available to the predator (0 - 100%). This equals the strength of the feeding relation and afterwards the term link with regards to tuning the diet will always refer to this number set for each possible prey-predator combination. Furthermore, an additional note on the terminology for this thesis is that the values to initialize and tune the model will constantly be phrased as parameters notwithstanding that these are both parameters and variables.

2.2.2 Tuning of the Northeast Arctic Cod Diet

Tuning of the diets is a major part of the work for implementing Atlantis. The initial set-up for all species was carried out prior to this study by C. Hansen and followed literature values in order to reach realistic and stable ecosystem dynamics. Nevertheless, more specific tuning is still lacking for some species. The most important parameters to adjust are the links between predator and prey (set-up in a diet matrix), consumption and growth rates, as well as gape size limits. Additionally, the abundances of the stocks, modifiable also by initial stock size and recruitment options, affect the feeding behavior because the availability of prey changes. The focus of this thesis lies on refining the diet matrix of cod. The available joint PINRO-IMR database of stomach contents for the Northeast Arctic cod in the Barents Sea (Mehl & Sunnanå, 1991; Mehl & Yaragina, 1992; ICES, 2012a) was valuable for this work owing to the detailed information and long time series going back to 1984. The survey covers most of the Barents Sea, especially southern, western, and central areas. However, it has extended and intensified over the last decade also northwards. On average, approximately 9 000 stomachs have been analyzed per year between 1984 – 2011. The consumption per capita cod is calculated for each half-year resolving prey age groups 0 – 6 and predator age groups 1 – 11+. For the spawning period, mature cod are assumed to be outside the Barents Sea, thus their consumption is excluded from calculations. The proportions of prey in the cod diet for Atlantis were calibrated in accordance with the average values from the stomach database.

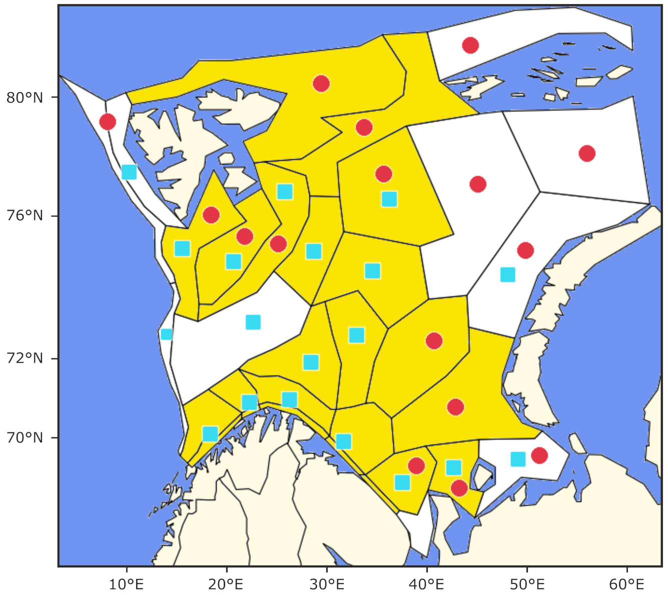
First, the prey species that should be considered for tuning were chosen. These are basically consistent with the presented species in the database. Redfish were considered as genus without distinguishing different species, though. In the model the species designations were redfish RED (hereafter beaked redfish) and other redfish REO (hereafter golden redfish). Hence, the proportion given for redfish from the database was split for the two functional groups. Additionally, numbers for other, unspecified prey consumed (listed as "Other") were excluded, although their proportion of the diet was about 18% on average. Squid (cephalopods, CEP) and the other large demersal (DEL) species (including monkfish, Atlantic halibut, Atlantic wolffish, northern wolffish, and spotted wolffish) were considered to be part of the diet within the initial set-up of the model. Nonetheless, both functional groups were neglected for tuning in this study, since no detailed information on the consumption of these species was available in the database. Labile detritus (DL) and refractory detritus at the bottom (drsed) were added to the diet as "bycatch" prey, since these are consumed continuously (Bj. Bogstad, pers. comm. via C. Hansen) and during feeding on other prey, particularly owing to the benthic habitat of cod. The links for DL and drsed should be kept constant and at low levels (diet proportions $< 1‰$). In summary, the tuning of this study considered 15 functional groups (Table 2.2). More species could be added after having understood how to tune the diet to a state where it is comparable to the survey data.

Table 2.1: Summary of the most important parameters for cod (NCO), capelin (CAP), polar cod (PCO) with regard to tuning of the cod diet. Some prey/predator species overlap and are given first for each of the three species, followed by the specific prey/predator "(no overlap)". A key to the acronyms is found in Table A.1.

	NCO	**CAP**	**PCO**
Parameters related to age:			
number of age groups	10	5	10
age class size	2	1	1
age (class) of maturity	6(3)	2(2)	3(3)
Parameters related to diet:			
lower/upper gape size*^{1}	10^{-10}/0.75	10^{-5}/0.42	10^{-5}/0.42
prey species	CEP, PWN ZL, ZM,	CEP, PWN ZL, ZM,	CEP, PWN ZL, ZM,
(no overlap)	DEL, REO, RED, LRD, GRH, HAD, BWH, SSH, NCO, PCO, CAP, DL, drsed	ZS	DF
predator species	PEL, SAI, REO, NCO, LRD, HAS, SSK, MWH, HWH, ZG*^{2}, CEP*^{2}	PEL, SAI, REO, NCO, LRD, HAS, SSK, MWH, HWH, ZG*^{2}, CEP*^{2}	PEL, SAI, REO, NCO, LRD, HAS, SSK, MWH, HWH, ZG*^{2}, CEP*^{2}
(no overlap)	GRH, RED, DEL, DEO, KWH, SBB, RIS	BWH, DEL, SSH, HAD, SBA, BES, FWH	BWH, RED, BES, SHO, SBB, HOS, RIS, FWH
Vertical and horizontal distribution: shown in Figures 2.2 and 2.2			

*^{1}Limits describe min/max allowed prey size in relation to own body size.

*^{2}Jellyfish and squid do not commonly consume adult fish, but are important predators for larval and juvenile stages of most fish species in the Barents Sea (Eriksen *et al.*, 2012).



0 - 50	0.1	0.5	0.05	0.05	0.1	0.5
50 - 150	0.2	0.4	0.1	0.1	0.25	0.4
150 - 250	0.2	0.1	0.6	0.6	0.25	0.1
250 - 375	0.2		0.15	0.15	0.2	
375 - 500	0.2		0.05	0.05	0.2	
500 - 1000	0.1		0.05	0.05		
1000 - Bottom						

Figure 2.2: Horizontal (top) and vertical (bottom) distribution of capelin, cod, and polar cod as set in the parameter files for all runs. The colors in the figures refer to capelin (yellow shading), cod (blue squares), and polar cod (red circles). Note the distortion of the latitude scale. For the vertical distribution, numbers in each depth layer refer to the fraction of the stock present at depth (columns are for adults and juveniles, respectively).

Table 2.2: Overview on all prey of cod used for tuning of the diet matrix: Species/group description, Atlantis specific acronym, diet proportion out of stomach database, initial (average) weight in model parameterization. The acronyms will be used for all following figures and tables without repeated explanation.

Species/Group	**Acronym**	**Diet %**	**Avg Wt [kg]**
Golden Redfish (*Sebastes marinus*)	REO	4.0*	0.99
Long rough dab	LRD	1.5	0.20
Greenland halibut	GRH	<0.1	3.30
Haddock	HAD	3.1	1.78
Beaked Redfish (*Sebastes mentella*)	RED	4.0*	0.57
Blue whiting	BWH	1.1	0.15
Norwegian spring-spawning herring	SSH	2.9	0.27
Northeast Arctic cod	NCO	3.8	9.09
Polar cod	PCO	5.8	0.05
Capelin	CAP	44.2	0.03
Shrimp (prawn)	PWN	8.2	–
Krill – large zooplankton	ZL	12.4	–
Amphipods/copepods – mesozooplankton	ZM	13	–
Labile detritus	DL	–	–
Refractory detritus at the bottom	drsed	–	–

Second, the proportions for each species within the cod diet that should be achieved after tuning were calculated from the stomach database (Table 2.2). The zooplankton species (ZL, ZM) and shrimp (PWN) in the diet as well as DL and drsed, are treated as biomass pools. For these, the abundance was expressed in terms of nitrogen concentration (N in mg/m^3). Later on, the consumption of cod will be examined by comparing both numbers of individuals and biomass consumed. The pooled species may only be considered for biomass comparison.

Third, the tuning process started by setting up different diet matrices. In total, five of all runs submitted were used to explore the tuning process. These five different parameterizations of the diet matrix are summarized in Table 2.3. The idea was to see what cod preyed upon without tuning the links (starting with links of 1 for all prey species). Certainly, this would reveal the feeding preferences of cod within the applied version of NoBa Atlantis for the study. Then, the links would be lowered in a stepwise manner with regard to both the discovered preferences in the model and the proportions from the stomach database. What was expected is that reducing a diet link would result in reducing the proportion of the consumption. Nevertheless, a linear response, i.e. changing a link from 1 to 0.1 and retrieving exactly 10 times smaller numbers of fish consumed, would be unlikely. Trophic interactions would most certainly strengthen or weaken the change of the link. The intention was not to reproduce the diet from the database in terms of exact numbers for the proportions but more likely equal proportions by order of magnitude. A link was decreased/increased until the correct order of magnitude would be reached. Subsequently, the link was either decreased/increased again but only within the same order of magnitude or kept constant because of the above mentioned secondary interactions that would alter the proportion in addition. In order to keep track of how the changed links affect the diet proportions not all links were modified at once but only for the species which needed strongest tuning. Then a refined tuning could rely upon the new results.

There are four possible parameters for the diet matrix to define age-specific feeding preferences: a) juvenile prey – juvenile cod, b) adult prey – juvenile cod, c) juvenile prey – adult cod, and d) adult prey – adult cod. All of these parameters were treated in the same way for the diet tuning. Hence, the naturally different diets of juvenile and adult cod or their preferences for juvenile or adult prey were neglected. Detailed descriptions for the specific runs of why and how the links were changed are given in the results.

2.3 Data Analysis

For analysis, only the Barents Sea boxes were used (Fig. 2.1). All other boxes of the Atlantis grid were neglected, including boundary boxes or islands such as Box 22 around Svalbard (black shading). The orange boxes in the map were included, which were in total 33 boxes: 4, 5, 12, 19, 21, 23 – 35, 37 – 49, 51, 52, and 58. These comprise an area of about 1.58 million km^2, which matches the estimate of Jakobsson *et al.* (2004). The boundaries towards the west and north align with the continental slope, the transition of shelf area to the deeper Norwegian Sea (>500 m) and the Arctic Basin, respectively (Fig. 1.1).

All runs in this study covered a period of 27 years that included a spin-up time of ten years, in order for the model to stabilize (J. Link, pers. comm. via C. Hansen). Consequently, the first ten years were not used for calculations. The length of the runs relates to the fact that when starting the runs for the current thesis version of Atlantis they were stable for 30 years. Even though this increased in later runs, the original scope was kept for simplicity of comparison. Likewise, it has to be noted that the last two years of the model output were neglected since, especially for the last year, the output is erroneous (B. Fulton, pers. comm. via C. Hansen). Therefore, the 15 years after the spin-up time were used for analysis, which includes approximately four full life cycles for capelin and almost two for polar cod. Cod has a longevity of 20 years in the model. So even though not an entire life cycle is covered, many cod will reach maturity (age 6) and spawn multiple times.

The analyzed output of the data was produced for December each year. August would be the best output to use, since at that time of year all species are within the Barents Sea area, including the migrating species such as blue whiting. At the same time, for the most important species of this work, the recruits would have entered the model earlier during the year and and population levels would have been stable. However, as the diet output could solely be printed for the last day of the year with the model version used, December had to be taken as the time of year for calculations. This has to be kept in mind when analyzing the data.

Data from the output files were read and processed by means of the "R" software (*http://www.r-project.org/*). The graphical programme "DIVE", especially made for Atlantis (*http://software.cmar.csiro.au/www/en/software/dive.html*), was used to visualize the distributions and abundances of the functional groups over time. However, maps were plotted in "R". The major variables of interest were numbers of individuals, individual structural and reserve weight written in the initial output-file. As the area was limited to the Barents Sea, the biomass and other variables had to be calculated for the desired boxes. Hence, all variables are read out for each box/depth layer and are then summed up for the age classes per year. Weight for vertebrate species is given in mg N. The total weight for each individual results in the sum of reserve and structural weight. By means of Equation 2.1, which is specific for the Atlantis model (Fulton *et al.*, 2004), the wet-weight was transformed into tonnes (from mg to tonnes – divisor 10^9), where w_w and w_d are wet and dry weight, respectively:

$$w_d = \frac{w_w \cdot 5.7 \cdot 20}{10^9} \tag{2.1}$$

Subsequently, the biomass of the vertebrate species was calculated by multiplying the average weight for an individual fish of each age class by the corresponding abundance. As additional information, the condition factor (structural/reserve weight) was calculated for all vertebrates. For invertebrates, functional groups treated as biological pools such as the plankton species, a concentration was given in nitrogen N [mg/m^3]. Thus, the biomass was calculated by multiplying the volume of each box by this concentration. The wet-weight transformation above yielded the biomass in tonnes.

Table 2.3: Predator-Prey Interaction – Links of cod diet all runs for each prey species. Initial run (Run 0) age specific links (a-d see text), rest of runs no distinction. Links for DL (1e-4) and drsed (1e-5) kept constant for all runs.

	REO	DEL	LRD	GRH	HAD	RED	BWH	SSH	NCO	PCO	CAP	PWN	CEP	ZL	ZM	cepj	pwnj
Run 0																	
a) juv -juv	0.01	1e-5	0	0.3	0.1	0.01	0.3	0.1	0.1	0.2	0.9	0.95	0.5	0.95	0.95	0.2	0.9
b) ad - juv	0.01	0	0	0.05	0.01	0.01	0.4	0.35	0	0.1	0.95	0.95	0.5	0.95	0.95	0.2	0.9
c) juv - ad	0.01	0.5	0	0.4	0.5	0.01	0.4	0.1	0.1	0.2	0.9	0.95	0.5	0.95	0.1	0.2	0.9
d) ad - ad	0.01	0.1	0	0.07	0.4	0.01	0.5	0.1	0.1	0.2	0.85	0.95	0.5	0.95	0.1	0.2	0.9
Run 1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1
Run 2	0.01	0	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	1	1	0	1	1	0	1
Run 3	1e-3	0	1e-3	1e-3	1e-3	1e-3	1e-3	1e-3	1e-3	1e-3	0.5	0.1	0	0.1	0.1	0	0.1
Run 3	1e-4	0	1e-4	5e-5	1e-5	1e-5	5e-5	5e-5	1e-4	1e-3	1	0.25	0	0	0	0	0.25
Run 4	7e-4	0	2e-4	2e-5	9e-5	1e-5	3e-5	6e-5	8e-5	1e-3	1	0.15	0	0	0	0	0.15

The predation mortality was quantified by mortality rates given for each prey group in relation to the predators. The mortality per predator multiplied by the abundance of the predator (here always cod) yielded the number of individuals or the biomass (for pooled species) taken out by predation. Consequently, for pooled species nothing else had to be calculated. However, to enable comparison of the amounts of these and fish eaten by cod, the number of individual fish preyed upon was multiplied by an average weight for each species. The latter was calculated for each run and species averaging all age groups. Considering the upper limit of the cod gape size, cod may prey on other species that are up 75% of its own maximum size. Hence, cod were able to consume all age classes of each prey species in the runs. Even though this has been the case for all investigated runs, the biomass calculated in this way can only be a rough estimate of the biomass taken out by predation. Therefore, the comparison of the entire diet with survey data including the pooled species was an approximation. Further analysis of the results was done with regard to predator-prey ratios compared to feeding behavior. Linear regression models were applied to examine the correlations between capelin, cod, and polar cod abundance and consumption.

The model output was then compared to known values from the literature, especially for cod stomach contents (as cited above and updated, pers. comm. Bj. Bogstad), abundances, weight, biomass (all for different year classes) from ICES (2012a); ICES (2000) and the IMR/PINRO joint report series (Anon., 2009, 2011; Eriksen, 2012) as well as Wienerroither *et al.* (2011) and Jakobsen & Ozhigin (2011).

3 – Results

3.1 Tuning the Diet Matrix of Cod

In the following, five selected runs are used to guide the reader through the tuning process. The runs summarize the major achievements towards a tuned diet matrix of cod in NoBa Atlantis that reflects the diet proportions from survey data. The changes compared to the initial set-up were the following:

Run 1, setting all links between cod and prey species to 1 thereby finding the feeding preferences in the used model version that originate independently from the diet matrix; Run 2, reducing all links by two orders of magnitude except for the main prey species (capelin, shrimp, krill, and mesozooplankton); Run 3, further reduction of links for all prey but capelin with the intention to refine the tuning with respect to the observed diet composition from the previous runs (also excluded runs); Run 4, final reduction of the links except for capelin to attempt to the correct diet proportions in terms of magnitude.

