Trophic vulnerability of 0-group Atlantic cod (Gadus morhua) and saithe (Pollachius virens)

A case study investigating the juveniles’ feeding pattern and identifying valuable nursery habitats in the Icelandic Westfjords

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Declaration

I hereby confirm that I am the sole author of this thesis and it is a product of my own academic research.

__________________________________________
Student’s name
Abstract

Rapid environmental change due to anthropogenic impacts currently threaten marine ecosystems and increase the pressure on the vulnerable early life stages of many marine organisms. In this study I examine trophic vulnerability of 0-group Atlantic cod (*Gadus morhua*) and saithe (*Pollachius virens*) during late summer and fall. This period coincides with the Atlantic cod juvenile settlement from the pelagic to the benthic habitat in the northwest of Iceland. It is a critical period for both species as growth in the first summer and fall may determine winter survival. Results from previous studies have identified clear habitat preferences of juvenile gadoids for structured habitats such as maerl beds and macro-algae. In Iceland, both habitat types are exploited and affected directly and indirectly by anthropogenic activities. In the current study, I review prior literature to identify potential threats to nursery habitats of Atlantic cod and saithe, execute a case study to investigate the diets of 0-group cod and saithe juveniles and discuss the relevance of trophic preferences and trophic competition for nursery ground conservation and management. For the case study, samples were taken with a beach seine in shallow coastal waters, and the stomach contents of 146 0-group cod and saithe were qualitatively and quantitatively analyzed. Dietary composition showed that copepods constituted the main diet for both species. Further important prey organisms were cladocera, insects (Chironomidae), gastropoda, cyprid larvae, amphipoda and ostracoda. The feeding patterns of the 0-group juveniles revealed that both species are opportunistic feeders with a wide range of prey organisms. Despite that, there is high overlap in the foraging niche of cod and saithe, suggesting the potential for trophic competition between and within the two species. Juveniles of both species exhibited similar feeding patterns during most of the study time. During the sampling period from late July until November, the proportion of benthic prey items gradually shifted until the diet mainly contained pelagic organisms. From late October on, cod and saithe feeding patterns started to diverge, which indicates more specialized foraging habits. 0-group saithe were larger throughout the sampling period. The results of the current study emphasize the need for further research investigating the early life stages of exploited fish species and the implementation of management measures for their nursery grounds.
„Man liebt nur, was man kennt, und man schützt nur, was man liebt.“

Konrad Lorenz

..AND:

Ęetta reddast!
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1. Introduction

Changes in environmental conditions due to anthropogenic impacts are challenging the earth’s ecosystems. Marine ecosystems seem to be particularly sensitive to those wide-ranging shifts of environmental conditions caused by climate change, pollution, resource extraction and various other anthropogenic activities (Edwards & Richardson, 2004). A vulnerable period in the life history of many marine fish is the early development stages, when juveniles are exposed to high predation pressure, and growth and survival are highly dependent on the availability of food and suitable habitats (Fjøsne & Gjøsæter, 1996). Despite the importance of the early life stages, the juvenile ecology of exploited fish species has seldom been considered in the evaluation of their population dynamics in fisheries management (Andrzej & Ragnarsson, 2006).

Atlantic cod is the most important exploited demersal fish stock in Icelandic waters (Astthorsson, Gislason, & Jonsson, 2007). Despite that, few studies have investigated the diet of the juvenile cod, and no study has investigated the interactions between 0-group cod and saithe, which have common nursery grounds. Juveniles of both species undergo ontogenetically driven changes in feeding habits when they start settling from the pelagic environment into the shallow coastal waters. The pelagic larvae phase is followed by a ontogenetic shift, when the juveniles move to shallow coastal waters and start feeding on benthic organisms (Bergstad, Jørgensen, & Dragesund, 1987). The transition stage is indicated by a mixed diet out of pelagic copepods and benthic organisms (Hüssy et al. 1997). Once the juveniles cod and saithe have settled in the benthic habitat, they mainly feed on amphipods, mysids, decapods, cumaceans, isopods, molluscs, polycheats and fish (Hüssy et al. 1997, Demain et al., 2011). Shallow coastal waters provide feeding habitats as well as sheltered areas to both 0-group cod and saithe. This spatial and temporal overlap of the two species can be expected to increase competition for food. The period of pre- and early benthic settlement, when competition between the two species is potentially high, constitutes a crucial time in the survival of 0-group juveniles (Tupper & Boutilier, 1995). During this early life stage, the juvenile cod and saithe might be particularly vulnerable to fluctuations or changes in prey abundance. The availability of food is dependent on various environmental conditions, biotic and abiotic factors, and the availability of suitable nursery
habitats. Preferred habitats of juvenile cod and saithe are structured habitats, such as maerl, macro-algae and seagrass, where the young fish find shelter from predation and rich feeding grounds (Kamenos, Moore, & Hall-Spencer, 2004a). The exploitation of maerl and macro-algae reduce the availability of valuable habitats and with that, negatively affect the growth and survival of the juvenile cod and saithe (Fjøsne & Gjøsæter, 1996). The feeding ecology of exploited fish species has seldom been considered as a way of evaluating population dynamics within fisheries management. As a consequence, little is known about trophic interactions between exploited fish species and their competitive interactions (Andrzej & Ragnarsson, 2006).

With this study, I aimed to identify the trophic vulnerability of 0-group cod and saithe inhabiting the shallow coastal waters in an Icelandic fjord. For this purpose, I designed the following research questions:

- Based on the current literature, which environmental changes and anthropogenic impacts potentially effect juvenile cod and saithe and their habitats during their early life stage?
- How do diet and feeding patterns change over time, and is trophic competition between species and size classes likely to occur?
- Do juveniles of each species preferentially forage in specific habitat types? How important is the availability of those different habitats as feeding grounds? Which conservation measures would be valuable to protect valuable habitat types?