A separate description of the results for the initial set-up, Run 0, is followed by a comprehensive analysis of the four tuning runs (Runs 1 – 4). Abundance, average individual weight, and biomass of all species included in the diet of cod are presented for each run. A comparison of the different diet compositions completes this section.

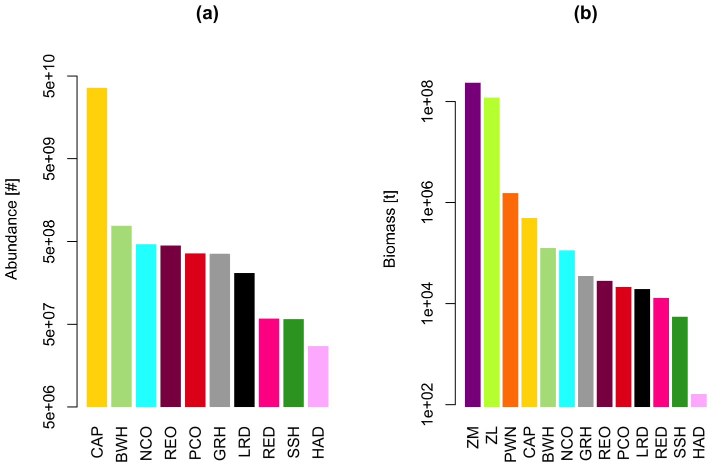


Figure 3.1: Run 0. (a) Magnitudes of abundances and (b) biomass for prey species of cod in decreasing order. For (b) pooled species are included. Note the logarithmic scale.

3.1.1 Run 0 - Initial Run

The starting point for tuning is set by Run 0, which represents the original parametrization by C. Hansen and yields the general picture for the species that are investigated. The distribution by species or group for abundance and biomass are given in Figure 3.1, which shows that most vertebrate species level at an average of $2 \cdot 10^8$ for abundance and $7 \cdot 10^4$ for biomass.

Capelin (CAP) is by far the most abundant and biomass-rich vertebrate stock, while especially haddock (HAD) as well as herring (SSH) and beaked redfish (RED) lie below the average. In terms of biomass the pooled species, krill (ZL), shrimp (PWN), and mesozooplankton (ZM) with the highest value, are all well above the vertebrate prey. Both squid and large demersals, which were excluded from the tuning process, matched the average numbers.

Additionally, it can be seen in Figure 3.1 that the relative rankings of abundance and biomass for polar cod (PCO) and halibut (GRH) have switched places, i.e. polar cod is higher in abundance but lower in biomass than halibut. This is because of their average weights. Polar cod is lighter than most of the other prey species while halibut is heavier (Fig. 3.2). Cod (NCO) has the maximum individual weight (neglecting the large demersals), on average approximately 30 – 100 times the weight of a polar cod or capelin (Table 3.1). Nevertheless, owing to the high abundance of capelin, cod does not have the largest stock biomass.

A comparison of the averaged output of Run 0 (over years 11 – 25) with data from surveys is given in Table 3.1. In general, stock size and biomass in the model are below the reference data, mostly by one order of magnitude, for cod and polar cod abundance even by two. The

Table 3.1: Comparison Atlantis output of Run 0 (all data averaged after spin-up time) with survey data for cod, capelin, and polar cod, (ICES, 2012a; Gjøsæter *et al.*, 2008).

Survey Data	Stock [#] (10^9)	Stock [t] (10^3)	Avg. Wt [kg]
NCO	10 – 13	800 – 1500	6 – 10
CAP	500 – 750	4000 – 7000	0.015
PCO	20 – 30	< 500	0.1
Run 0	Stock [#] (10^9)	Stock [t] (10^3)	Avg. Wt [kg]
NCO	0.55	80	1.408
CAP	35	500	0.013
PCO	0.37	20	0.049

initial abundance of cod in the model is approximately $5.5 \cdot 10^8$, stays at this level throughout the run, and therefore remains below survey data. The capelin stock starts at a size of circa $2.5 \cdot 10^{11}$ individuals and stabilizes at $3.5 \cdot 10^{10}$. For polar cod abundance the initial value is roughly $1.3 \cdot 10^9$, which then stabilized at about $3.7 \cdot 10^8$. Considering weights, the individual weight of capelin differs slightly by 15%, which is in the acceptable ±50% range for working with Atlantis (pers. comm. C. Hansen). The individual weights of cod and polar cod are low on average, 50% below the natural average for polar cod and up to 90% for cod.

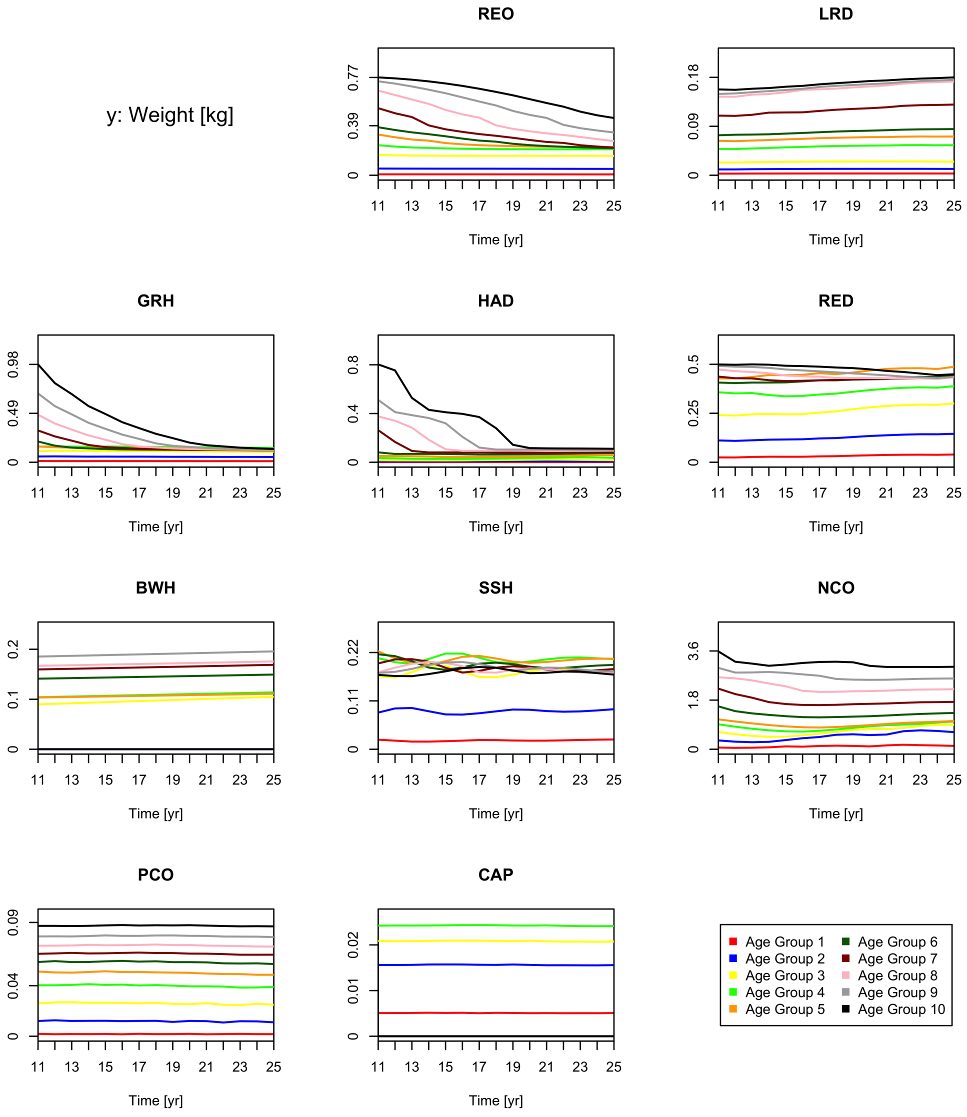


Figure 3.2: Run 0. Weights per age group for each prey species of cod after spin-up time. Note the different scales for the weight.

Likewise, these observations account for the tuning runs (Run 1 – 4) in the following section.

Figures 3.3, 3.4, and 3.5 show the development of abundance, average weight, and biomass over the time of the run. The biomass of capelin and polar cod increase slightly over time despite their stable weights. However, both increase in numbers at the same time, consequently the stocks are constantly growing.

For cod, the age groups 1 – 5 increase their weights (Fig. 3.2), which is most obvious for the second age group after year 16. This is when the abundance of cod generally decline while the stock biomass increases. Consequently, individual fish gain weight, which is expected from density dependent regulation. For older age groups of cod (5+), the opposite is observed as their weights decrease within the first years down to stable levels at the end of Run 0. Therefore, the cod stock is declining in terms of numbers of individuals, but increasing in biomass, since young cod increase their condition and the old cod remain their weights after a certain period.

The latter is equally true for the golden redfish, halibut, and haddock. The individuals of age groups 5 – 10 lose weight in accordance to higher abundance, hence competition. Additionally, the stock biomass of halibut and golden redfish declines. The opposite behavior, such as for young cod, is observed for beaked redfish, blue whiting (BWH), and long rough dab (LRD). Whilst their abundances decrease, biomass and weight increase. For the remaining species, abundance and biomass respond concordantly. In summary, few stocks decline, whereas most grow either in terms of abundance and/or weight, especially for the last five years, e.g. haddock and herring, or beginning within year 14, e.g. cod and capelin. The pooled species are comparably stable over time apart from the krill, which begin to increase in year 14 and gain biomass by two orders of magnitude until the end of the run. The mesozooplankton also vary. For year 21 to 22 the population size sinks almost one order of magnitude.

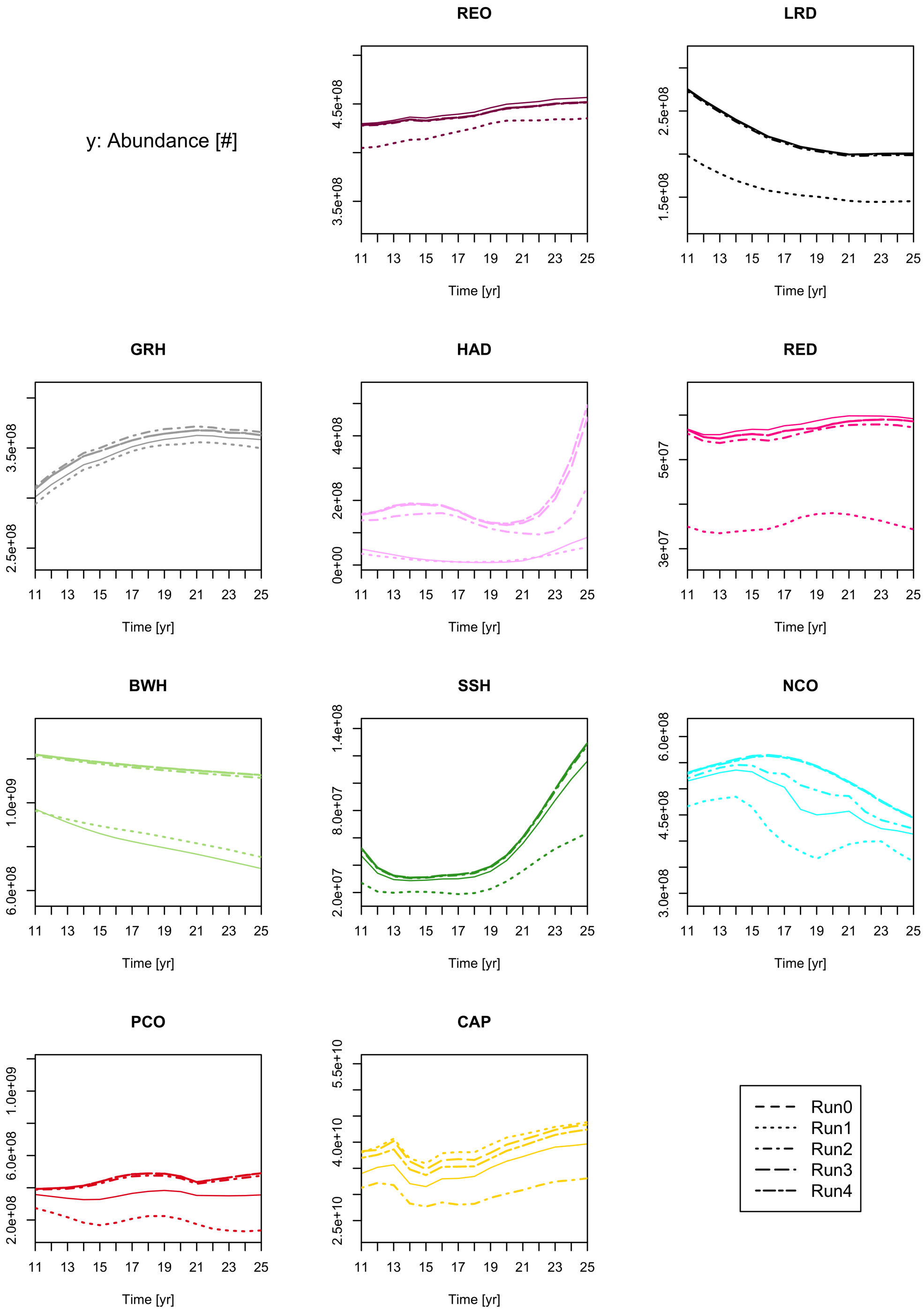


Figure 3.3: Runs 0 – 4. Abundance for each prey species of cod after spin-up time. Note different scales for y-axes.

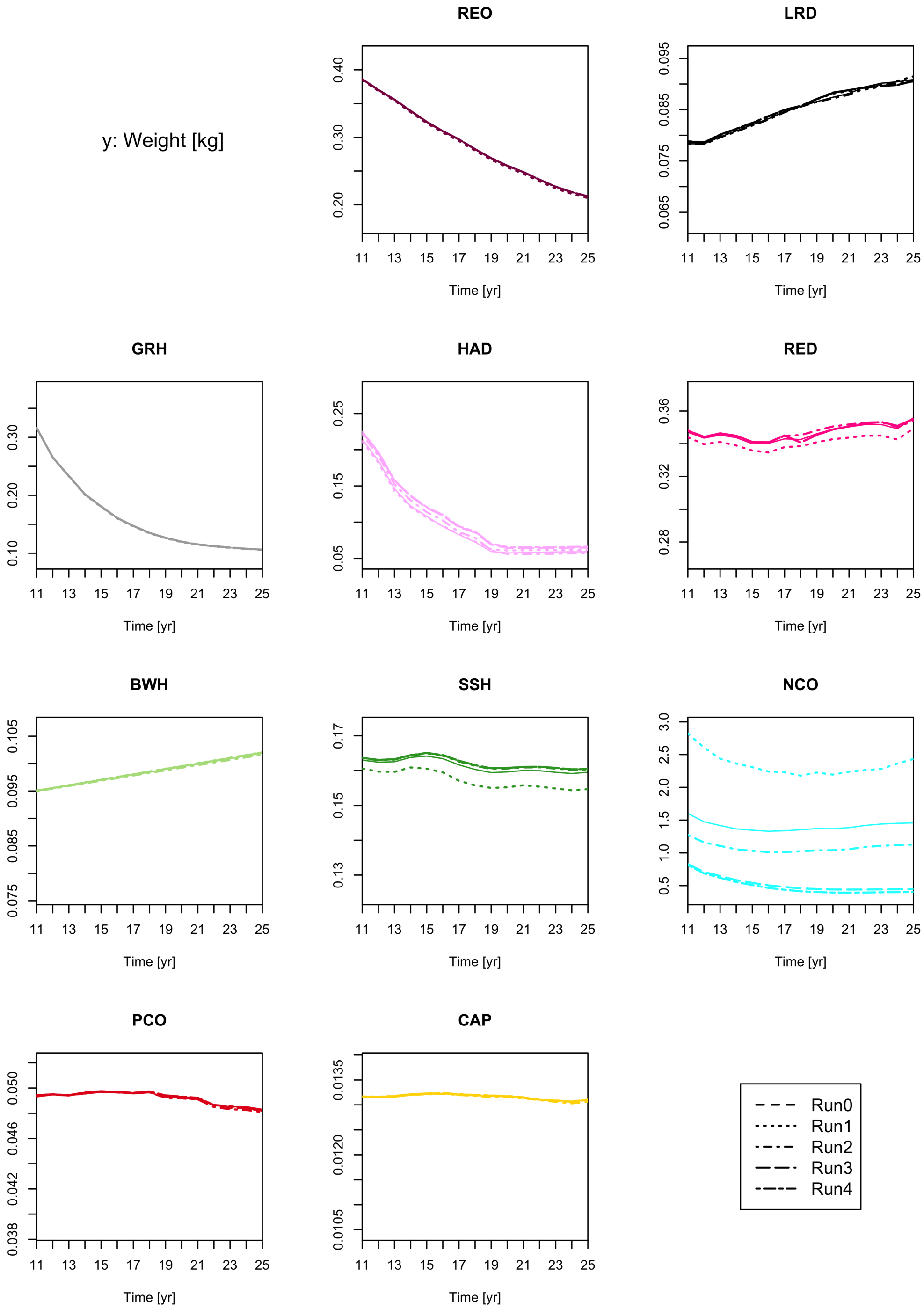


Figure 3.4: Runs 0 – 4. Average weight for each prey species of cod after spin-up time. Note different scales for y-axes.

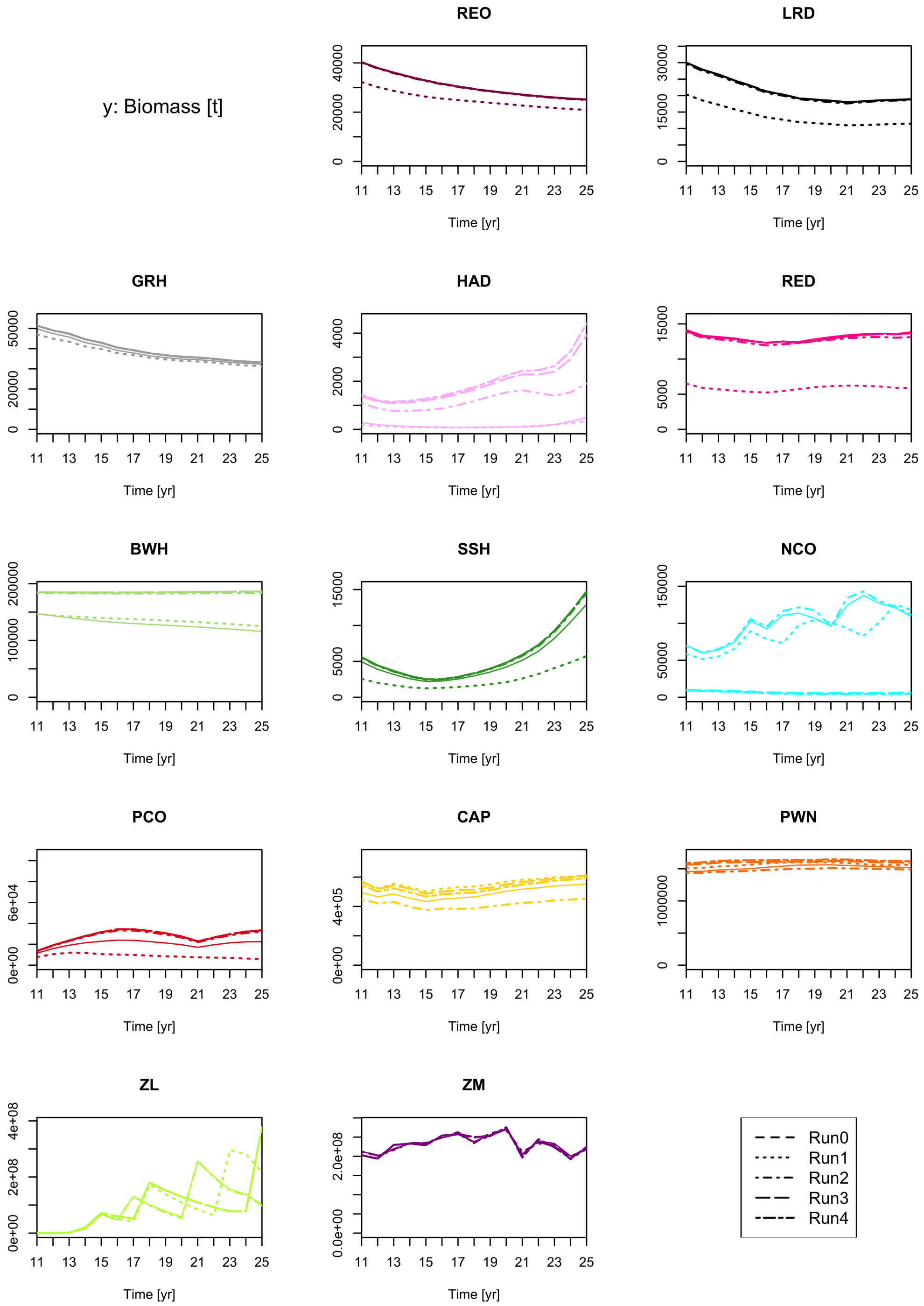


Figure 3.5: Runs 0 – 4. Biomass for each prey species of cod after spin-up time. Note different scales for y-axes.

Table 3.2: Run 0. Links in the diet matrix for cod prey. Age specific links according to prey-predator. Red = REO/RED.

	Red	DEL	GRH	HAD	BWH	SSH	NCO	PCO	CAP	PWN	CEP	ZL	ZM
jv-jv	0.01	1e-5	0.3	0.1	0.3	0.1	0.1	0.2	0.9	0.95	0.5	0.95	0.95
ad-jv	0.01	0	0.05	0.01	0.4	0.35	0	0.1	0.95	0.95	0.5	0.95	0.95
jv-ad	0.01	0.5	0.4	0.5	0.4	0.1	0.1	0.2	0.9	0.95	0.5	0.95	0.1
ad-ad	0.01	0.1	0.07	0.4	0.5	0.1	0.1	0.2	0.85	0.95	0.5	0.95	0.1

Considering the number of fish and biomass consumed by cod, some interesting observations can be made. In general, the link defines the fraction of the prey population available to the predator. Therefore, cod should prey predominantly upon species with a strong link and high abundance, whereas for weak links and low abundance less prey is available.

All links for Run 0 were set according to the feeding preferences of cod from literature. This was the original parameterization of the cod diet from which the tuning started. The strongest links were assigned to the major prey species, which are capelin, together with shrimp, krill, and mesozooplankton. This is especially valid for the juvenile cod. Generally, the prey size increases with the body size of the predator, which in the model can be judged by the average weights. Hence, an age-specific distinction was made, for example: no predation by juvenile cod on adult cod (link 0); the adult cod link for mesozooplankton was much lower than for juvenile cod (0.1 vs. 0.95); the link for adult cod preying on juvenile haddock was set five/fifty times higher than for juvenile cod on juvenile/adult haddock. In general, moderate links were set for blue whiting, herring, polar cod, and squid. Links for cod, both redfish, large demersals, and halibut were low. A more detailed overview on the links is given in Table 3.2.

From the results in Table 3.3 it follows that species with the highest links in the diet matrix do not necessarily make up the highest proportion in the diet (both with regard to numbers/biomass consumed). The proportions of individual fish/biomass consumed are averaged for each species over the time of the run (15 years) after spin-up time. Pooled species are only considered for biomass, since numbers are not available.

Most important for the diet of the cod in Run 0 are blue whiting, haddock, and herring, both in terms of individuals and biomass consumed, as well as polar cod (# of individuals) and cod (biomass). Blue whiting is the dominant prey species with proportions of 44% for individuals consumed and 36% for biomass, whereas the other range between 10 and 20%, respectively. Minor prey species with proportions of the diet below 10% are halibut

Table 3.3: Run 0. Results for: Average weight of each prey species; Amount of individuals consumed (and diet proportion %); Biomass consumed (and diet proportion % (a) Run 0, (b) Survey data). *REO and RED not distinguished in stomach database (amount is sum of both).

	Av. weight [g]	Individuals [#]	%	Biomass [t]	%	
					(a)	(b)
REO	289	83102	0.06	24	0.14	4.0*
DEL	3611	8285	0.01	30	0.18	–
LRD	85	0	0.00	0	0.00	1.5
GRH	162	4283102	2.98	696	4.11	< 0.1
HAD	96	23390739	16.25	2238	13.21	3.1
RED	346	1833401	1.27	636	3.75	4.0*
BWH	98	62669925	43.55	6171	36.45	1.1
SSH	161	23454530	16.30	3782	22.34	2.9
NCO	1408	1538742	1.07	2167	12.80	3.8
PCO	49	23980568	16.66	1179	6.97	5.8
CAP	13	2671612	1.86	35	0.20	44.2
PWN	–	–	–	0.0042	0.000025	8.2
CEP	–	–	–	0.0001	0.000001	–
ZL	–	–	–	0.6813	0.004025	12.4
ZM	–	–	–	0.0270	0.000160	13
DL	–	–	–	0.0001	0.000001	–

and beaked redfish, as well as capelin and cod (# of individuals), and polar cod (biomass). With less than 1%, the golden redfish, large demersals, capelin, and all pooled species (even $< 0.01\%$) are of negligible importance for the diet.

The observed proportions are inconsistent with the set up in the links, where capelin, for example, is set up to nine times higher numbers than herring. In further consequence capelin should be consumed in higher amounts than herring, since both links and abundance of capelin are high. Nonetheless, the results for Run 0 show the opposite. Consistency of links and consumption accounts for polar cod, golden redfish, and the large demersal species. Significantly different is the observation for the pooled species, capelin, halibut, and beaked redfish in comparison to the links. Accordingly, the diet proportions in Run 0 do not yet match observations from the stomach database (Table 3.3).

In total, the numbers of fish consumed by cod are roughly 143 million individuals and 17 thousand tonnes on average per year. Compared to the historical record of, for example, year 1984 with 2.3 million tonnes consumed by cod (Dolgov *et al.*, 2011), the model output is significantly lower.

Over time, the predation by cod changes significantly for some species (Fig. 3.6). After year 14 the consumption of halibut, beaked redfish, blue whiting, capelin, shrimp, and mesozooplankton decreases. At the same time, year 14, the consumption of krill, haddock, but also capelin peaks. The consumption for blue whiting, herring, and polar cod increases during the second half of the run. For years 19 to 21, higher cannibalism can be observed. The consumption of labile detritus is neglectable, however it declines by more than half after year 16. For large demersals and squid no plot is given because of their minor importance in the diet of Run 0 and they are excluded in the following runs.

3.1.2 Tuning Runs

The results for the tuning runs, Run 1 – 4, are given together with Run 0 in the same plots for better comparison, i.e. for abundance, weight, and biomass of the species in Figures 3.3, 3.4, and 3.5. Table 3.1 provides survey data for comparison of the results with natural stock size and weight. The results concerning the biomass consumed by cod for each prey are shown in Figures 3.6 – 3.8. The trends for consumption of individuals are similar to the ones of consumed biomass and therefore no plots are given. An overview on numbers and biomass consumed is given in Table 3.4.

ABUNDANCE A similar pattern for most species can be observed with regards to Run 1 as the run with the lowest numbers in abundance (Fig. 3.3). Exceptions are blue whiting and capelin. For both of these species the abundances for the initial run, Run 0, are lower. In Run 1 all links for predator-prey interaction were set to maximum 1.

The ranking of the runs is more variable in terms of highest abundances reflecting the specific tuning for each species. The abundances for all runs of capelin, halibut as well as cod and haddock are separable, whereas for the remaining species, abundances of Runs 2–4 are highest and differ only slightly. For both redfish and long rough dab the highest abundance is seen in Run 0. Polar cod, herring, and blue whiting are highly abundant in Runs 2–4. Run 0 is not highest for these three species, though. For all species, except capelin, the diet links were lowered by several orders of magnitude for Runs 2–4.

Capelin is most abundant in Run 1, followed closely by Runs 3 and 4. Run 0 is lower and Run 2 well below all of them. A similar distribution applies to halibut with the difference of Runs 1 and 2 being switched in regards to most and least abundant. Similar to capelin and halibut, cod and haddock can be grouped. In Runs 3 and 4 their abundances are highest, followed by Run 2. Run 0 and then Run 1 are lowest, as for most of the other species.

The temporal development of the stocks can be roughly split into two groups: either species increase or decrease in abundance over time. Those increasing comprise redfish (RED, REO), halibut, haddock (years 20+), herring (years 18+), polar cod (with a significant minimum for year 21, though), and capelin (years 14+). Those decreasing include long rough dab (stabilized years 20+), blue whiting, and cod. For cod, the start of declining abundance differs among the runs and lies between 14 (Run 1) and 16 years (Runs 3,4).

WEIGHT All observations made for the abundance are the opposite for the average weights of the species, as seen by comparing the two sets of plots in Figures 3.3 and 3.4. Apart from capelin, polar cod, and beaked redfish with relatively stable average weights, the weights increase whenever the abundances decrease over time and vice versa.

Differences between the runs are likewise small for capelin and polar cod, as well as for golden redfish, long rough dab, halibut, and blue whiting. For the rest of the species the weights changed, most obviously for cod. For beaked redfish and herring the average weight in Run 1 is lower than for the rest of the runs. For haddock this distinction is not as clear, but likewise for Runs 3 and 4 the average weight is higher than for the rest. The ranking of runs for cod is exactly the opposite to the order in terms of abundance: Run 4 < Run 3 < Run 2 < Run 0 < Run 1.

BIOMASS Most species have similar distribution and behavior over time of the runs for biomass and abundance (compare Figures 3.3 and 3.5). The temporal development of the biomass is generally less variable and therefore smoother in comparison to the abundance for all species.

Differences between patterns of abundance and biomass only occur for the predator cod as well as for halibut and golden redfish. The cod biomass is lowest for Runs 3 and 4, which are the runs with highest abundance. Significantly higher biomass for cod is seen in the other runs in the following order: Run 1 < Run 0 < Run 2. Halibut and golden redfish have increasing abundances over time. Their biomass, however, declines for the period of the run. But the ranking of the runs remains the same for these two species.

Finally, also the invertebrates can be included and investigated in terms of their biomass. The shrimp biomass is mostly stable over time and varies little among the runs. The order is from lowest to highest: Run 2, 0, 1, 3, 4. Likewise, the differences between the runs for mesozooplankton biomass is low but varies temporally up to one order of magnitude, with minima in years 12, 15, 18, 21, and 24. The krill biomass undergoes the most distinct development. After year 13 the amount increases by two orders of magnitude. The curve is similar for all runs with an offset for the maxima, though:

Runs 0 and 2 - maxima in years 15, 18, 25; Run 1 - maxima in years 15, 18, 23; Run 3 and 4 - maxima in years 15, 17, 21. The variability of krill biomass is therefore negatively correlated with the mesozooplankton biomass, which reflects their feeding on similar species.

CONSUMPTION In comparison to the biomass, the patterns of consumption are quite similar for most of the species. Therefore, the described differences between biomass and abundance apply to consumption also. Exceptions are found for beaked redfish, where the biomass is stable while the consumption declines. Most interestingly, the pattern of capelin and polar cod, as well as the invertebrates, are the opposite - a generally decreasing consumption versus increasing biomass. For cod, the trends within each run for both biomass and consumption are rising constantly.

Additionally, it can be said that the consumption for the tuning runs decreases from Run 1 to Run 4. The highest consumption during Run 1, declining afterwards, is in accordance with the step-wise weakening of the links in the diet matrix. This is valid for both individuals and biomass preyed upon. A summary on total amounts is given in Table 3.4.

In Figure 3.6 the decreasing consumption among the different runs becomes obvious. Run 1 is well above all others. Exceptions are the consumption for invertebrates (PWN, ZL, ZM) and capelin. For these, most biomass is consumed by cod in Run 2, and second in Run 0. Otherwise, the initial Run 0 lies below Run 1 as well and higher than Run 2. For the majority of the species Run 3 still has higher consumption than Run 4 (Fig. 3.7). However, again the consumption of capelin as well as for haddock and golden redfish is different. For these, consumption in Run 3 is lowest. For mesozooplankton and krill the links were set to 0 for Runs 3 and 4, and for labile detritus the link was low enough to obtain no consumption.

Over time the pattern of consumption equals the descriptions above for Run 0. For most of the prey the consumption decreases during the run, especially before year 16. At the end consumption increases again for long rough dab, halibut, and golden redfish. Increasing consumption throughout the entire run is observed for herring and polar cod. However, the consumption of polar cod shows a minimum between years 16 and 18. This is similar for beaked redfish and most of the remaining prey only less pronounced. Compared to cannibalism the pattern is opposite. Cannibalism increases for all runs after year 16 and during the last five years decreases again, except for Run 3. Then however, the consumption of cod by cod is negligible. For Run 2 minimal cannibalism occurs in year 22.

The consumption of capelin and polar cod seems to correlate with the invertebrate groups mesozooplankton and krill, respectively. The consumption of the invertebrates shows several peaks. These maxima are similar for capelin and mesozooplankton, whereas the consumption of polar cod and krill seems negatively associated (best observable for Run 3, Fig. 3.7). For example, the peak in krill consumption for year 15 is followed by a low consumption of polar cod the year after. Both, capelin and mesozooplankton, are consumed at a maximum in year 14.