The literature review compiles a broad overview of the anthropogenic impacts and further describes the impacts that would potentially affect the early life stages of juvenile cod and saithe, varying from a global to a local scale. The utilization and exploitation of valuable habitat, specifically in the Westfjords, is then discussed based on available information about the industries currently in operation. Understanding the outcomes of the dietary analysis requires some basic knowledge from previous studies that investigated the early life stages of cod and saithe. This is described in the last part of the literature review. Subsequently, I will describe the methodology of my case study with a broad introduction of the northwest Icelandic marine ecosystem and present my results of the dietary analysis. In the discussion, I first interpret the results of the stomach content analysis and connect
these results to the outcomes of previous studies. I then connect the biological results to potential conservation measurements and discuss the legal background for their implementation.
2. State of Knowledge

2.1. Climate Change

Ecosystem dynamics are complex and nonlinear [...] and unexpected phenomena may arise as we push the planet into this unknown climate state (Doney, 2006: 696).

Variation in the earth’s climate is a natural phenomenon and can occur in seasonal, annual or long-term patterns across a range of temporal scales (Harley et al., 2006). Since the industrial revolution in the late eighteenth century (Sabine et al., 2004), the amount of anthropogenic emission of greenhouse gases has increased to an alarming extent and caused an increase in average global temperature that has exceeded by far natural temperature fluctuations (Harley et al., 2006). Data provided by the Intergovernmental Panel for Climate Change (Jones et al., 2007) on the rise in global temperature show that during the period from 1880 to 2012, the global air and surface temperatures rose by 0.85°C. This significant temperature increase can have tremendous effects on the environment and has already caused dramatic shifts in marine and terrestrial ecosystems (Hughes, 2000; Walther et al., 2002; Thomas et al., 2004).

Marine pelagic environments seem particularly sensitive to climate change relative to terrestrial communities (Edwards & Richardson, 2004). One third of the anthropogenic carbon-dioxide (CO$_2$) emitted during the last two centuries has been dissolved by the oceans, which is why the oceans are often referred to as a sink for greenhouse gases (Sabine et al., 2004). The uptake of high amounts of CO$_2$ and the increase of ocean surface temperatures are changing the physical and chemical conditions of the oceans (Harley, 2006), and experts are increasingly concerned about the development of marine ecosystems (Feely et al., 2004; Faasse & Bayha, 2006; Orr et al., 2005). The high mobility of organisms living in the ocean may allow them to respond to environmental changes faster than freshwater species (Rahel & Olden, 2008). This has resulted in rapid changes to the geographical and temporal distributions of species, which have had tremendous effects on marine ecosystems (Cohen, Carlton, & Fountain, 1995; Stachowicz, Terwin, Whitlatch, & Osman., 2002).
2.1.1. Global warming and the oceans

One effect that has been attributed to global warming is a change in the geographic distribution of marine organisms (Beaugrand, 2009; Lindley, Gamble, & Hunt, 1995; Perry, Low, Ellis, & Reynolds, 2005). With the increase in ocean temperature, marine organisms have been observed to undertake a poleward shift in latitudinal distribution toward cooler marine regions (Perry et al., 2005; Parmesan & Yohe, 2003). These shifts might be a response to physiological stress occurring in environmental conditions that are at the edge of the species’ physiological tolerance ranges. For example, intertidal organisms, which are already living close to their physiological tolerance limits due to constant exposure to the impacts of different environments, are faced with a fast geographical shift (Birchenough et al., 2015). The consequences of distribution shifts, due to both new invasions and species loss, include changes in ecosystem functioning (Reef, 2012), reorganization in the food web (Faasse & Bayha, 2006) and the loss of native species (Kortsch, 2012). Climate change’s impacts on the ocean are not equally distributed all over the globe, but vary with latitude and longitude (Jones et al., 2007). Northern regions appear to be particularly vulnerable to temperature changes, and measurements have identified a temperature rise in the Arctic at twice the global average rate (Kortsch, 2012). In turn, the response of marine organisms to changing temperatures seems to be particularly fast at higher latitudes (Beaugrand, Edwards, Brander, Luczak, & Ibanez, 2008; Berge, Johnsen, Nilsen, Gulliksen, & Slagstad, 2005; Rose, 2005).

Another reaction of marine organisms to temperature increases in their environment is a phenological shift that implies a change in temporal abundance. Edward and Richardson (2004) conducted a study on marine phenology and the very individual distribution pattern of plankton species. They identified large phenological shifts of five functional groups across three trophic levels due to an increase of the sea's surface temperature. Since the recruitment success of higher trophic levels is highly dependent on synchronization with the seasonal planktonic production (Cushing, 1990), these results suggest that climate-driven phenological shifts will highly affect trophic interactions, altering food-web structures and leading to eventual ecosystem-level changes. Those changes may have tremendous effects on the whole marine environment.

The geographical and phenological shifts of marine organisms in response to global warming have already led to a mismatch between interdependent trophic levels from
primary, secondary and tertiary production (Edwards, 2004). Edwards and Richardson (2004) deduce that marine trophodynamics may have already been radically altered and will continue to change in the coming decades if the climate continues to warm at its present rate.

2.1.2. Circulation of the atmosphere and weather regime

According to the IPPC, “Changes in the circulation of the atmosphere and ocean are an integral part of climate variability and change” (Jones et al., 2007: 280). According to Scheffer and Carpenter (2003), changes in temperature are likely to alter the amount and distribution of the world’s freshwater supply, due to changes in key processes such as evaporation, water vapor transport and precipitation. During the last century, a distinct upward trend in precipitation at higher latitudes has been observed (Jones et al., 2007). Coastal areas are the most vulnerable marine ecosystems to changing precipitation patterns since they are directly affected by an increase of water runoff from land (Birchenough et al., 2015). Potential consequences for coastal ecosystems include high alterations in the salinity, turbidity, nutrient inputs (i.e., eutrophication) and pollutants (Harley, 2004).

A number of studies investigating storm track location in both hemispheres have shown that storm events in the second half of the twentieth century underwent a poleward shift and increased in intensity (Simmonds & Keay, 2000; Gulev, Zolina, & Grigoriev, 2001; McCabe, Clark, & Serreze, 2001). High wave action loosens small sediments, which then become distributed in the water column. One consequence is a higher turbidity in the sea water, which prevents the sunlight from penetrating deeper water layers and, thus, changes the environmental conditions for the marine organisms that inhabit the epipelagic zone. Furthermore, recent storms on the east coast of Central America have destroyed vast areas of coral reefs (Wilkinson & Souter, 2008).