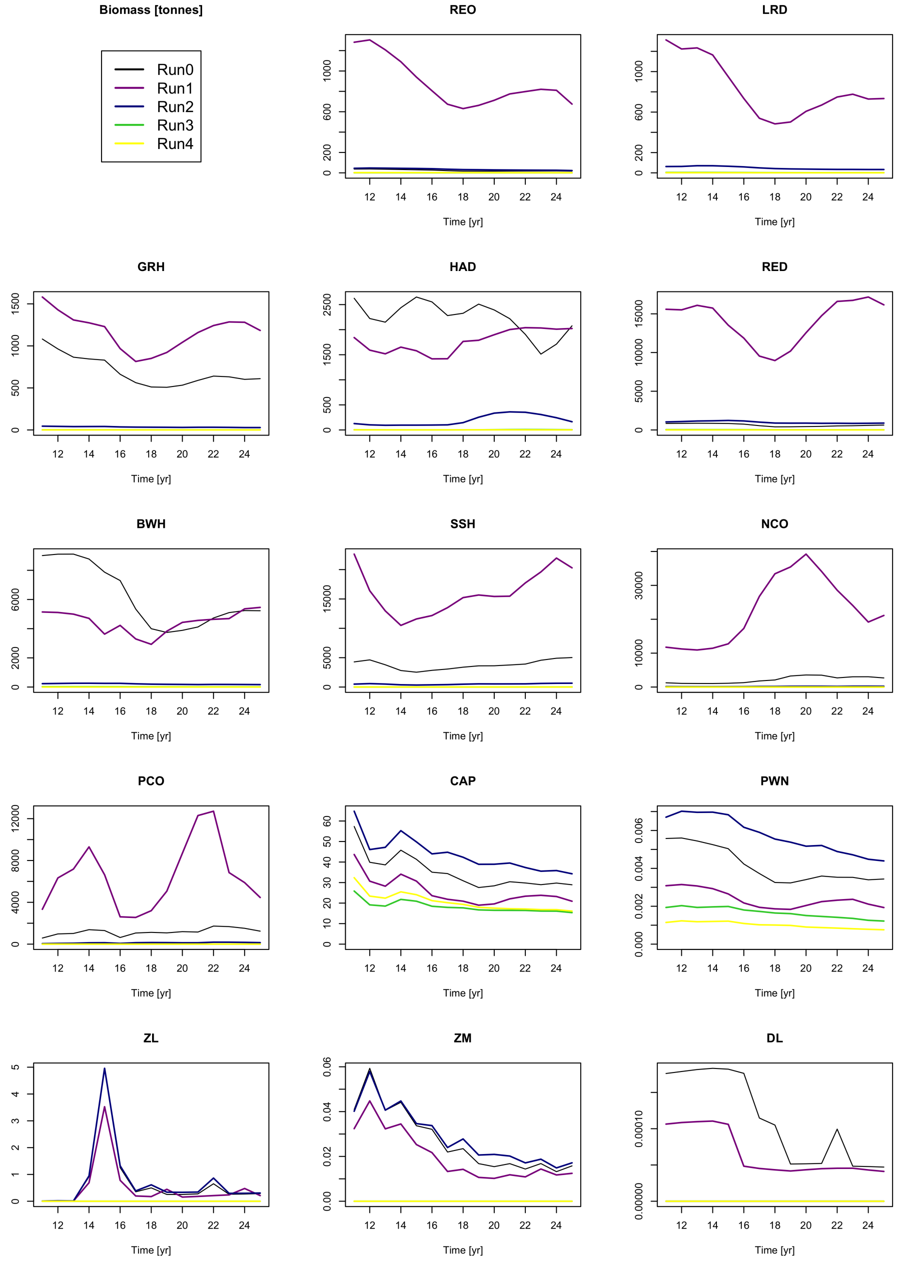


Figure 3.6: Consumption of biomass by cod for Runs 0 – 4 after spin-up time. Note different scales for y-axes.

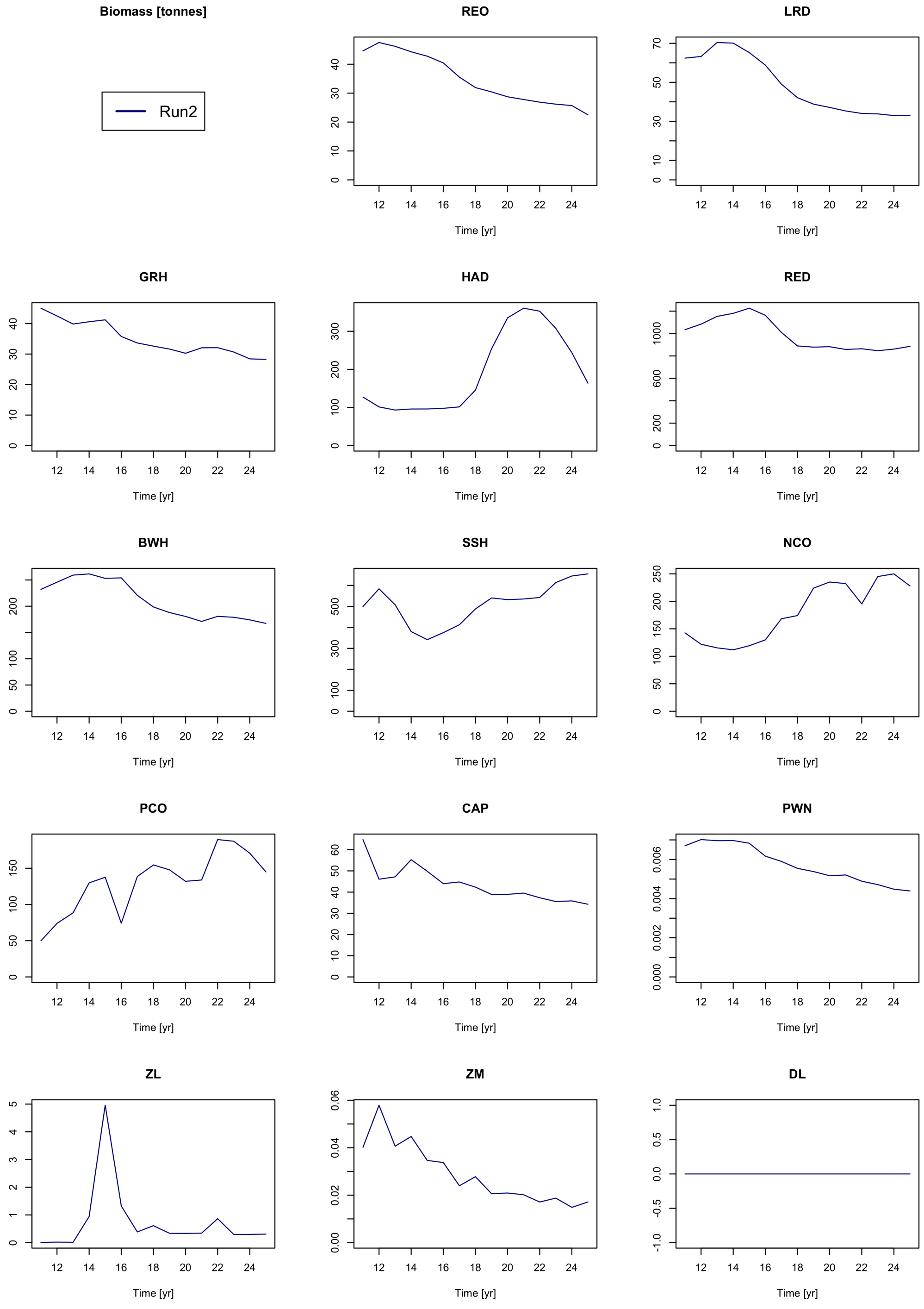


Figure 3.7: Consumption of biomass by cod for Run 2 after spin-up time. Note different scales for y-axes.

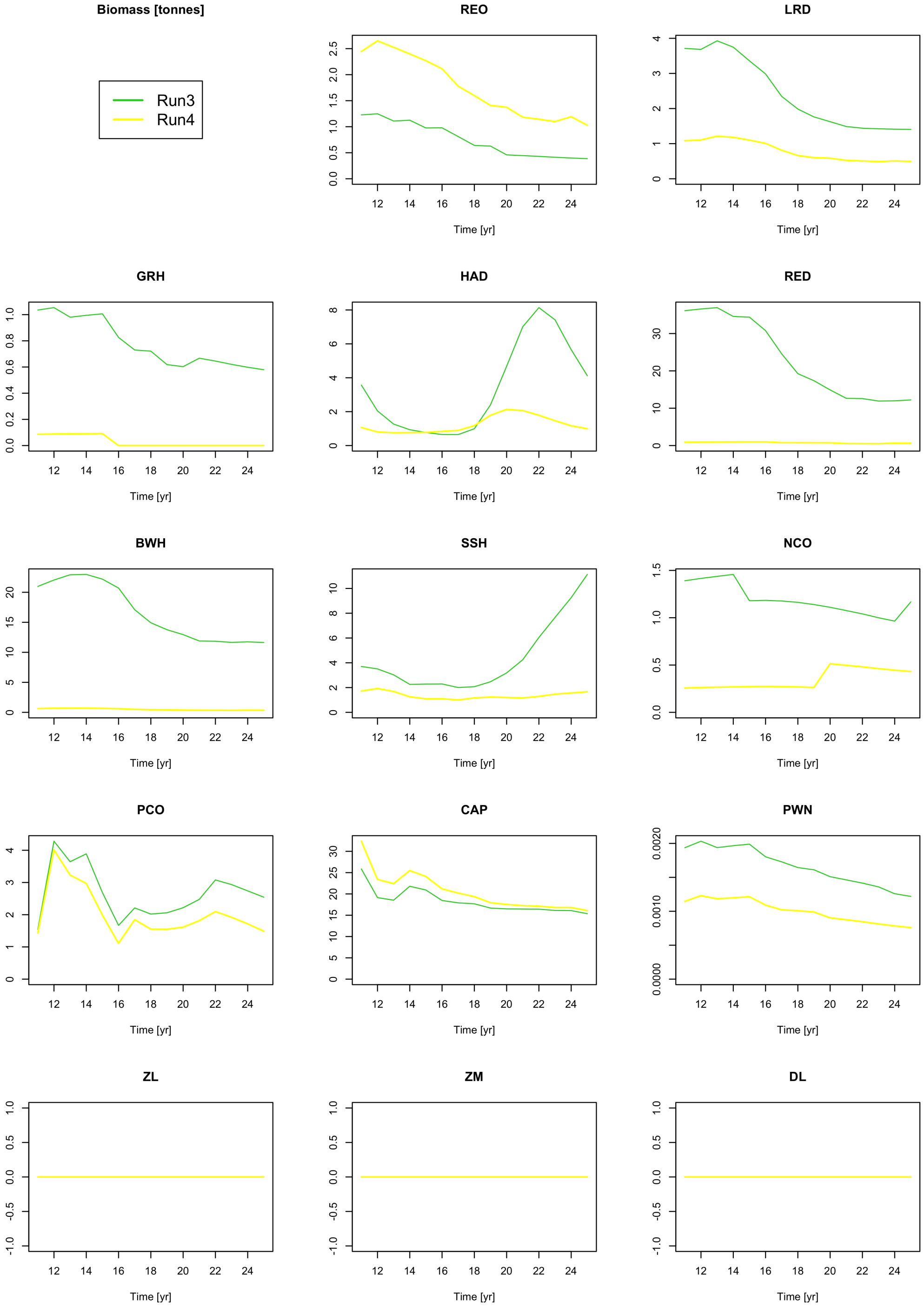


Figure 3.8: Consumption of biomass by cod for Runs 3 – 4 after spin-up time. ZL, ZM, and DL were excluded from the diet matrix for these runs and consumption is therefore zero. Note different scales for y-axes.

Table 3.4: Diet compositions for Runs 0 – 4. Top: individuals consumed, bottom: biomass consumed. The sum is given for each below all the species.

	RUN 0	RUN 1	RUN 2	RUN 3	RUN 4
			Individuals [#]		
REO	83102	3067593	120404	2603	6048
LRD	0	9705508	570545	28390	9274
GRH	4283102	7238317	215344	4791	182
HAD	23390739	18393242	1948063	31915	11588
RED	1833401	41216638	2840653	66607	2217
BWH	62669925	45318908	2146756	168669	5045
SSH	23454530	102240614	3146824	26764	8425
NCO	1538742	9586013	165710	2278	718
PCO	23980568	131623332	2649655	54174	41073
CAP	2671612	1954556	3320107	1387661	1560083
SUM	143905721	370344721	17124061	1773852	1644654
			Biomass [t]		
REO	24.0	879.3	34.8	0.75	1.75
LRD	0.0	827.3	48.4	2.42	0.79
GRH	695.7	1171.4	35.0	0.78	0.03
HAD	2238.5	1772.3	191.8	3.35	1.23
RED	635.5	14069.1	987.9	23.12	0.77
BWH	6170.7	4467.5	211.0	16.62	0.50
SSH	3782.0	16079.0	510.0	4.34	1.37
NCO	2166.6	22488.7	179.5	1.19	0.35
PCO	1179.5	6473.6	130.2	2.67	2.02
CAP	35.1	25.7	43.6	18.27	20.54
PWN	0.00415	0.00238	0.00576	0.00166	0.00100
ZL	0.68131	0.48739	0.73570	0.00000	0.00000
ZM	0.02702	0.02004	0.02888	0.00000	0.00000
DL	0.00011	0.00007	0.00000	0.00000	0.00000
SUM	16928.3	68254.4	2373.1	73.5	29.3

3.1.3 Summary for Diet Proportions

In summary, the absolute consumption (Table 3.4) goes down by weakening the links for most of the prey species, leaving strong links for the major prey, such as capelin. The decline of the total amount consumed is not linearly related to the amount of decrease in the links, neither for individuals nor biomass consumed. Cod loses weight with decreasing consumption. However, the proportions of the species within the diet become closer to the desired numbers, which are given for comparison in Table 3.5. The line *Atlantis* in the table gives the proportions for comparison of the results for (a) with and (b) without invertebrates. The other data refer to the original proportions from the stomach database.

Reducing the links for the minor prey species leads to an increase of the proportion of capelin in the diet. The numbers of individual capelin preyed upon remain at the same order of magnitude for all runs. Nevertheless, the consumption of capelin reacts to changes in the links. In Run 3, the link for capelin was halved as was the resulting consumption for both numbers and biomass. For the pooled species, weak differences between the runs were observed. Even though the changes were below 0.1%, it can be noted that the consumption increased from Run 1 to Run 2. Figure 3.9 summarizes the changes of diet proportions for the different runs with regard to

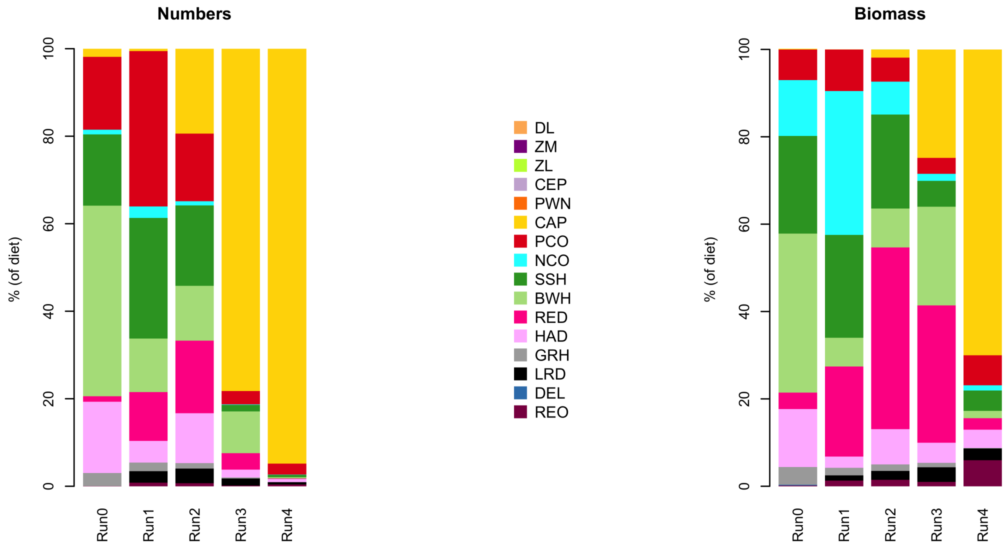


Figure 3.9: Diet proportions for Runs 0 – 4. The left plot is for numbers of individuals consumed, the right plot for biomass.

» consumption of individuals:
The species that is preyed upon strongest shifts from blue whiting in the initial run, Run 0, to herring and polar cod in Run 1. The following two runs result in a decreasing importance of these three species, while capelin increases as does beaked redfish and long rough dab. In Run 4 almost 95% of the individuals in the cod diet are capelin, followed by 2.5% polar cod.

» consumption of biomass:
Capelin becomes more present in the diets of Runs 2 and 3, but not as strong as for the numbers. This is also true for beaked redfish, which is the major diet component for the Runs 2 – 3. Run 1 is dominated by cannibalism if only looked at in terms of the biomass consumed. However, cod is also the heaviest prey. Whereas blue whiting is less dominant in the diets of Runs 1 and 2, the consumption is high again in Run 3. This is opposite to the herring consumption. Long rough dab increases in the diet for all three runs (Runs 1–3). Halibut and golden redfish remain similar in all runs. The final run, Run 4, gives similar proportions as in the diet from the stomach database (Table 3.5). The results, that can be read from Figure 3.9, are the following: capelin 70%, polar cod 8%, herring 4.7%, cod 1.2%, haddock 4.2%, redfish 8.6%, blue whiting 1.7%, long rough dab 2.7%, halibut 0.1%. Capelin is the most important prey biomass-wise (50%). More than three quarters of the remaining diet are split among polar cod, herring, haddock, and golden redfish in almost equal parts. Cod, beaked redfish, blue whiting, and long rough dab make up the rest, thus are minor prey for Run 4.

Table 3.5: Average diet proportions (%) for most important prey species of cod. All values are means for the period 1984 – 2011. "*Atlantis*" shows diet proportions that the results of this study were compared with: (a) excluding data for "Other", (b) additionally excluding data for all invertebrates (ZL, ZM, PWN). Red designates REO and RED together. From stomach database.

	Other	**ZM**	**ZL**	**PWN**	**CAP**	**SSH**	**PCO**
Min	9.75	1.16	1.59	2.87	8.07	0.11	0.08
Ave	17.68	10.66	10.21	6.78	36.42	2.37	4.75
Max	34.95	44.68	27.82	18.70	62.24	6.77	12.63
Atlantis							
(a)	–	12.95	12.40	8.24	44.24	2.88	5.77
(b)	–	–	–	–	66.62	4.34	8.69

	NCO	**HAD**	**Red**	**GRH**	**BWH**	**LRD**
Min	0.28	0.09	0.02	0.00	0.00	0.19
Avg	3.13	2.52	3.26	0.05	0.92	1.24
Max	12.88	6.81	15.60	0.40	6.03	5.82
Atlantis						
(a)	3.81	3.06	3.97	0.06	1.12	1.51
(b)	5.73	4.61	5.97	0.09	1.68	2.27

3.2 Further Analysis of Results

The closer investigation of the relationships between cod, capelin, and polar cod was achieved by evaluating correlations between abundances and consumption of the three species. Figure 3.10 visualizes that the capelin abundance (red) was negatively correlated with the capelin consumption (green) as well as with the polar cod abundance (light blue). The cod abundance (blue) correlated positively with the consumption of capelin. To determine the strength of the correlations, linear regression models were applied.

First, for each species the correlation between abundance and consumption by cod was investigated, i.e. whether the consumption of prey was a function of the prey abundance. Figures 3.11 and 3.12 show five plots (Runs 0 – 4) for each of the three species. The consumption was correlated with abundance and the R^2 values are given for each run (Table 3.6). Several correlations, especially for polar cod, had to be rated as insignificant owing to p-values > 0.05 (**) and were excluded from further analysis.

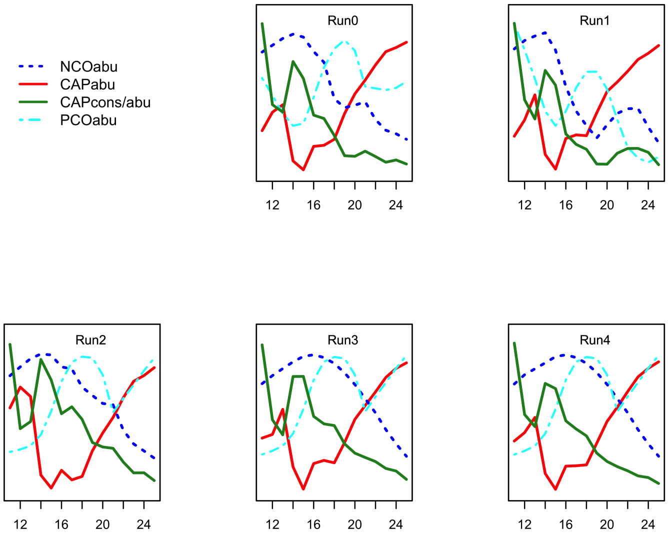


Figure 3.10: Abundances of cod, polar cod, and capelin as well as capelin consumption in relation to capelin abundance for Runs 0 – 4. No scale is given for the y-axis, since relations are more important than absolute values for this overview.

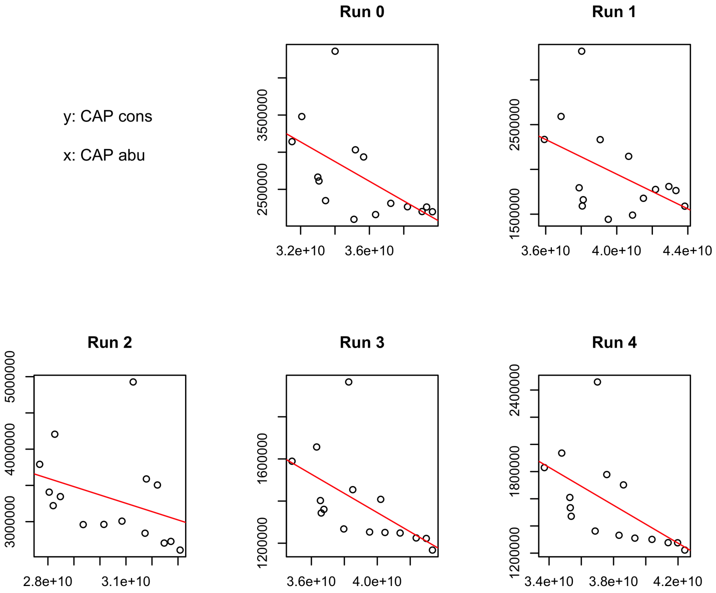


Figure 3.11: Overview on the correlation for abundance and consumption of cod on capelin.

If the predation by cod was effective, the correlation should be negative, thus the more prey consumed the lower the abundance of the prey. Overall, this relationship was observed, but with a much higher correlation for cod than for polar cod and capelin. For the latter two the runs with highest correlation were Runs 2 and 4 and Runs 0, 3, and 4, respectively. Capelin became a major part of the diet in Runs 3 and 4, whereas cannibalism decreased to very low levels for those. In relation to the low cannibalism in Runs 3 and 4, the trend for cod is also positive showing that the predation on the population did not affect the abundance. Such a trend can however only be observed, if the data are not correlated for the entire period. The consumption of cod for these runs followed a sigmoid curve over time, hence for correlation the data were split in two sets, which are of perfect correlation each. In summary, the consumption of cod and capelin is a function of the species abundances. For polar cod this is only true for Runs 2 (positive trend) and 4 (negative trend). It has to be noted that for the capelin data in year 11 (first year after spin-up time) the consumption were always highest. However, abundance was lower than for the end of the run. Therefore, year 11 could be regarded as an outlier of the dataset. Linear regression that excluded this year gave higher correlation (e.g. Runs 3 and 4: $R^2 = 0.6$) that reassured that the capelin abundance was dependent on the cod predation.

Second, the ratio of capelin consumption and capelin abundance was correlated with cod abundance (CAP consumption / CAP abundance versus NCO abundance) (Fig. 3.13). The same was done for capelin correlated with polar cod as well as for polar cod and cod. Only the first two models had correlations > 0.3 (Table 3.6). Therefore, no correlation between polar cod and cod was found. Again, correlations with capelin could be improved by excluding year 11 from the analysis.

Figure 3.13 (upper box) shows positive trends for the correlation between capelin and cod. This refers to higher consumption of capelin proportional to the capelin stock for higher abundance of cod. Thus, the consumption increased with increasing numbers of predators. The analogue correlation for polar cod consumption and cod abundance was low and is not shown.

The second box in Figure 3.13 (bottom) presents the correlation of polar cod abundance with capelin consumption proportional to the capelin stock. The trends are negative, apart from Run 1, and of lower correlation than for capelin and cod. Additionally, Runs 0 and 1 were of insignificant correlation. Nonetheless, the results indicate that more capelin was consumed when the polar cod stock was smaller.

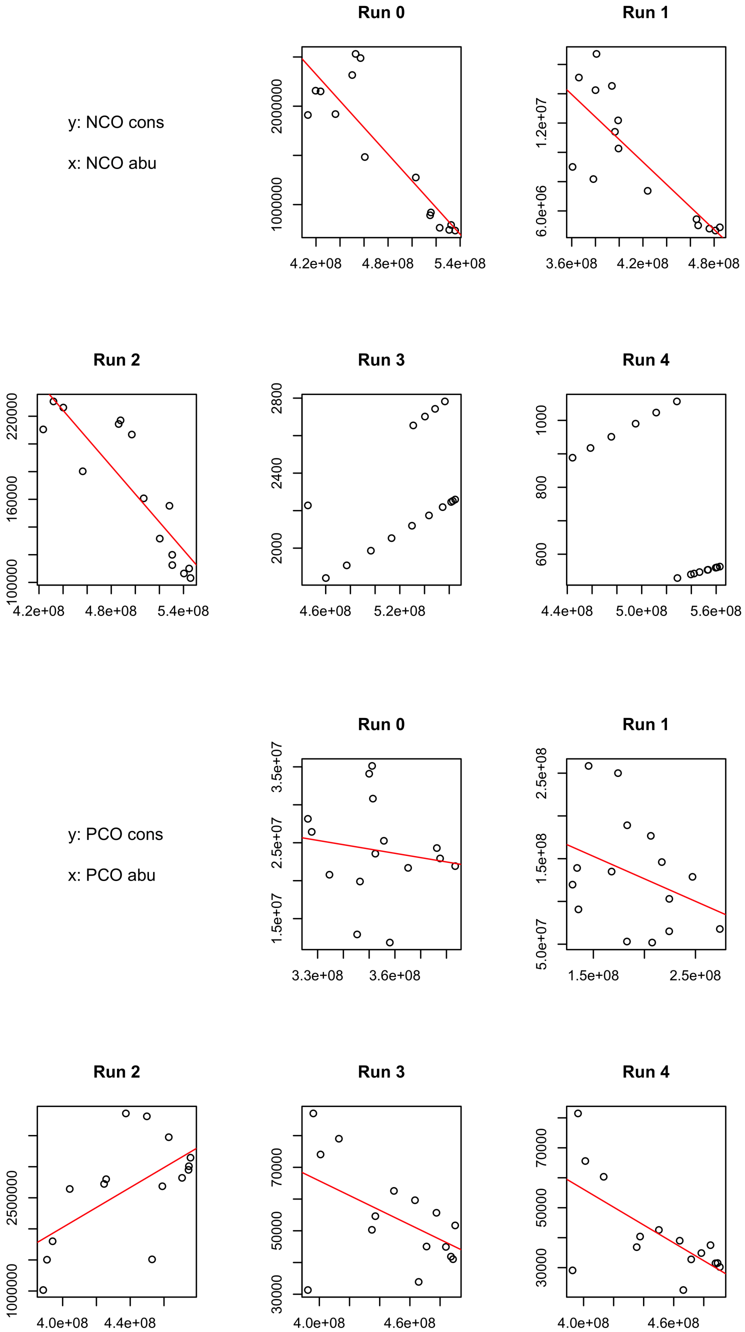


Figure 3.12: Overview on the correlation for abundance and consumption of cod on: top – cod, bottom – polar cod.

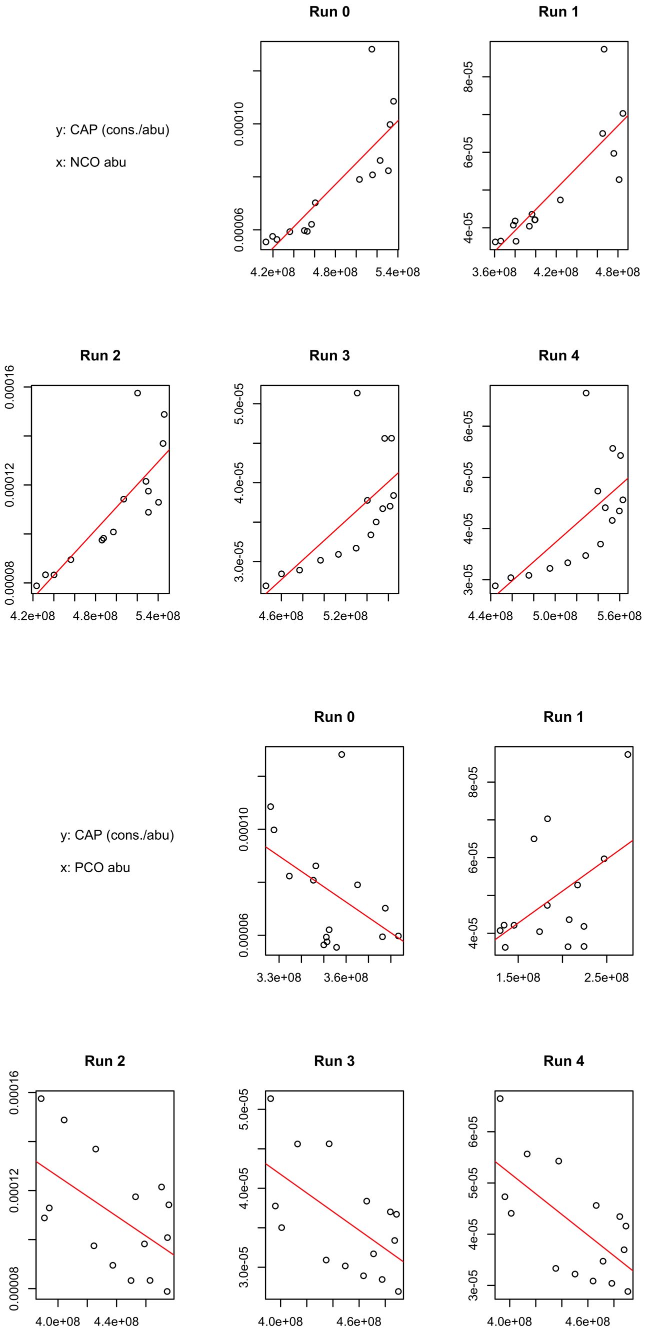


Figure 3.13: Correlation of consumption (as a function of stock size) and abundance: top – capelin versus cod, bottom – capelin versus polar cod.

Table 3.6: R^2 for linear regression models applied for different correlations: (a) consumption versus abundance, (b) consumption/abundance versus abundance. *p-value 0.01 – 0.05 **p-value > 0.05. (No labeling for p-value < 0.01)

RUN			0	1	2	3	4
(a)							
	CAP –	CAP	0.33*	0.22**	0.12**	0.33*	0.33*
	PCO –	PCO	0.02**	0.12**	0.38*	0.26*	0.45
	NCO –	NCO	0.78	0.67	0.76	–	–
(b)							
	CAP/CAP –	NCO	0.69	0.71	0.68	0.46	0.44
	CAP/CAP –	PCO	0.20**	0.24**	0.30*	0.35*	0.44

3.3 Excluded Runs with Contribution to Tuning Process

As indicated in the methods, most of the runs submitted for this thesis contributed to the results without being described. Explanation of the several steps that lead to the final runs are included for completeness.

In total, 96 runs were submitted, 39 of which used the latest update of the code (including Runs 0 – 4). Besides the five final runs that were analyzed, 23 (19 old code, 4 new code) runs can be mentioned as a major contribution to the results presented. A list of all these is attached in the Appendix (Table A.2) and explains the runs that are specified in the description below. Apart from the contribution to the results, the runs also helped to discover some bugs in the parameter files and code. For example, the horizontal distribution of capelin, the lower gape size of cod or the migration of the shrimp from the overwintering area in the Norwegian Sea to the Barents Sea were revised. Code corrections were performed by Cecilie Hansen. Moreover, from the close examination of the cod diets questions arose about the predation output. This led to an update of the code by the developers in Australia and to the revision that has been used for the final runs.

In the beginning of the tuning work for the cod diet, cod consumed far more polar cod than capelin, no matter how the links were set. Consequently, a first step was to check whether it could be a bug in the code. All diet links were set to 0 and only capelin was allowed as prey (Run 5). Indeed, the absolute consumption was low. Another possibility was to check upon a potential lack in the spatial overlap of cod and capelin. This was done by exchanging the values for distribution of capelin with the ones of polar cod (several modifications of distributions, Runs 6 – 8). The only mentionable effect was that polar cod was in better condition when being distributed similarly to capelin since other predators of polar cod besides cod, e.g. bearded seals, could not prey upon the polar cod any longer. However, the capelin consumption did not increase in relation to polar cod. To be sure that no mistake occurred within the distribution, cod, capelin, and polar cod were distributed in limited boxes, eventually. Thereby it was investigated whether the diet composition would change with the 100% overlap and feeding preferences of cod exclusively for capelin and polar cod. Because the results remained the same, further investigations with modified recruitment parameters for polar cod that reduced the stock size and gave higher initial numbers for capelin were carried out. The change of the recruitment of polar cod helped as did the additionally lowered gape size of cod. Upscaling of initial capelin abundance seemed to be less useful (runs with distribution to limited boxes: Runs 9 – 13). To evaluate the changes for the modified parameters, initial runs were submitted and compared (e.g. Runs 14 and 15).

Furthermore, consumption rates for cod were increased in two runs, to observe whether the total consumption would increase. Runs 20 and 21 therefore were parameterized with ten-fold consumption rates for cod and both cod and capelin, respectively. This resulted in enhanced condition of the cod for both runs, but more in Run 21 than 20. Likewise, owing to higher condition of capelin with increased consumption rates for this species, a preference for capelin was achieved. Since these changes, however, involved various resulting tuning steps, the idea of enhancing consumption rates must be left for further study.