However, changing precipitation patterns and more intense storm events are not the only consequences of climate-driven alterations in atmospheric circulation. The water system, when affected by disturbances and changes in the weather regime, can produce anything from small-scale water motions to the immense water masses of ocean currents. Other conditions that can develop as consequences of climate change include high bottom water temperatures, reduced water circulation, changing characteristics of ocean currents and upwelling and reduced water circulation leading to stratification (Harley, 2006).
2.1.3. Ocean acidification

The ratio of airborne CO$_2$ to the dissolved CO$_2$ in waterbodies is balanced by a chemical equilibrium reaction. If the amount of CO$_2$ in the air rises, e.g., due to anthropogenic pollution, the system will balance the air-water ratio by increasing the uptake of CO$_2$ in the world’s oceans (the so-called “CO$_2$ sink”). The atmospheric CO$_2$ dissolves passively into ocean surface waters and dissociates to hydrogen and bicarbonate ions. The dissolved hydrogen ions break up the bindings of CaCO$_3$ in the ocean to form HCO$_3^-$ (Doney, Fabry, Feely, & Kleypas, 2009). Foraminifera, corals, sea urchins, coralline red algae and pteropods are just a few of those marine organisms that rely on CaCO$_3$ to form their body structures (Feely et al., 2004). According to Harley (2006), a continued uptake of atmospheric CO$_2$ could severely impact the many marine invertebrates and algae that build carbonate structures.

Since the level of acidification is higher in colder waters, polar regions are likely to be more affected by worldwide ocean acidification than equatorial areas (Bates & Mathis, 2009). Pteropods (planktonic mollusks) constitute an important item in the diet of the marine fauna in Arctic waters. Even though only a few species of these free-swimming pelagic sea snails are found at high latitudes, the fact that they group together in large quantities makes them important prey organisms for economically important fish species, particularly in the North Atlantic and Arctic (Bé & Gilmer, 1977; Jespersen, 1940). Their shell structure, made of calcium carbonate, makes them highly vulnerable to a decrease in the pH of their environment. An experiment by Orr et al. (2005) showed that a pteropod's shell is dissolved at acidification levels within the predicted scope of models for future climate change scenarios (Feely et al., 2004). If these organisms are lost due to extinction or a geographical shift, the northern marine ecosystem would lose an important group of organisms in the food chain (Orr et al., 2005). There is also cause for concern about other marine organisms, such as sea urchins, a keystone species whose loss could reduce habitat complexity and the biological regulation of competition (Orr et al., 2005; Widdicombe & Spicer, 2008). Large-scale decreases in carbonate saturation values in oceans worldwide could have profound impacts on calcification rates for many species of organisms that use CaCO$_3$ to form their shells (Feely et al., 2004). Calcification rates of corals and coralline red algae (maerl), which form specific types of ecosystems and provide nursery ground, feeding area and habitat to a large variety of other marine organisms (Hall-Spence, Grall,
Moore, & Atkinson, 2003; Moberg & Folke, 1999), are likely to drop by 10\%-40\% in the future (Feely et al., 2004). The loss of these ecosystems would have a tremendous effect on marine biodiversity, since they are among the most productive and biologically diverse ecosystems on Earth and provide ecological and economical services (Moberg & Folke, 1999).

2.2. Anthropogenic Impacts on the Coastal Environment in the Westfjords

This study takes place in the Icelandic Westfjords, a remote area in the northwest of the country, just south of the Arctic Circle and surrounded by the mixing water masses of the Polar and Atlantic currents. Ísafjarðardjúp is the main body of a fjord system in the Westfjords, from where shallower fjords branch off. The whole area of Ísafjarðardjúp is sparsely populated, with only four towns of which two have more than 900 inhabitants. Low population numbers might convey the impression of a pristine and unspoiled nature; however, a deeper look into the marine conditions reveals human footprints. Settlements, infrastructure and land-based activities lead to the runoff of pollutants and nutrients into coastal waters. Untreated waste waters from households and industries are drained straight into the sea and lead to alteration and destruction of marine habitats (Halpern et al., 2008). Big sections of the roads in the Westfjords follow the coastline and disrupt the natural transition zone between land and coastal waters and add pollutants to the runoffs that enter the marine environment. Industries in the Westfjords are highly dependent on the marine ecosystem for important and valuable goods and services. Ocean-based activities such as fish farming, trawling and harvesting marine resources, however, are several pressures that affect marine areas and lead to the alteration and destruction of habitats due to a complex web of chemical, physical, and biological factors (Pearson & Rosenberg, 1978). Contaminants entering the marine environment that are of major concern include persistent organic pollutants, nutrients, oils, radionuclides, heavy metals, pathogens, sediments, litter and debris, etc. (Williams, 1996). In the following review, several potential anthropogenic impacts are described, and the consequences for affected coastal marine ecosystems will be discussed based on the results of previous studies. Not all of the factors identified may be applicable to the Westfjords at the present time, but they may rather reflect future risks to the fjord system.
2.2.1. Organic materials

The input of organic materials might be considered to be one of the principal causes of faunal change in nearshore benthic environments (Pearson & Rosenberg, 1978). Studies investigating the effects of household and industrial sewage discharge on marine environments (Tester & Costlow, 1981; Grant et al., 1995; Gorostiaga and Díez, 1996; Haya et al., 2005; Cromey et al., 2009) have found that few ephemeral species with high reproductive capability and tolerance to pollution occur within short distances from the sources of pollution. At increasing distance, species richness and biomass increase while the abundance of benthic organisms declines to the steady-state level usually found under normal conditions. Similar results were achieved by Grant et al. (1995), who conducted a study about the impact of mussel farming and the high influx of organic material (feed and feces) from aquaculture facilities on the benthic community. In the area investigated, the biodiversity of benthic organisms decreased at sample sites underneath the mussel rafts whereas the biomass of marine organisms at the same site increased. The input of organic wastes changes the physiochemical properties of the sediments and causes low oxygen concentrations in the bottom water due to decomposition of organic material (Cromey et al., 2009; Pearson & Rosenberg, 1978). Only a few small, opportunistic species are able to deal with the anaerobic conditions in areas with high organic loading, while the natural species diversity decreases.