Finally, the latest update of the code (revision 3728) guaranteed a reliable diet output of the model. To ensure a possible, at least comprehensive, and relative comparison between runs with the old and new code, all parameters where kept as similar as possible to the former code. Still changes, especially in the lower trophic levels (pers. comm. C. Hansen) could not be fixed entirely for the thesis version of the code. Nevertheless, with the update, for the first time tuning of the links made a notable difference for capelin consumption and the final tuning process started. Several runs were submitted to test the response within the diet proportions to changes in the links (Runs 16 – 19). From Run 18, for example, it was observed that setting the link to $1{\cdot}10^{-8}$ for haddock and beaked redfish and $1{\cdot}10^{-6}$ for blue whiting and herring, reduced the proportion to zero. None of these species were eaten for such a weak link. Hence, the links were carefully increased again in Run 19. The links set in Runs 3 and 4 that were finally used for analysis in the thesis are referable to the observations from those previous runs.

Initially, work on the capelin collapses in relation to fisheries had started as part of this thesis as well (Runs 22 – 28). The idea was to increase natural capelin mortality simulating fishing mortality as preliminary work to the implementation of the fisheries submodule. This could have been a first approach to test the hypothesis whether fisheries were a major cause of the capelin collapses, e.g. as indicated by Ushakov & Prozorkevich (2002). With the tuning of the cod diet being more important, though further investigations were left for future work, since after all, the tuning state of the cod diet determines most of the interpretations for results of this tuning.

4 – Discussion

When it comes to summarizing and evaluating the results, the question arises which of all the runs submitted were best. Clearly, this is dependent on the definition of "best". In the following the evaluation of the runs will regard tuning the diet matrix towards the relative (percental) and absolute diet proportions given in the stomach database. Likewise, the interactions between cod, capelin, and polar cod are investigated in terms of linkage in the model and in nature. Additionally, the state of all prey species of cod referring to their stock sizes and condition of the individuals is considered in relative comparison and compared to survey data. The limits of the applied set-up of the model and parameter files for this study are discussed as well as suggestions for improving this specific part of the tuning work within NoBa Atlantis. Eventually, general advantages and limits to Atlantis are reviewed.

Relative Diet Proportions

The aim of the tuning work was to capture the diet proportions from the stomach database within an order of magnitude before exploring different biological interaction or climate and fisheries scenarios. Run 4 reproduces the observed diet proportions most closely. Within this run, capelin is the most important component and its consumption lies one order of magnitude above the other prey. Polar cod and both redfish groups rank second, followed by herring, cod, and haddock. Of minor importance are blue whiting and long rough dab. Halibut consumption is negligibly small and the pooled species are not included. In total, the succession of prey fits the survey data well (Figure 3.9, Table 3.5).

The runs with the worst match with the observed diet composition are Run 0 and especially Run 1. As mentioned previously, Run 1 reflects the prey preferences of cod in the model without specific tuning (all links equal to one). In that case only about 4‰ of the diet consists of capelin. The minimal consumption of capelin in historical records still made up 8% of the diet (Table 3.5). The consumption of invertebrates is equally low, while cod and herring together constitute more than half of the diet. Survey data shows that the consumption of herring as well as cannibalism never in the record exceeded 7 and 13%, respectively, even for the years when the capelin collapses caused reduced prey availability for cod. Further, the dominant position of blue whiting in the model diet is unrealistic. In addition to a rather minor consumption in reality, blue whiting was not recorded in the stomachs of cod in the Barents Sea before the early 2000s. The presence of blue whiting in the cod diet in the model can be explained by the spatial overlap of the stocks off the northern coast of Norway. Even though the initialization of the stock size in NoBa Atlantis was done according to the early 1980s, the distribution of stocks considered averages through until the present.

Total Consumption of Cod

Opposite to the results for diet proportions, the runs that best match the total consumption of cod, i.e. absolute amount of prey, are Runs 0 and 1. This was because cod was allowed (by setting the links high) to eat as much as possible within the scope of the set of other parameters such as growth rate. In the other runs, the links are reduced (for some species by up to four orders of magnitude) resulting in declines in the total consumption. In terms of numbers of individuals consumed, the total is reduced from Runs 1 to 4 by two orders of magnitude, while for the biomass the difference is three orders.

Comparing these to the observed consumption, the model predicts values that are at a minimum thirty times too small. The highest sum in the model, for Run 1, is 70 000 tonnes. The initial set-up in Run 0 gives 16 000 tonnes and in Run 4 consumption equals only 29 tonnes (Table 3.4). The reasons are mainly found in the strongly reduced links, which without changing other parameters such as the individual weights of the prey species, will prevent the total consumption from increasing.

Nevertheless, several observations remain unexplained, for example, regarding the consumption of invertebrates in Runs 0 – 2. A possible explanation for the total low consumption might be found in the lower gape size limit of cod, since a response to changes in the links is observed, e.g. from Run 1 to Run 2 the consumed shrimp biomass doubled (from 0.0024 – 0.0058). However, the absolute change is diminishing small compared to the remaining prey (Table 3.4). The value for the lower gape size limit is small (10^{-10}) and also smaller than it would be in nature (approximately 10^{-3}), cod length meters versus plankton length millimeters). Regardlessly, natural proportions for setting the parameters in the model might not be an appropriate guidance level by absolute means, as observed from this diet tuning work.

Furthermore, an interesting observation is the stable consumption of capelin throughout the runs. The range of the total amount remained within the same order of magnitude as the link remained the same for capelin. Relative to the other links in Run 2, the link for capelin was only two orders of magnitude higher, but its total consumption highest for all runs. By increasing the difference relative to the links for the other prey the total consumption did not increase further. Additionally, in Run 0, when difference between the links was smallest, the consumption ranked second for all runs. This indicates the need for a broader consideration of different parameters for diet tuning.

Stocks and Individual Weight

Stock size and biomass as well as the individual weights for cod, capelin, and polar cod in the model are below the reference data as shown in the previous chapter. Especially cod is too light in weight, but the initialization of the weights is reasonable (Table 2.2), except for polar cod, for which the weights should be doubled for future work with the model.

Explanations for why the average stock sizes (after spin-up time) are low compared to the survey data lie first of all in mortality, starvation, and predation. Nevertheless, for example for cod, the time of year for the model output is of importance, which is in December. The time for the model output is hard coded into the model version used in this study. In December cod adults migrate out of the Barents Sea to spawn along the western coast of Norway. This reduces the cod abundance in the Barents by at least one order of magnitude. Further explanation of the lower than observed model abundances relates to the initial values for cod that are set to $5.5 \cdot 10^8$ individuals and remain at this level. For capelin the abundance is initialized with a value of circa $2.5 \cdot 10^{11}$ individuals. The number is reduced via a specific parameter for stock sizes, which for this model version is set to 0.22 (changing it to one would result in five times the current biomass). Polar cod abundance has been tuned to lower levels by means of recruitment options. As stated above, the initial setting results from former tuning work on the model providing the here applied version of NoBa Atlantis, which could not be adjusted for these parameters within the scope of this study.

Trophic Interactions - Cod, Capelin, Polar Cod

The links for predator-prey interactions are set according to the known strength from the stomach database. From the results of the tuning runs it follows that differences between the links for minor and major prey species have to be several orders of magnitude to achieve a signal in reduced/increased consumption. This is especially obvious for the initial run (Run 0). Even though the links are tuned to reasonable proportions compared to stomach data, desired diet proportions are not reached. This relates to the discovered prey preferences of cod in the model by means of Run 1, which for polar cod and herring are highest but besides comprise the heavier species, such as blue whiting and redfish. The lighter species such as invertebrates and capelin are not preferred. The resulting diet proportions do not match the survey data and therefore are unrealistic. Likewise, what would have been expected was a strong predation on species for which both the links were set high and the stocks were high in abundance. A large fraction of prey would be available to the predator. The case of low consumption of capelin and invertebrates has shown that this was not observed despite their high links and abundances in the model.

Regardless of the diet proportions and total amount of consumption, increased predation leads to reduced prey abundance. Regression analysis shows that especially for the tuned Runs 2 – 4, capelin abundance is affected by cod predation. In accordance, the capelin consumption is higher than for Runs 0 and 1. For polar cod, though, the same correlation is low or insignificant. One possible explanation might be that because of the short lifespan of capelin, predation affects the population stronger than for other prey, owing to recruitment failure. Polar cod have more age groups defined in the model than capelin and hence show less feedback. Another possibility could be a suppression of the signal owing to stronger predation on polar cod by other species, hence a potential for outcompeting cod.

Further regression analysis shows a clear linear relationship for cod between cannibalism and cod stock size. Thus, cannibalism is captured in the model. Also, due to a strong reduction in the links, cannibalism is lowered in Runs 3 – 4 to such a level that the correlation proves the predation to be of minor importance. To summarize, the capelin consumption in relation to (a) cod and (b) polar cod abundances, shows that: (a) the capelin stock is clearly affected by predation and abundance of the predator cod, (b) there is an inverse relation found between capelin and polar cod, e.g. high polar cod abundance coincides with high capelin predation and therefore reduced abundance of the capelin stock.

In addition to the observed species interactions, density-dependent regulation of individual fish weight is observed from the tuning runs. A large proportion of prey available to the predator will result in good condition (stable or increasing weights) for the predator only if the predator abundance is not too large. Higher abundance of predators will reduce the per capita consumption and therefore the individual condition. For example, whenever the cod weight declines owing to an overall decreased consumption, this is amplified by stable or even increasing numbers of cod. As the amount of prey available per capita declines by reduction of consumption through the diet matrix, cod lose weight. For similar reasons, blue whiting, long rough dab, and beaked redfish, gain in biomass and weight. Being preyed upon strongly in the first years of the runs, abundances decrease, and with reduced predation by cod in the course of the run the populations recover, if not to say increase remarkably.

Two runs that were excluded from the analysis (Runs 20 and 21) show that with increased consumption rates the cod condition improves. Higher consumption rates and adapted tuning for other predator-prey interactions in the model have to be regarded as solution to establish realistic feeding conditions in general. All of these observations are important characteristics of basic food web interactions. Capturing these relations builds a foundation for further runs exploring more complex dynamics within the Atlantis model, which also includes close examination of more species.

Future Work

In summary, the tuning work on the cod diet was successful in achieving the diet proportions as found in the stomach database. Basic feeding relations were captured for capelin and cod. The results show that the method applied can be a first approach to a final tuned diet matrix. Additionally, the work helped to understand the necessary parts for diet tuning within Atlantis better. More realistic predator-prey interactions might be achieved by implementing the following suggestions of improvement. Furthermore, future research ideas are described.

One solution for enhancement of the results is a more comprehensive tuning of the parameters instead of solely adjusting the diet matrix links as has been done in this study. Likewise, overcoming some limitations to the version of Atlantis used in the thesis could be done through using an updated version of the code and parameter files. This will provide a more dynamic working situation for dealing with new findings from the tuning results. The limitations resulting from the time scope of this thesis, however, emphasized advantages of using fixed versions of Atlantis for retrieving results.

An update of the code and parameter files would lead to a more complete state of the tuning of the species, retrieve output of the model at different times to capture the temporal variations in the cod diet, use a more detailed output of the diet matrix including age specific predation (fine tuning of juvenile and adult diets), and the inclusion of invertebrates for cod consumption. A better resolution of the predator-prey interactions would follow.

Another approach to the diet tuning of cod in Atlantis would be to include the main prey species from the stomach database one by one in the diet matrix, in decreasing order of importance. Thereby, the relation for each species would be tuned until the level of observations in nature were reached. However, because of secondary interactions this process might be rather slow and the combined tuning of all prey species more worthwhile instead. Most convenient might be an initial examination of the predator-prey interactions by applying links of equal strength for all prey to observe significant problems of tuning, e.g. unrealistic consumption of a prey species owing to untuned spatio-temporal overlap or unrealistic proportions of prey in the diet because of untuned weights. Afterwards, setting up the links might be easier and more effective.

One example from the runs of this study concerns testing the importance of the strength of the diet matrix links on consumption behavior. In Runs 9 – 13 spatial overlap is maximized by including capelin, polar cod, and their predator cod in a limited number of boxes. Cod is allowed to prey upon capelin and polar cod as defined by the diet matrix. Even though capelin is more abundant and stronger links for consumption are set, the polar cod remains the most preferred prey for these runs. As a consequence, the fraction of prey available to the predator is not the most important parameter in Atlantis if other interactions are not yet tuned. These include parameters such as growth and consumption rates, recruitment options, and gape size limits (pers. comm. C. Hansen).

Similarly, improvements could be achieved by setting the links for capelin not exactly to the maximum despite leaving it higher than for the other prey. This would open the possibility of increasing the link eventually for fine tuning. Not least, secondary effects have to be considered more closely, especially as the links in the Barents Sea ecosystem are so close. Capelin, for example, is prey for most of the carnivores of the area. Years of lower predation pressure by cod would give other capelin predators potential to increase feeding.

Moreover, extending the observations from focussing on primary interactions to secondary levels is rewarding and more species should be considered in the analysis. Also, the interactions in the trophic web should be regarded for the entire model grid, thus including the entire area of the cod distribution such as the spawning grounds of cod. Longer runs would ensure the coverage of several life cycles of cod and most likely better reflect the ecosystem dynamics in completeness.

Ongoing research with NoBa Atlantis, besides the general implementation work and development of the fisheries submodule, covers impacts of the feeding behavior of migrating species on the Barents Sea food web, e.g. baleen whales (Hansen & Skern-Mauritzen, 2012). This implies the reconstruction of more complex trophic interactions. Another interesting possibility to pursue would be to examine the capelin collapses. The reduction of initial abundances of capelin could be a first approach. Such an exercise could be expanded to cover all cod prey including changing the proportion of species to determine their effects on cod. Would a switch in prey occur if capelin was less abundant than polar cod? Could other pelagic fish compensate the lack of capelin as a prey? Would cannibalism or consumption of other non-pelagic prey species increase?

Further aspects for investigations of trophic interactions include the 0-group fish. The youngest fish constitute a large proportion of the pelagic food web and serve as a food source for many of the species in the area. As the larval stage of the fish is not included in NoBa Atlantis at present, this is a promising avenue of research. Including the 0-group fish in the model would also help to simulate well-studied and known processes such as the predation of juvenile herring on capelin larvae, which contributed strongly to the capelin collapses (Gjøsæter & Båmstedt, 1998; Pedersen *et al.*, 2009; Wiedmann *et al.*, 2012), which contributed strongly to the collapses of the capelin stock. Additionally, the importance of jellyfish for the ecosystem in relation to climate and the 0-group fish, was proposed recently for the Barents Sea (Eriksen *et al.*, 2012). Atlantis could help to better understand interactions with species such as jellyfish, which are difficult to observe from field work.

All previous suggestions could then be coupled with climate change scenarios to examine, for example, ocean temperature affecting stock dynamics and feeding behavior. Runs for changing climate conditions would be a proper way to explore different hypotheses concerning regime shifts or resilience of the Barents Sea ecosystem, e.g. in Hop & Gjøsæter (in press); Yaragina & Dolgov (2009); Johannesen *et al.* (2012).

Working with NoBa Atlantis as a model under development resulted in numerous runs that could not be included in the thesis but revealed promising fields for future work with the model, such as investigating capelin collapse dynamics by increasing natural mortality to represent added fishing mortality. Future work should comprise fisheries scenarios to investigate the impacts on the ecosystem on a more holistic scale. Scenarios in combination with climate change should accomplish the list of future work as intended by setting up NoBa Atlantis. The diet tuning of cod seems to be rather far removed from such holistic investigations but contributes to establishing a solid basis for Atlantis modeling in the Barents Sea.

Limits and Advantages of Atlantis

Challenges while working with Atlantis are manifold, but most commonly relate to the deterministic nature of the model. Not least, this includes the need for sufficient experience through training and guidance from implementing the model until the interpretation of the results (Fulton, 2010). Being an end-to-end model, Atlantis includes an accordingly long list of parameters to be defined. This allows many options. However, all initial conditions, be it stock size, growth or stock-recruitment parameters, depend on the quality of field and laboratory observations. Often, data may be incomplete or experimental work assumes conditions not observed in the wild (Kaplan *et al.*, 2010). Furthermore, Plagányi (2007) points out that for most of the marine ecosystems insufficient data might be available to implement such models. Norway and Russia, however, have a long record of stocks in the Barents Sea owing to the strong historical role of fisheries in these countries (Jakobsen & Ozhigin, 2011). Still, when initializing Atlantis certain values have to be estimated by means of the “most appropriate guess” such as, for example, the biomass of jellyfish where data are difficult to capture from the field. Likewise, detailed data do not always resolve problems within Atlantis, as the model itself often is much coarser in resolution than the data. Rose (2012) proposes the important question of how to deal with the error from the parameterization put into the model. The author stated that theoretically-oriented models might be a better start to unravel ecosystem dynamics, such as shown in a model developed for the Barents Sea by Lindstrøm *et al.* (2012).