2.2.2. Chemicals from aquaculture

The aquaculture discharge from remaining food and fish feces enter the surrounding environment and add high amounts of nitrates (Grant et al., 1995). In addition to the influx of organic waste, aquaculture constitutes a source of pollutants that includes various synthetic chemicals. Farmed fish are treated with pesticides and drugs to prevent diseases and parasites. Furthermore, antifoulants, anesthetics and disinfectants are substances used in aquaculture activities that can have harmful effects on the marine community and cause mortality of non-target species. While the application of antibiotics poses a risk to human health due to resistance bacteria, the input of parasitic agents has a direct negative effect on the marine environment (Burridge, Weis, Cabello, Pizarro, & Bostick, 2010). The uptake of contaminants can negatively affect the survival and spawning of several groups of invertebrates and zooplankton (Haya, Burridge, Davies, & Ervik, 2005) that constitute the base of the marine food web. The application of chitin synthesis inhibitors, for example, is
an effective treatment against larval and pre-adult stages of sea lice. However, sea lice represent only a few species of the group of copepods, whereas the most affected, but non-target species from that group are an important component of the marine food web. Tester and Costlow (1981) investigated the effect of a chitin synthesis inhibitor on the marine copepod Acartia tonsa, which is, “where abundant, possibly the major planktonic herbivore.” (Tester & Costlow, 1981: 1). Results have shown that the treatment of juvenile copepods diminished their hatching success significantly.

### 2.2.3. Persistent organic pollutants

Persistent organic pollutants (POPs) are a group of many thousands of chemicals that are persistent in the environment. Due to their resistance to metabolism and their lipophilic character, POPs are accumulating throughout the food chain (Jones & Voogt, 1999). Most POPs are synthesized for industrial uses or as agrochemicals, and once they are released into the environment, they travel long distances before they deposit in soil, water or organisms’ tissues. According to Ørbæk et al. (2007), POP levels in marine invertebrates are low compared to higher trophic positions. Regarding the whole trophic relationship, most negative effects of POPs have been determined in top predators, such as marine mammals and birds. Studies have determined the negative effects of POPs on the reproduction of birds (Giesy, Ludwig, & Tillitt 1994; Bosveld & Van den Berg, 1994), seals (Reijnders, 1986) and beluga whales (Béland et al., 1993). They have also been found to damage the immune system of top predator species (Safe, 1994; Ross et al., 1995) and genotoxicity (Peterson, Theobald, & Kimmel, 1993; Boening, 2000).

Coastal roads are crucial in their function as transportation system for humans, but they have negative effects on the surrounding environment. The toxicity of road runoff containing organic pollutants from fuel residues that flows into adjacent aquatic ecosystems was identified by Maltby, Boxall, Forrow, Calow, & Betton (1995), who analyzed the contamination of amphipods in affected ecosystems. The abundance of the species investigated was greatly reduced where motorway runoff entered the stream. Furthermore, subtle effects arise from the combined effects of PCBs and TNT, an antifouling biocide used in marine paints, and these affect the performance and subsequent survival rate of organisms (Kaiser et al., 2011). Striking symptoms, such as the occurrence of imposex at dogwhelks (Nucella lapillus) in highly polluted areas, reduced egg
production in Littorina littorea and the development of thickened and deformed shells at oysters, provide evidence for the harmful impacts of chemical pollutants within the invertebrate community (Matthiessen, Wallock, Thain, Waite, & Scropehowe, 1995). The consequences include population decline and even extinction of local populations worldwide (Gibbs and Bryan, 1986).

2.2.4. Oil pollution

Oil pollution derives from various sources both land- and sea-based. In addition to the land-based municipal and industrial sources for oil run-off entering the marine environment, global shipping traffic contributes a high ratio of the millions of tons of oil that are being added into coastal and marine waters from the residue of heavy fuel oil, oil spills from leakages, breakages and tanker accidents, oil loads in ballast waters and the discharge of oily waste waters (Islam & Tanaka, 2004). A great number of studies have provided evidence that oil pollution poses serious adverse effects on marine ecosystems (Au, Chiang, & Wu, 2000; D en Besten, Herwig, Zandee, & Voogt, 1989; Taysse, Troutaud, Khan, & Deschaux, 1995; Tsutsui, Hayashi, Maizumi, Huff, & Barrett, 1997; Buttino, 1994; Vos et al., 2000; Day et al., 1997). The extent of affected organisms reaches all trophic levels and can endanger whole populations of key species in the marine environment. Investigations into the effects of oil pollution have reported mortality and elimination of sea-stars and sea-urchins (Au et al., 2000; Den Besten et al., 1989), irritations of gills and disorders in the central nervous and endocrine systems in fish (Taysse et al., 1995; Tsutsui et al., 1997), reduction of egg production in copepoda (Buttino, 1994), impairment of reproduction and immune functions in marine mammals (Vos et al., 2000) as well as direct effects on the population size and structure of sea birds (Day et al., 1997). Worldwide shipping traffic is likely to increase in importance and extent in the coming years, even entering the sensitive polar region as ice melt facilitates the opening of Arctic trade routes. Thus, the amount of environmental impacts brought about by shipping and the size of the impacted areas are expected to increase.

2.2.5. Heavy metals

The definition of heavy metals originally describes elements with a high specific gravity. Now, however, the expression carries a connotation of toxicity and refers to elements such as lead, cadmium, mercury, arsenic, copper, manganese and zinc (Ansari, Marr, & Tariq,
2004). Human activity has inevitably increased the levels of heavy metals in the marine and freshwater environments. A variety of heavy metals derived from industrial and human waste waters, fisheries and agricultural runoff accumulate in the coastal waters. Environmental fluctuations, physical parameters, metal concentration, speciation and biotic factors including the physiology of the target species are all factors that impact the degree of toxicity, and as such make it difficult to determine the health implications of specific incidents of heavy metal contamination (Boyd, 2010). Evidence of the lethal and sublethal effects of heavy metals on marine organisms has been provided by several studies (Boyd, 2010; Hollis, McGeer, McDonald, & Wood, 1999; Howarth & Sprague, 1978). Investigations of environments with high mercury loading revealed oxidative stress and biotransformation responses in the seasonal fish populations in Portugal (Guilherme, Válega, Pereira, Santos, & Pacheco, 2008), the attenuation of the immune response of *Mytilus edulis* due cadmium exposure (Coles, Farley, & Pipe, 1995) and changes in growth, respiration rate and degree of lysosome latency in marine organisms due to heavy metals from gasoline (Rainbow & Phillips, 1993). Studies have also investigated behavioral changes due to exposure to the elements Cd, Cu and Hg. All studies revealed changes in the escape behavior of prey species as a consequence of inhibited physiological response in fish to alarm substances (Carreau and Pyle, 2005; Kusch, Krone, & Chivers, 2008; Scott, Sloman, Rouleau & Wood, 2003; Smith & Weis, 1997). Concentrations of heavy metals in sediments usually exceed those in the overlying water by between three and five orders of magnitude and, thus, are of special concern for benthic organisms (Pereira et al., 2014). Therefore, in several benthic species, physiological detoxification mechanisms have developed to enable the organisms to tolerate some contamination. However, the solubility of heavy metals, and thereby the availability of heavy metals for marine organisms, is controlled by several factors, such as pH, temperature, salinity and the nature of different anions (Ansari et al., 2004). Those parameters are expected to change as a consequence of global warming (see 2.1.1. and environmental impacts, which will increase the physiological stress on the organisms and the toxicity of the toxic elements and eventually exceed the threshold of the detoxification mechanisms of marine organisms. The interplay of various factors affecting the toxicity of heavy metal pollution gives reason for concern regarding how marine organisms will deal with the increase of marine pollution in connection to climate change in the future.
2.2.6. Invasive species

The worldwide distributional shifts in marine species as a consequence of global warming are a current problem in Icelandic waters. In the period 1996-2005, 22 rare fish species normally found in waters farther south were recorded around Iceland. Many species were found for the first time in Icelandic waters, and nine of them were caught at more than one location within Iceland’s Exclusive Economic Zone (EEZ) (Astthorsson & Palsson, 2006). The Atlantic rock crab (Cancer irroratus) is a non-indigenous species that was recently found in Icelandic waters. Its introduction happened most likely through ballast water, and the species is now distributing along the southwestern and western coasts of Iceland. The expected effects on the native benthic organisms are predation, competition for habitat and indirect trophic cascades (Thorarinsdottir, Gunnarsson, & Gíslason, 2014).

Not all species that enter and establish themselves in a new ecosystem have negative effects on the native community (Simberloff and Von Holle, 1999). Studies from around the world, however, have revealed the tremendous negative impacts by invasive species on natural ecosystems (Shiganova, 1998; Grosholz, 2000; ENO, 1996; McMinn, Hallegraeff, & Thomson, 1998). The term invasive species usually refers to introduced organisms that come to dominate the native flora and fauna. It also refers to viral and bacterial pathogens that can lead to harmful algal blooms and shellfish poisoning and that can be distributed with human vectors (Bax, Williamson, Aguero, Gonzalez, & Geeves, 2003). Those human vectors can be ballast water, anchor chains, hull fouling, mariculture, discarded debris and fishing gear. (Bax et al., 2003). Aquaculture net pens are a highly debated vector for the introduction of new species in the Westfjords, where farmed fish regularly go astray from their pens. Escapees from sea-cages have been reported for almost all species presently cultured around the world. They can have detrimental genetic and ecological effects on the natural ecosystems and may heighten the potential for the transfer of diseases and parasites to wild populations (Jensen, Dempster, Thorstad, Uglem, & Fredheim, 2010). Rainbow trout (Oncorhynchus mykiss) is an example of a non-native species that has been introduced into the Icelandic ecosystem due to fish escaping from farms. Reports about catches of this species in popular fishing rivers have caused concern about potential effects that the new species will have on the local fish stocks (Arnarsdóttir, 2015). Species replacement and fragmentation as well as the introduction of parasites are other potential threats that come along with the introduction of rainbow trout and other farmed fish.
species (Crowl, Townsend, & McIntosh, 1992). A study by Shelton et al. (2015) about population dynamics and size structure in streams has shown that the invasion of rainbow trout significantly diminished the abundance of fish with a size <40mm. Since rainbow trout is an anadromous fish species, similar effects can be expected in the marine environment, and these effects pose a threat to juvenile fish in shallow coastal waters.

2.2.7. Turbidity

Turbidity is a recurring topic when it comes to anthropogenic disturbance in the marine environment. Coastal settlements and industries multiply the natural turbidity in the nearshore waters by discharge and runoff that carry small particles into the sea, where they are distributed in the water column. Road and bridge construction can increase sediment loading to the coastal waters and, thus, lead to alterations in hydrodynamics and sediment deposition (Trombulak & Frissell, 2000). Also, offshore activities such as fish farming and resource extraction affect sediment loading in marine environments. The high amount of organic matter from aquaculture (feces and food) is distributed in wide areas around the sea cages, and dredging for marine resources loosens sediments and increases the turbidity (Glemarec, Lefau, & Cuq, 1997). Suspended or dissolved particles scatter and absorb light and, therefore, reduce visibility in the water column (Lythgoe, 1980). Several studies were conducted about the effects on feeding success within turbid waters; however, results vary with each specific condition and species investigated. Studies by Gregory and Northcote (1993), Utne-Palm (2002) and Engström-Öst & Mattila (2008) are in accord about the beneficial impact of turbidity on predation and higher feeding success due to an increased encounter rate between predator and prey. Sweka and Hartman (2003) determined that turbidity had no influence on the foraging success of the visual predator Micropterus dolomieu. Studies by Vinyard and O’Brien (1976) and Pekcan-Hekim and Lappalainen (2006) identified a substantial reduction in the reactive distance of several predators and, by that, a reduced feeding efficiency due to increased illumination and turbidity. Discussing the effects of turbidity based on the two factors of optical properties and predation risk, turbidity benefits small juvenile fish and planktivores with a small visual field and high predation pressure, whereas turbid conditions are not optimal to adult piscivores (Utne-Palm, 2002). By comparing the foraging, growth and habitat choice of pike larvae (Esox lucius) in the Baltic Sea, Engström-Öst and Mattila (2008) identified a significant higher weight gain for pike larvae in low-turbidity waters compared to waters
with high turbidity. Furthermore, the larvae exhibited considerably greater feeding activity and displayed a reduced need for sheltered habitat in turbid conditions. The latter effect might be a consequence of the fact that reduced water transparency provides shelter against predators (Gregory & Northcote, 1993). Hart (1987) conducted a study about population dynamics and production of zooplankton in response to fluctuating turbidity. The main effects of turbidity affected population density and biomass of the zooplanktonic crustacean. Both factors were significantly higher during less turbid conditions. The broad variety of consequences stand to reason when looking at the cause. Turbidity is an environmental impact that can be highly variable in its source, its contents and their degree of negative environmental effects.