Similar concern is drawn by Fulton (2010), who is outlining the dimensions of end-to-end modeling (up to 14 orders of magnitude - from microbial to ocean basin scales) and the potentially inaccurate understanding of the usage of these models. Being aware of the weaknesses of the modeling approach is pivotal to understand the approach and communicate the results properly (Fulton *et al.*, 2011). Atlantis has been developed to achieve long-term trends for a more holistic view on the studied system rather than a detailed prognostication of the dynamics. Rose (2012) acknowledges the long-term benefits gained from end-to-end models and thereby requests their further development “with appropriate caution and thoughtfulness”. Advantages of these models comprise the combined exploration of ecosystem, climate, and humankind, smoothing the way for better understanding of the system dynamics in a broad sense. Fulton (2010) summarizes the overall advantages in three points: first, enhancing the holistic thinking about the system; second, exploring system dynamics that are mostly non-linear; third, evaluating appropriate management of a system with respect to its non-stationarity. Until the performance of models like Atlantis is better understood, the results are most suitable for examination of “what if” scenarios (Rose *et al.*, 2010). The comprehension of end-to-end models might be broadened by studying the combinatorial and feedback effects on sensitivity in these complex models (Pantus, 2007).

5 – Conclusion

A first approach of tuning the cod diet within the NoBa Atlantis model was successful and pointed out the method and parameters that are of major importance for continued diet tuning in the model. The study focused on cod, capelin, and polar cod as the major diet components for the tuning process because of their strong predator-prey relationship and ecological role. Basic food web interactions were captured. Pivotal considerations before future work on the diet can be carried out are summarized here.

- Tuning the links within the diet matrix of cod can achieve the proportions of the natural diet.

- The accuracy to generate the diet proportions in the model is referred to in orders of magnitude.

- The basis for the predation of cod on other species is given by spatial and temporal overlap in distribution, which has to be achieved prior to diet tuning.

- The accomplishment of the absolute diet composition with respect to realistic scales is dependent on additional parameters, presumably consumption and growth rates, and gape size limits.

- A more comprehensive approach, i.e. combining the tuning of several parameters, most likely will lead to an appropriate generation of the cod diet in NoBa Atlantis.

- Density dependent regulation of population characteristics and basic predation behavior are both impacted by changing the strength of predation links in the diet matrix.

Bibliography

ACIA (2005). *Arctic Climate Assessment*. Cambridge University Press.

Aglen, A., Bakketeig, I., Gjøsæter, H., Hauge, M., Loeng, H., Sunnset, B.H. & et al. (2012). Havforskningsrapporten 2012. *Fisken og Havet*, 158 pp.

Anon. (2009). Survey report from the joint Norwegian/Russian ecosystem survey in the Barents Sea August-October 2008. Tech. Rep. No. 1/2009, IMR/PINRO.

Anon. (2011). Survey report from the joint Norwegian/Russian ecosystem survey in the Barents Sea August-October 2011. No. 3/2011. issn 1502-8828. 118 pp., IMR/PINRO.

Blanchard, J., Pinnegar, J. & Mackinson, S. (2002). Exploring marine mammal-fishery interactions using 'Ecopath with Ecosim': modelling the Barents Sea ecosystem. Tech. Rep. 117, CEFAS Lowestoft.

Bogstad, B. & Gjøsæter, H. (2001). Predation by cod (Gadus morhua) on capelin (Mallotus villosus) in the Barents Sea: implications for capelin stock assessment. *Fisheries Research*, **53**, 197–209.

Bogstad, B., Haug, T. & Mehl, S. (2000). Who eats whom in the Barents Sea? *NAMMCO Scientific Publications*, **2**, 98–119.

Brand, E., Kaplan, I., Harvey, C., Levin, E., P.S. andFulton, Hermann, A. & Field, J. (2007). A spatially explicit ecosystem model of the California Current's food web and oceanography. Nmfs-nwfsc-84, U.S. Dept. Commerce NOAA.

Browman, H.I. & Stergiou, K.I. (2004). Perspectives on ecosystembased approaches to the management of marine resources. *Marine Ecology Progress Series*, **274**, 269–303.

Browman, H.I. & Stergiou, K.I. (2005). Politics and socio-economics of ecosystem-based management of marine resources. *Marine Ecology Progress Series*, **300**, 241–296.

Carmack, E., Barber, D., Christensen, J., Macdonald, R., Rudels, B. & Sakshaug, E. (2006). Climate variability and physical forcing of the food webs and the carbon budget on panarctic shelves. *Progress in Oceanography*, **71**, 145–181.

Carscadden, J.E. & Vilhjálmsson, H. (2002). Capelin- What are they good for? *ICES Journal of Marine Science*, **59**, 863–869.

Christiansen, J.S., Dalmo, R.A. & Ingebrigtsen, K. (1996). Xenobiotic excretion in fish with aglomerular kidneys. *Marine Ecology Progress Series*, **136**, 303–304.

Craig, P.C., Griffiths, W.B., Haldorson, L. & McElderry, H. (1981). Ecological Studies of Arctic Cod (Boreogadus saida) in Beaufort Sea Coastal Waters, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, **39**, 395–406.

Devries, A.L. (1982). Biological antifreeze agents in coldwater fishes. *Comparative Biochemistry and Physiology Part A: Physiology*, **73**, 627–640.

Dolgov, A.V. (2009). Trophic structure of the Barents Sea fish assemblage with special reference to the cod stock recoverability. *Progress in Oceanography*, **81**, 165–173.

Dolgov, A.V., Johannesen, E., Heino, M. & Olsen, E. (2010). Trophic ecology of blue whiting in the Barents Sea. *ICES Journal of Marine Science*, **67**, 483–493.

Dolgov, A.V., Orlova, E.L., Johannesen, E. & Bogstad, B. (2011). Chapter 8.4 Piscivorous fish. In *The Barents Sea - Ecosystem, Resources, Management*, Tapir Academic Press.

Drinkwater, K. (2005). The response of Atlantic cod (Gadus morhua) to future climate change. *ICES Journal of Marine Science*, **62**, 1327–1337.

Eide, A. (2008). An integrated study of economic effects of and vulnerabilities to global warming on the Barents Sea cod fisheries. *Climatic Change*, **87**, 256–262.

Ekman, S. (1953). The boreal fauna of the North Atlantic. In Sidgwick & Jackson, eds., *Zoogeography of the Sea*, 100–141.

Erga, S.R., Ssebiyonga, N., Hamre, B., Frette, Ø., Rey, F. & Drinkwater, K. (2012 (in press)). Nutrients and phytoplankton biomass distribution and activity at the Barents Sea Polar Front during summer near Hopen and Storbanken. *Journal of Marine Systems*.

Eriksen, E., Prozorkevich, D. & Dingsør, G.E. (2009). An Evaluation of 0-Group Abundance Indices of Barents Sea Fish Stocks. *The Open Fish Science Journal*, **2**, 6–14.

Eriksen, E., Prozorkevich, D., Trofimov, A. & Howell, D. (2012). Biomass of Scyphozoan Jellyfish, and Its Spatial Association with 0-Group Fish in the Barents Sea. *PLOS ONE*, **7**.

Eriksen, E.E. (2012). Survey report from the joint Norwegian/Russian ecosystem survey in the Barents Sea August-October 2012. 139 pp., IMR/PINRO Joint Report Series.

Fulton, E. (2010). Approaches to end-to-end ecosystem models. *Journal of Marine Systems*, **81**, 171–183.

Fulton, E.A., Fuller, M., Smith, A. & Punt, A.E. (2004). Ecological Indicators of the Ecosystem Effects of Fishing: Final Report. Tech. Rep. Report Number R99/1546, CSIRO, Australian Fisheries Management Authority.

Fulton, E.A., Smith, A. & Smith, D. (2007). Alternative Management Strategies for Southeast Australian Commonwealth Fisheries: Stage 2: Quantitative Alternative Management Strategies for Southeast Australian Commonwealth Fisheries: Stage 2: Quantitative Management Strategy Evaluation. Tech. rep., CSIRO, Australian Fisheries Management Authority.

Fulton, E.A., Link, J., Kaplan, I., Savina-Rolland, M., Johnson, P., Ainsworth, C., Horne, P., Gorton, R., Gamble, R.J., Smith, A. & Smith, D. (2011). Lessons in modelling and management of marine ecosystems: the Atlantis experience. *Fish and Fisheries*, **12**, 171–188.

Gjøsæter, H. (1995). Fish and the Ecological Impact of the Modern Fishing Industry in the Barents Sea. *Arctic*, **48**, 267–278.

Gjøsæter, H. (2009). Commercial fisheries (fish, seafood and marine mammals). In *Ecosystem Barents Sea*, Tapir Academic Press.

Gjøsæter, H. & Båmstedt, U. (1998). The population biology and exploitation of capelin (Mallotus villosus) in the barents sea. *Sarsia*, **83**, 453–496.

Gjøsæter, H., Dommasnes, A., Båmstedt, U. & Røttingen, B. (1998). The Barents sea capelin stock 1972–1997. A synthesis of results from acoustic surveys. *Sarsia*, **83**, 497–510.

Gjøsæter, H., Bogstad, B. & Tjelmeland, S. (2002). Assessment methodology for Barents Sea capelin, Mallotus villosus (Mueller). *ICES Journal of Marine Science*, **59**, 1086–1095.

Gjøsæter, H., Huse, G., Robbestad, Y. & Skogen, M. (2008). Havets ressurser og miljø 2008 (in Norwegian). *Fisken og Havet.*

Gjøsæter, H., Bogstad, B. & Tjelmeland, A. (2009). Ecosystem effects of the three capelin stock collapses in the Barents Sea Published in collaboration with the University of Bergen and the Institute of Marine Research, Norway, and the Marine Biological Laboratory, University of Copenhagen, Denmark. *Marine Biological Research*, **5**, 40–53.

Gjøsæter, H., Ushakov, N.G. & Prozorkevich, D.V. (2011). Chapter 5.2 Capelin. In *The Barents Sea - Ecosystem, Resources, Management*, Tapir Academic Press.

Godiksen, J.A., Hallfredsson, E.H. & Pedersen, T. (2006). Effects of alternative prey on predation intensity from herring Clupea harengus and sandeel Ammodytes marinus on capelin Mallotus villosus larvae in the Barents Sea. *Journal of Fish Biology*, **69**, 1807–1823.

Haidvogel, D.B., Arango, H., Budgell, W., Cornuelle, B., Curchitser, E., Lorenzo, E.D., Fennel, K., Geyer, W., Hermann, A., Lanerolle, L., Levin, J., McWilliams, J., Miller, A., Moore, A., Powell, T., Shchepetkin, A., Sherwood, C., Signell, R., Warner, J. & Wilkin, J. (2008). Ocean forecasting in terrain-following coordinates: Formulation and skill assessment of the Regional Ocean Modelling System. *Journal of Computational Physics*, **227**, 3595– 3624.

Hallfredsson, E.H. & Pedersen, T. (2007). Growth of the Barents Sea capelin, Mallotus villosus, in relation to climate. *Canadian Journal of Fisheries and Aquatic Sciences*, **64**, 1710–1722.

Hallfredsson, E.H. & Pedersen, T. (2009). Effects of predation from juvenile herring (Clupea harengus) on mortality rates of capelin (Mallotus villosus) larvae. *Canadian Journal of Fisheries and Aquatic Sciences*, **66**, 1693–1706.

Hamre, J. (1994). Biodiversity and exploitation of the main fish stocks in the Norwegian- Barents Sea ecosystem. *Biodiversity and Conservation*, **3**, 474–492.

Hansen, C. (2010a). Atlantis: socioECOnomics and ECOsystem-based fisheries management (@ECO). Proposal for Havet og kysten, delprogram V: Grunnlag for verdiskapning (VERDI).

Hansen, C. (2010b). Setting up Atlantis in the Barents and Nordic Seas. Working Document.

Hansen, C. & Skern-Mauritzen, M. (2012). Studying the effect of migrating whales on the ecosystem of the Barents Sea using an endtoend model. In *Book of Abstracts*, ICES CM 20120/M:14.

Hedeholm, R., Grønkjær, P. & Rysgaard, S. (2011). Energy content and fecundity of capelin (Mallotus villosus) along a 1,500-km latitudinal gradient. *Marine Biology*, **158**, 1319–1330.

Hjermann, D.Ø., Bogstad, B., Dingsør, G.E., Gjøsæter, H., Ottersen, G., Eikeset, A.M. & Stenseth, N.C. (2010). Trophic interactions affecting a key ecosystemcomponent: a multistage analysis of the recruitment of the Barents Sea capelin (Mallotus villosus). *Canadian Journal of Fisheries and Aquatic Sciences*, **67**, 1363–1375.

Hop, H. & Gjøsæter, H. (in press). Polar cod (Boreogadus saida) and capelin (Mallotus villosus) as key species in marine food webs of the Arctic and the Barents Sea.

Hop, H., Welch, H.E. & Crawford, R.E. (1997). Population Structure and Feeding Ecology of Arctic Cod Schools in the Canadian High Arctic. In *Fish ecology in Arctic North America*, American Fisheries Society.

Horne, P.J., Kaplan, I.C., Marshall, K.N., Levin, P.S., Harvey, C.J., Hermann, A.J. & Fulton, E.A. (2010). Design and Parameterization of a Spatially Explicit Ecosystem Model of the Central California Current. Tech. rep., U.S. Dept. Commerce NOAA.

Howell, D. & Bogstad, B. (2010). A combined Gadget/FLR model for management strategy evaluations of the Barents Sea fisheries. *ICES Journal of Marine Science*.

Hunt, G.L., Blanchard, A.L., Boveng, P., Dalpadado, P., Drinkwater, K., l. Eisner, Hopcroft, R.R., Kovacs, K.M., Nocross, B.L., Renaud, P., Reigstad, M., Renner, M., Skjoldal, H.R., Whitehouse, A. & Woodgate, R.A. (2012). The Barents and Chukchi Seas: Comparison of two Arctic shelf ecosystems. *Journal of Marine Systems*.

Huse, G. & Toresen, R. (2000). Juvenile herring prey on Barents Sea capelin larvae. *Sarsia*, **85**, 385–391.

Huse, G., Johansen, G.O., Bogstad, B. & Gjøsæter, H. (2004). Studying spatial and trophic interactions between capelin and cod using individual-based modelling. *ICES Journal of Marine Science*, **61**, 1201–1213.

ICES (2000). Report of the Arctic Fisheries Working Group (AFWG), 23 August - 1 September 1999. Tech. rep., ICES, ICES Headquarters, Copenhagen.

ICES (2012a). Report of the Arctic Fisheries Working Group 2012 (AFWG), 20 - 26 April 2012. Tech. rep., ICES, ICES Headquarters, Copenhagen.

ICES (2012b). Report of the Working Group on Interactive Physical-biological and Ecosystem Modelling (WGIPEM), 13–16 March 2012. Tech. rep., ICES, ICES Headquarters, Copenhagen.

Ingvaldsen, R., Asplin, L. & Loeng, H. (2004). The seasonal cycle in the Atlantic transport to the Barents Sea during the years 1997–2001. *Continental Shelf Research*, **24**, 1015–1032.

IPCC (2007). *Climate Change 2007: the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press.

Jakobsen, T. & Ozhigin, V., eds. (2011). *The Barents Sea - Ecosystem, Resources, Management*. Tapir Academic Press.

Jakobsson, O.R., Grantz, M., Kristoffersen, A. & Macnab, Y. (2004). Bathymetry and physiography of the Arctic Ocean and its constituent seas. In M.R. Stein R., ed., *The Arctic Ocean Organic Carbon Cycle: Present and Past*, pp. 1–6, 336p., Springer, Berlin–Heidelberg–New Yor.

Johannesen, E., Ingvaldsen, R.B., Bogstad, B., Dalpadado, P., Eriksen, E., Gjøsæter, H., Knutsen, T., Skern-Mauritzen, M. & Stiansen, J.E. (2012). Changes in Barents Sea ecosystem state, 1970–2009: climate fluctuations, human impact, and trophic interactions. *ICES Journal of Marine Science*, **69**, 880–889.

Johansen, G., Bogstad, B., Mehl, S. & Ulltang, Ø. (2002). Consumption of juvenile herring (Clupea harengus) by cod (Gadus morhua) in the Barents Sea: a new approach to estimating consumption in piscivorous fish. *Canadian Journal of Fisheries and Aquatic Sciences*, **61**, 343–359.

Kaplan, I., Levin, P., Burden, M. & Fulton, E. (2010). Fishing catch shares in the face of global change: a framework for integrating cumulative impacts and single species management. *Canadian Journal of Fisheries and Aquatic Sciences*, **67**, 1968–1982.

Klyashtorin, L. & Lyubushin, A. (2007). *Cyclic Climate Changes and Fish Productivity*. VNIRO.

Lindstrøm, U., Smout, S., Howell, D. & Bogstad, B. (2009). Modelling multi-speciesinteractionsintheBarentsSeaecosystemwith special emphasisonminkewhalesandtheirinteractionswithcod, herring andcapelin. *Deep-Sea Research II*, **56**, 2068–2079.

Lindstrøm, U., Planque, B. & Subbey, S. (2012). A dynamic stochastic foodweb model for the Barent Sea ecosystem. In *Book of Abstracts*, ICES CM 2012/A:19.

Link, J., Fulton, E.A. & Gamble, R. (2010). The northeast US application of ATLANTIS: A full system model exploring marine ecosystem dynamics in a living marine resource management context. *Progress in Oceanography*, **87**, 214–234.

Loeng, H. (1979). A review of the sea ice conditions of the Barents Sea and the area west of Spitsbergen. *Fisken og Havet*, **2**, 29–75.