2.2.8. Exploitation of and threats to maerl and kelp in the Westfjords

In addition to the many general risks to juvenile marine fish by environmental change and anthropogenic impacts, which have been identified in the above review, benthic habitat loss may be of particular importance. This study was conducted in the shallow coastal waters in the Westfjords, where kelp and maerl are important habitats that provide crucial ecosystem services to the marine environment (Hall-Spencer, 2010). Even though their importance has been identified in several previous studies, the habitat loss due to anthropogenic destruction and industrial utilization is still continuing. As these habitats are likely to be of high importance as nursery grounds for juvenile cod and saithe, I will now describe current the exploitation of and threats to maerl and kelp in Iceland with a specific focus on the Westfjords, referring to the risks already reviewed above as appropriate.

About maerl
Maerl habitats comprise various species of non-joined coralline red algae (Corallinales, Rhodophyta) that can form extensive beds found in coastal waters (Hall-Spencer, Kelly & Maggs, 2008). The Convention for the Protection of the North-East Atlantic (OSPAR) designated maerl as a marine habitat of high value for a wide variety of marine animals and plants and with a disproportionally high biological diversity and biomass compared to the surrounding habitats (Hall-Spencer, Kelly & Maggs, 2010). Disturbance and destruction from anthropogenic impacts have caused an increased substrata loss in recent years and give cause for concern about the future extent and quality of this slow-growing habitat (Hall-Spencer & Moore, 2000; Hall-Spencer et al., 2010). Due to the slow growth, maerl is
described as a non-renewable resource that cannot sustain direct exploitation (Barbera et al., 2003). Despite that, maerl is being exploited in several countries, and it is commercially used as in fertilizer and dietary supplements. The exploitation of maerl does not only destroy the direct maerl beds, but also affects the surrounding areas and adjacent habitats. The dredging processes swirl up sediments that are distributed by the ocean currents and increase turbidity in the surrounding areas. Turbidity in the water column has several effects on the environment as has been discussed in the literature review (2.2.7.). One effect is the decrease of population density and biomass of the zooplanktonic crustaceans (Hart, 1987). As zooplankton constitutes the majority of prey organisms of juvenile cod and saithe (Nedreaas, 1985; Demain, Gallego, Jaworski, Priede, & Jones, 2011), a decrease in the amount of crustaceans is likely to negatively affect the juvenile fish by causing them to lose a food resource.

A recent effort has been made to mine these red algae in Icelandic waters (Hill et al., 1998). The extraction of maerl in the Westfjords is conducted by Halfkalk (http://www.hafkalk.is/), a company that is currently located with all extraction sites in Arnarfjörður. Hafkalk has recently applied for permission to establish new extraction sites in Ísafjarðardjúp (Figure 2.1), where it is planning to mine about 120.000m³ of maerl per year (VSÓ ráðgjöf, 2015). According to Hall-Spencer (2010), such habitat removal has major effects on the species occurring on maerl and, consequently, on the whole trophic chain that is connected to them.

**Scallop dredging**

The Icelandic scallop has been harvested mainly in the West and Northwest of the country and yielded an annual maximum return of 17,000 tons (Valtýsson, n.d). Scallop dredging is conducted with heavy gear that is dragged over the sea floor and destroys topographical features (Garcia & Ragnarsson, 2007). The gear is mainly deployed in the shallow waters where maerl can be found (Valtýsson, n.d). The fragile branches of maerl species in combination to its extremely slow growth makes this biotope highly vulnerable towards the impacts of demersal fishing gear. A study by Hall-Spencer and Moore (2000) identified that scallop dredging led to a >70% reduction of live maerl, with no sign of recovery within the four years of the study period. The trawling is not only expected to destroy the habitats, but also lead to a “decrease in species richness and species diversity as a result of the gear and the increased mortality of the gear” (Garcia & Ragnarsson, 2007: 81). Hall-
Spencer (2010) confirmed these findings through his extensive studies on maerl, its value and its threats, concluding that scallop dredging reduces the complexity, biodiversity and long-term viability of maerl.

Aquaculture sea cages
Marine aquaculture, the process through which fish are farmed in floating sea cages, have become an important business in Iceland during the last 20 years. Particularly in the Westfjords, the number of sea cages has increased tremendously, and aquaculture companies have applied for aquaculture licenses to increase the amount of farmed fish. For example, the local company Hraðfrystihúsið Gunnvör in 2013 applied for licenses that would allow it to increase the amount of farmed fish from 2,000 tons to 7,000 tons in Ísafjarðardjúp (Jónsson, 2013).

Figure 2.1 Map of the Ísafjarðardjúp showing the distribution of aquaculture sea cages in 2015 (black rectangles), planned sea cages (hachured rectangles) and proposed areas for maerl extraction (diagonals) (VSÓ Ráðgjöf, 2015)
Hall-Spencer, White, Gillespie, Gillham and Fogg (2006) conducted an extensive study in the United Kingdom about the impact of fish farms on maerl and associated fauna. The results showed that the organic waste from remaining food and fish faeces is distributed with the currents and accumulates on the sea floor, where it attracts scavenging organisms that out-compete the natural fauna. The organic waste matter that builds up on maerl caused significant reductions in biodiversity, especially in small crustaceans (ostracods, isopods). The effects of the fish farms were traceable up to 100 meters from the sea cages.

**Harvesting macro-algae**

Seaweed is harvested in several areas around Iceland, and the dried thalli are used for the production of fertilizer and for human consumption. The two species that are harvested are *Ascophyllum nodosum* and *Laminaria digitata*. *A. nodosum*, is highly relevant in connection to the current study, since it was one of the prevailing species at the study site, next to *Fucus vesiculosus*, which was the most abundant macro algae species. Between 50,000-100,000 tons of *A. nodosum* are already harvested in Iceland. According to estimations by Matís (an Icelandic institute specializing in food and biotechnology research and design), *F. vesiculosus*, which is not yet harvested in Iceland but is utilized in other countries, has a potential harvest of between 1000 and 5000 tons per year (Elíasson, 2012). A new company plans to harvest seaweed in Breiðafjörður, indicating the increasing interest in the seaweed business and with that, the increasing pressure on the macro-algae habitat.

**2.3. About Atlantic cod**

**2.3.1. Early life history**

The main spawning grounds of Atlantic cod in Icelandic waters are located off the southwest coast (Marteinsdóttir & Björnsson, 1999). During the first 40 to 45 days after hatching, the larvae feed in pelagic waters and drift with the currents towards the northwest and the north of Iceland (Thorisson, 1989; Salvanes, Giske, & Nordeide, 1994). The most important nursery grounds around Iceland are shelf areas in the north and northwest of the country as well as the fjords on the east coast in Breiðafjörður (P álsson, 1980). Moving from the pelagic waters, the juveniles start settling into shallow coastal waters during early September and start feeding on benthic organisms in littoral and sub-littoral habitats. For their first two to four years, the cod juveniles stay in the shallow coastal waters, often
inside the protected environment of the fjords, from where they perform seasonal migrations between shallow summer feeding grounds and deep winter areas (Bergstad, Jørgensen, & Dragesund, 1987). The availability of food is a factor that determines the distribution of 0-group cod. Astthorsson, Gislason and Gudmundsdottir (1994) identified a significant correlation between the abundance of 0-group cod and the biomass of zooplankton in the southwest of Iceland. 0-group cod were found at a depth from 0 to 200 m during surveys in the north of Iceland (Astthorsson et al., 1994). By far, the highest numbers of 0-goup cod were caught at depths of <50 m. In the study by Pálsson (1980) about the biology of juvenile gadoids in Icelandic waters, most 0-group cod were caught at depths of between 0 to 100 m.

2.3.2. Foraging of juvenile cod

Analyses of the juvenile cod diet during the pelagic stages have shown that calanoid copepods are the dominant component among the smallest cod (<5 cm) (Demain et al., 2011). The most common species within the pelagic calanoids and the dominant diet compound are different stages of *Calanus finmarchicus* (Demain et al., 2011; Heath & Lough, 2007; Bainbridge & McKay, 1968), a copepod that constitutes the major part of the diet for many pelagic fish (Bainbridge & McKay, 1968; Prokopchuk & Sentyabov, 2006). Beside *C. finmarchicus*, studies have identified *Para* and *Pseudocalanus*, *Oithona*, *Temora* and *Acartia* species as the most important prey for pelagic cod larvae around Iceland (Thorisson, 1989; Bainbridge & McKay, 1968). The pelagic larvae phase is followed by a transition period, during which the juveniles move to shallow coastal waters and start feeding on benthic organisms. The transition stage is indicated by a mixed diet comprised of pelagic copepods and benthic organisms (Hüsey et al. 1997). Once the fish have settled in their benthic habitat, studies conducted in the North Sea and the Baltic Sea identified amphipods, mysids, decapods, cumaceans, isopods, molluscs, polychaetes and fish as their main prey groups (Hüsey et al. 1997, Demain et al., 2011). Studies about the diet of juvenile cod in Icelandic waters identified fish larvae, mainly capelin, euphausiids and copepods, as the most important prey species (Thorisson, 1989; Pálsson, 1980). Fjosne and Gjosæter (1996:763) described the 0-group cod as “generalists with the highest niche width of all fish.” This wide prey spectrum allows the 0-group to feed in different environmental conditions. Demain et al. (2011) conducted a study about the changing prey preferences of juvenile cod with increasing depth. The juveniles consume mainly copepods
in the shallowest depths, while the proportions of fish, shrimp, the larvae of decapods and crabs increased with depth. The fact that juveniles feed on different organisms at different depths reveals a high adaptability within the 0-group to different feeding conditions.

2.3.3. Size classes during settlement

Body size is an additional factor that factors into the habitat and prey preferences in the 0-group juveniles’ ecology. The size-habitat correlation seems to follow the same patterns in different cod stocks throughout the world (Hüsey et al. 1997; Demain et al., 2011; Lomond, Schneider, & Methven, 1998). The ontogenetic shift that juveniles undergo when settling to the benthic habitat occurs when they reach a length of about 4.0 to 6.5 cm (Hüsey & Tomkiewicz, 1995; Hüsey et al., 1997; Demain et al., 2011). During the beginning of their shift towards the benthic environment, pelagic copepods were still the most important food items. Their utilization dropped when juveniles reached the size interval between 6.0 and 9.0 cm, and a diet mainly consisting of benthic organisms indicates a completed transition to the benthic habitat (Hüsey et al., 1997; Lomond et al., 1998). Hüsey et al. (1997) set the size class of juvenile cod in relation to the dominant individual prey species and determined an increase in the prey size simultaneously with an increase in the juveniles’ body sizes. Bromley, Watson and Hislop (1997) found a similar outcome with their study about diel feeding patterns and the development of food webs of pelagic 0-groups.