Loeng, H. (1991). Features of the physical oceanographic conditions of the Barents Sea. In E. Sakshaug, C.C.E. Hopkins & N. Britsland, eds., *Proceedings of the Pro Mare Symposium on Polar Marine Ecology*.

Loeng, H. & Drinkwater, K. (2007). An overview of the ecosystems of the Barents and Norwegian Seas and their response to climate variability. *Deep-Sea Research II*, **54**, 2478–2500.

Mehl, S. & Sunnanå, K. (1991). Changes in growth of Northeast Arctic cod in relation to food consumption in 1984-1988. *ICES Marine Science Symposion*, **193**, 109–112.

Mehl, S. & Yaragina, N.A. (1992). Methods and results in the joint PINRO-IMR stomach sampling program. In B. Bogstad & S. Tjelmeland, eds., *Interrelations between fish populations in the Barents Sea*.

Nakken, O., ed. (2008). *Norwegian Spring-Spawning Herring and Northeast Arctic Cod*. Tapir Academic Press.

Olsen, E.M., Gjøsæter, H., Røttingen, I., Dommasnes, A., Fossum, P. & Sandberg, P. (2007). The Norwegian ecosystem-based management plan for the Barents Sea. *ICES Journal of Marine Science*, 599–602.

Orlova, E.L., Dolgov, A.V., Rudneva, G.B., Oganin, I.A. & Konstantinova, L.L. (2009). Trophic relations of capelin Mallotus villosus and polar cod Boreo gadus saida in the Barents Sea as a factor of impact on the ecosystem. *Deep-Sea Research II*, **56**, 2054–2067.

Ozhigin, V.K., Ingvaldsen, R.B., Loeng, H., Boitsov, V.D. & Karsakov, A.L. (2011). Chapter 2 The Barents Sea. In *The Barents Sea - Ecosystem, Resources, Management*, Tapir Academic Press.

Pálson, O.K. (1994). A review of the trophic interactions of cod stocks in the North Atlantic. *ICES Marine Science Symposia*, **198**, 553–575.

Pantus, F.J. (2007). *Sensitivity analysis for complex ecosystem models*. Ph.D. thesis, School of Physical Sciences, University of Queensland - http://espace.library.uq.edu.au/view/UQ:158483 (accessed 02.06.13).

Pedersen, O.P., Pedersen, T., Tande, K. & Slagstad, D. (2009). Integrating spatial and temporal mortality from herring on capelin larvae: a study in the Barents Sea. *ICES Journal of Marine Science*, **66**, 2183–2194.

Piatt, J. & Methven, D.A. (1992). Threshold foraging behavior of baleen whales. *Marine Ecology Progress Series*, **84**, 205–210.

Plagányi, É.E. (2007). Models for an ecosystem approach to fisheries. Tech. rep., FAO.

Ridgeway, L. & Maquieira, C. (2006). Report on the work of the United Nations Open-ended Informal Consultative Process on Oceans and the Law of the Sea at its 7th meeting.

Rose, K.A. (2012). End-to-end models for marine ecosystems: Are we on the precipice of a significant advance or just putting lipstick on a pig? *Scientia Marina*, **76**, 195–201.

Rose, K.A., Allen, J.I., Artioli, Y., Barange, M., Blackford, J., Carlotti, F., Cropp, R., Daewel, U., Edwards, K., Flynn, K., Hill, S.L., HilleRisLambers, R., Huse, G., Mackinson, S., Megrey, B., Moll, A., Rivkin, R., Salihoglu, B., Schrum, C., Shannon, L., Shin, Y.J., Smith, S.L., Smith, C., Solidoro, C., John, M.S. & Zhou, M. (2010). End-To-End Models for the Analysis of Marine Ecosystems: Challenges, Issues, and Next Steps. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*, **2**, 115–130.

SÆTRE, R., ed. (2007). *The Norwegian Coastal Current - Oceanography and Climate*. Tapir Academic Press.

SAKSHAUG, E. & SKJOLDAL, H.R. (1989). *Life at the ice edge*. Ambio.

SAKSHAUG, E., JOHNSEN, G. & KOVACS, K., eds. (2009). *Ecosystem Barents Sea*. Tapir Academic Press.

SHCHEPETKIN, A.F. & MCWILLIAMS, J.C. (2005). The regional oceanic modeling system (ROMS): a split-explicit, free-surface, topography-following-coordinate oceanic model. *Ocean Modelling*, **9**, 347–404.

SKAGSETH, Ø., FUREVIK, T., INGVALDSEN, R., LOENG, H., MORK, K.A., .ORVIK, K. & OZHIGIN, V. (2008). Volume and heat transports to the Arctic via the Norwegian and Barents Seas. In R. Dickson, J. Meincke & P. Rhines, eds., *Arctic-Subarctic Ocean Fluxes: Defining the role of the Northern Seas in Climate*, 45–64, Springer.

SKOGEN, M.D. & SØILAND, H. (1998). A user's guide to NORWECOM V2.0 the Norwegian ecological model system. *Fisken og havet*.

SKOGEN, M.D., SVENDSEN, E., BERNTSEN, J., AKSNES, D. & ULVESTAD, K.B. (1995). Modelling the Primary Production in the North Sea using a Coupled Three-dimensional Physical-Chemical-Biological Ocean Model. *Estuarine, Coastal and Shelf Science*, **41**, 545–565.

SØREIDE, J.E., H., H., CARROLL, M.L., FALK-PETERSEN, S. & HEGSETH, E. (2006). Seasonal food web structures and sympagicpelagic coupling in the European Arctic revealed by stable isotopes and a two-source food web model. *Progress in Oceanography*, **71**, 59–87.

STENEVIK, E. & SUNDBY, S. (2007). Impacts of climate change on commercial fish stocks in Norwegian waters. *Marine Policy*, **31**, 19–31.

STENSETH, N., MYSTERUD, A., OTTERSEN, G., HURRELL, J., CHAN, K.S. & LIMA, M. (2002). Ecological Effects of Climate Fluctuations. *Sience*, **297**, 1292–1296.

STIANSEN, J.E. & FILLIN (2006). Joint PINRO/IMR report on the state of the Barents Sea ecosystem 2005/2006. Tech. rep., IMR/PINRO.

SUNDBY, S. & NAKKEN, O. (2008). Spatial shifts in spawning habitats of Arcto-Norwegian cod related to multidecadal climate oscillations and climate change. *ICES Journal of Marine Science*, **65**, 953–962.

TJELMELAND, S. & BOGSTAD, B. (1998). MULTSPEC - a review of a multispecies modelling project for the Barents Sea. *Fisheries Research*, **37**, 127–142.

TRAVERS, M., SHIN, Y.J., JENNINGS, S. & CURY, P. (2007). Towards end-to-end models for investigating the effects of climate and fishing in marine ecosystems. *Progress in Oceanography*, **75**, 751–770.

UNITED NATIONS, N.Y. (2005). Plan of Implementation of the World Summit on Sustainable Development (Johannesburg declaration).

Ushakov, N.G. & Prozorkevich, D.V. (2002). The Barents Sea capelin - a review of trophic interrelations and fisheries. *ICES Journal of Marine Science*, **59**, 1046–1052.

Vinje, T. (2001). Anomalies and Trends of Sea-Ice Extent and Atmospheric Circulation in the Nordic Seas during the Period 1864–1998. *Journal of Climate*, **14**.

Wang, M. & Overland, J. (2009). A sea ice free summer Arctic within 30 years? *Geophysical Research Letters*, **36**.

Wassmann, P., Bauernfeind, E., Fortier, M., Fukuchi, M., Hargrave, B., Moran, B., Noji, T., Nothig, E.M., Peinert, R., Sasaki, H. & Shevchenko, V. (2004). Particulate organic carbon flux to the sea floor. In *The Organic Carbon Cycle in the Arctic Ocean*, Springer, Heidelberg–Berlin–New York.

Wassmann, P., Reigstad, M., Haug, T., Rudels, B., Carroll, M.L., Hop, H., Gabrielsen, G.W., Falk-Petersen, S., Denisenko, S.G., Arashkevich, E., Slagstad, D. & Pavlova, O. (2006). Food webs and carbon flux in the Barents Sea. *Progress in Oceanography*, **71**, 232–287.

Wiedmann, M.A., Pedersen, O.P. & Nilssen, E.N. (2012). The recruitment process of the Barents Sea capelin (Mallotus villosus) stock, 2001–2003. *Fisheries Oceanography*, **21**, 379–392.

Wienerroither, R., Johannesen, E., Langøy, H., Eriksen, K.B., de Lange Wenneck, T., Høines, Å. & Bjelland, O. (2011). Atlas of the Barents Sea Fishes. Tech. rep., IMR/PINRO.

Yaragina, N.A. & Dolgov, A.V. (2009). Ecosystem structure and resilience - A comparison between the Norwegian and the Barents Sea. *Deep-Sea Research II*, **56**, 2141–2153.

Yaragina, N.A., Aglen, A. & Sokolov, K.M. (2011). Chapter 5.4 Cod. In *The Barents Sea - Ecosystem, Resources, Management*, Tapir Academic Press.

Zhang, J., Lindsay, R., Schweiger, A. & Steele, M. (2013). The impact of an intense summer cyclone on 2012 Arctic sea ice retreat. *Geophysical Research Letters*, **40**, 720–726.

Appendix

Run Setup

Table A.1: Functional groups defined within NoBa Atlantis. Types of groups: marine mammals (MAM), sea birds (BIR), fish (VERT), shark, and invertebrates and other groups treated as biomass pools ("pooled species", POOL). Some groups are still lacking specific parametrization. Prmd = parameterized as. *[1]DL, DR, and DC are no species but treated as functional groups. *[2]These five groups are treated within their main groups and are not parameterized separately in the model.

#	Acronym	Included Species	Type/Age Grp
1	POB	Polar Bear (*Ursus maritimus*)	MAM/10
2	KWH	Orca (*Orcinus orca*)	MAM/10
3	SWH	Sperm whale (*Physeter macrocephalus*)	MAM/10
4	HWH	Humpback whale (*Megaptera novaeangliae*)	MAM/10
5	MWH	Minke whale (*Balaenoptera acutorostrata*)	MAM/10
6	FWH	Fin whale (*Balaenoptera physalus*)	MAM/10
7	BES	Bearded Seal (*Erignathus barbatus*)	MAM/10
8	HAS	Harp Seal (*Pagophilus groenlandicus*)	MAM/10
9	HOS	Hooded Seal (*Cystophora cristata*)	MAM/10
10	RIS	Ringed Seal (*Pusa / Phoca hispida*)	MAM/10
11	SBA	Arctic Sea birds, prmd *Fratercula arctica*	BIR/10
12	SBB	Boreal Sea birds, prmd *Uria lomvia*	BIR/10
13	SHO	Other Sharks, include picked dogfish and porbeagle	shark/10
14	DEO	Other Demersals, include *Molva molva* and *Brosme brosme*	VERT/10
15	PEL	Large Pelagics, prmd *Salmo salar*	VERT/10
16	PES	Small Pelagics, include lumpsucker, greater argentine and norway pout	VERT/10
17	REO	Other Redfish, prmd (*Sebastes marinus*	VERT/10
18	DEL	Large Demersals, include monkfish, Atlantic halibut, Atlantic wolffish, Northern wolffish and spotted wolffish	VERT/10

#	Acronym	Included Species	Type/Age Grp
19	FLA	Flatfish, prmd *Pleuronectes platessa*, include righteye flounder, the turbot, and true sole	VERT/10
20	LRD	Long Rough Dab (*Hippoglossoides platessoides*)	VERT/10
21	SSK	Skates and Rays, include Arctic skate, thorny skate, sailray, thornback ray, round skate, and spinytail skate	VERT/10
22	MES	Mesopelagics, include pearlside, glacier lanternfish, and barracudina	VERT/10
23	GRH	Greenland Halibut (*Reinhardtius hippoglossoides*)	VERT/10
24	MAC	Mackerel (*Scomber scombrus*)	VERT/10
25	HAD	Haddock (*Melongrammus aeglefinus*)	VERT/10
26	SAI	Saithe (*Pollachius virens*)	VERT/10
27	RED	Redfish, prmd (*Sebastes mentella*)	VERT/10
28	BWH	Blue Whiting (*Micromesistius poutassou*)	VERT/10
29	SSH	Norwegian Spring-Spawning Herring (*Clupea harengus*)	VERT/10
30	NCO	Northeast Arctic Cod (*Gadus morhua*)	VERT/10
31	PCO	Polar Cod (*Boreogadus saida*)	VERT/10
32	CAP	Capelin (*Mallotus villosus*)	VERT/5
33	PWN	Prawns, Shrimp (*Pandalus borealis*)	POOL/2
34	CEP	Cephalopodes, Squid (*Gonatus fabricii*)	POOL/2
35	KCR	Red King Crab (*Paralithodes camtschaticus*)	POOL/1
36	ZG	Gelantinous Zooplankton, include *Aurelia aurita*, *Cyanea capillata*	POOL/1
37	ZL	Large Zooplankton, prmd *Thysanoessa inermis*	POOL/1
38	ZM	Mesozooplantkon, prmd *Calanus finmarchicus*	POOL/1
39	ZS	Small Zooplankton, prmd *Oithona similis*	POOL/1
40	DF	Dinoflagellates, prmd *Ceratium* family	POOL/1
41	PS	Small Phytoplankton	POOL/1
42	PL	Large Phytoplankton	POOL/1
43	BC	Predatory Benthos, include echinoderms, sea urchins, annelids, and anemones	POOL/1
44	BD	Detrivore Benthos	POOL/1
45	BFF	Benthic Filter Feeders, prmd (*Tridonta borealis*)	POOL/1
46	SPO	Sponges, prmd (*Geodia baretti*)	POOL/1
47	COR	Corals, prmd (*Lophelia pertusa*)	POOL/1
48	PB	Pelagic Bacteria	POOL/1
49	BB	Benthic Bacteria	POOL/1

#	Acronym	Included Species	Type/Age Grp
50	DR*[1]	Refractory Detritus	POOL/1
51	DL*[1]	Labile Detritus	POOL/1
52	DC*[1]	Carrion	POOL1
53	drsed*[2]	Refractory Detritus, bottom sediment	POOL/1
54	dlsed*[2]	Labile Detritus, bottom sediment	POOL/1
55	dcsed*[2]	Carrion, bottom sediment	POOL/1
56	cepj*[2]	Juvenile Squid (cephalopods)	POOL/1
57	pwnj*[2]	Juvenile Shrimp (prawn)	POOL/1

Table A.2: Overview on all runs submitted for thesis, which are mentioned/discussed. Run 0 – 5 used for analysis. * These runs used the latest revision/update of the code for NoBa Atlantis model in this study. For the remaining runs earlier version of the code were used. Note that the numbers do not refer to the order in which the runs were originally performed.

	RUN	PARAMETER MODIFICATION
y*	0	**Run 0**, Initial run, unchanged parameters
y*	1	**Run 1**, links all prey = 1
y*	2	**Run 2**, links major prey (CAP, ZL, ZM, PWN) = 1, rest 0.01
y*	3	**Run 3**, refined tuning with regard to Run 18
y*	4	**Run 4**, refined tuning with regard to Run 19
n	5	Links all prey = 0 except CAP = 1
n	6	Links all prey = 1 / horizontal distribution switched for CAP with PCO
n	7	Links all prey = 1 / horizontal distribution of CAP equals PCO, PCO normal
n	8	Links all prey = 1 / horizontal distribution CAP covers PCO and CAP area, PCO normal
n	9	Links all prey = 0 except for CAP and PCO = 1/ horizontal distribution of NCO, CAP, and PCO limited to boxes 42–44, 47, 48 / upscaled initial abundance CAP
n	10	Same as Run 9, but initial abundance CAP original level and old BHalpha_PCO
n	11	Same as Run 10, but no competition for NCO, i.e. diet links of all species in Atlantis = 0 apart from CAP, PCO and their prey
n	12	Same as Run 11, but new BHalpha_PCO 4.35e9
n	13	Same as Run 12, but with lower gape size for NCO, KLP_NCO 1e-5
n	14	Initial run set-up
n	15	Initial run set-up, changed Bev.Holt recruitment PCO BHalpha_PCO = 4.35e9 (from initial BHalpha_PCO = 6.5e12)
n	16	Links CAP = 0.5, other major prey = 0.1, rest = 0.001
n*	17	Same as Run 16, but links for ZL and ZM = 0
n*	18	Refined tuning I with regard to Run 17
n*	19	Refined tuning II with regard to diet of Run 18, ZL and ZM = 0
n*	20	Same as Run 18, but consumption rates NCO enhanced ten-fold (C_NCO)
n*	21	Same as Run 19, but consumption rates CAP enhanced ten-fold (C_CAP)

	RUN	PARAMETER MODIFICATION
n	22	Initial run, natural quadratic mortality mQ_CAP, original mQ_CAP = 1e-21
n	23	Increased value for added fishing mortality (all following runs), mQ_CAP = 1e-20
n	24	mQ_CAP= $1e-19$
n	25	mQ_CAP= $1e-18$
n	26	mQ_CAP= $1e-17$
n	27	mQ_CAP= $1e-16$
n	28	mQ_CAP= $1e-15$