2.3.4. Habitat choice of 0-group cod

Algae beds grow in shallow coastal waters and provide sheltered habitats for juvenile fish (Lomond et al., 1989). Borg, Pihl and Wennhage (1997) investigated the habitat choice of juvenile cod, and results showed a significant preference for vegetation, particularly for Fucus vesiculosus during daylight. However, the habitats that Borg et al. (1997) compared in their study did not include maerl. Kamenos et al. (2004a), who investigated the distribution of juvenile gadoids in shallow inshore waters, compared the juveniles densities over maerl, heavily vegetated rock and gravel substrata. According to their results, maerl was the habitat with the highest densities of juvenile cod. Keats (Keats, Steele, & South, 1987; Keats, 1990; Keats & Steele, 1992) examined the changes in diel habitats in Newfoundland and compared his results to previous studies conducted in the North Sea. According to Keats and Steele (1992), the results do not exhibit any clear patterns of the
juveniles’ distribution and, therefore, suggest that “juvenile cod have a flexible diel cycle of feeding activity and habitat utilization” (Keats & Steele, 1992: 12). Ringler (1983) endorses this outcome with his theory about tactical variability in foraging behavior. Instead of claiming that this variability is simply “noise,” Ringler suggests that certain behavioral, physiological or morphological adaptations to the environment are “sources” for the foraging habitat variability. Demian et al. (2011) found similar results in their study on the feeding ecology and habitat preference of juvenile cod, stating that “diets are influenced by environmental factors and developmental changes” (Demian et al., 2011:17). That would explain why the studies from different locations in the world show conflicting results regarding the variation in the habitat choice of juvenile cod. The habitat preference of juveniles under certain conditions can deviate from the ones described above. Gotceitas, Fraser, & Brown (1995) conducted experiments about the habitat use of juvenile fish under predation pressure. The juveniles’ response to active predators was a significant shift in habitat use from open sand/gravel to kelp, where the juveniles were able to hide and reduce predation risk.

2.4. About Saithe

The main spawning grounds for Saithe (Pollachius virens) around Iceland are off the southeast to the northwest coasts. Of all gadoid species living in Icelandic waters, saithe is the one that spawns the earliest (Jónsson, 1996). Spawning season begins in late January, peaks in February and ends around mid March (Armannsson, Jonsson, Neilson, & Marteinsdottir, 2007). After the larval life stage spent in pelagic waters, 0-group juvenile saithe settle in the littoral area. While their most important prey has been the pelagic copepod C. finmarchicus in June (Nedreaas, 1985), the 0-group has been found to vanish from the plankton in July/August (Clay, Stobo, Beck, & Hurley, 1989). That implies that the habitat shift from pelagic to the near shore waters occurs in mid-summer. A study conducted in Nova Scotia revealed that inshore juveniles that occurred first around mid-July were 7 to 11 cm in length (Clay et al., 1989). However, 0-group saithe collected in southwest Scotland varied in length from 5 to 15 cm (Kamenos et al., 2004a). Nedreaas (1985) conducted a study about the feeding habits of young saithe and tried to identify their foraging habitats. He concluded that the juveniles mainly fed in the epi-fauna and hyper-benthos, since amphipods and isopods played an important role in their diet. Also Steele (1963), who studied saithe in the Bay of Fundy (Canada), found 0-group juveniles in
the shallow sub-littoral zone feeding mainly on algae-inhabiting organisms and to a lesser extent on plankton. According to Nunn, Tewson and Cowx (2012) the main diet of juvenile saithe are calanoid copepods, decapoda (larvae, adults), amphipoda, euphausiacea and polychaeta. Only one study by Pálsson (1983) investigated the diet of juvenile saithe in Iceland. The results emphasized the importance of euphausiacea for the smaller length groups and the general dietary patterns demonstrated the highly pelagic nature of saithe, which prey mostly on zooplankton during the juvenile phase.

The juvenile saithe spend their first two to four years in the coastal waters, where they display seasonal migration in their depth distribution. Similar to other gadoid species such as cod, the juvenile fish migrate from shallow to deeper water during autumn and winter (Mello & Rose, 2005; Armannson et al., 2007). With an age of 2 to 4 years, saithe perform large-scale and long-range migrations towards feeding areas from the coastal waters into the pelagic environment (Bergstad et al., 1987; Nedreaas, 1985).

### 2.5. Competition between juvenile cod and saithe

During their early life stages, Atlantic cod and saithe occur in the same coastal habitats and follow similar seasonal distribution patterns (Mello & Rose, 2005; Armannson et al., 2007). This spatial and temporal niche overlap can be expected to increase competition between the two species. Bergstad et al. (1987) highlighted that the co-existence of fish species with similar life history strategies is possible. He suggests that competition can be limited by evolving physiological and ecological strategies such as variations in the feeding habits, prey preferences or foraging niches.

In a study about diel feeding patterns of 0-group juveniles from five fish species, including cod and saithe, Bromley at al. (1997) presented evidence for inter- and intra-specific interactions. One type of interaction was the competition for food, since the study revealed a considerable overlap in the prey identified in the stomachs of the gadoids. Since all small stages fed on copepods, mainly Calanus finmarchicus, the authors assumed that “competition for food could be most intense at the early stages of 0-group development” (Bromley et al. 1997: 853). Once cod settled to the benthic environment, different feeding preferences of the 0-group size classes seemed to reduce the intraspecific competition for food. Size-dependent feeding patterns of cod have been investigated by several studies (Bergstad et al., 1987; Bromley et al., 1997). The studies revealed that the stomachs of the
smaller juveniles contained high numbers of small prey organisms, whereas stomach contents of the larger juveniles revealed fewer but bigger prey items. Different prey preferences between the size classes within a fish population are assumed to decrease intraspecific competition (Bergstad et al., 1987). Lomond et al. (1989) reasoned that different feeding preferences occur due to physical limitations. They suggest that prey preferences are determined by the mouth opening and that the choice of prey organisms by smaller size classes of cod is limited by the mouth gape. One possible consequences of physical limitations for small body sized juveniles has been mentioned by Thorisson (1989), who set a relative small body size and a slow growth rate in relation to the growth rate of the prey organisms. Based on previous studies, he suggested that the growth rate of cod larvea is parallel to the growth rate of Calanus, which potentially leads to the increased risk for young cod of small size and with slow growth rates to lose the ability to feed on C. finmarchicus. As a consequence, small-sized cod might “lose the race for the most common food” (Thorisson, 1989: 271) during their early life stage.

Kamenos et al. (2004a) argued that the different foraging niches of cod and saithe allow the two species to inhabit the same sites. While saithe utilize bentho-pelagic food sources, cod seemed to mainly feed on benthic organisms. This ability of co-existing species to utilize different resources in order to reduce the interspecific competition is described as ecological character displacement (Svanbäck & Bolnick, 2006). With the idea that a similar behavior also occurs within species, Svanbäck and Bolnick (2006) manipulated the population density of Gasterosteus aculeatus in a natural environment to reduce the prey availability and therefore increase competition. The authors identified that the diversification of the juveniles’ feeding patterns can arise as a mechanism to solve competition between and within species and that this adaptation can be developed within a short time and on an individual level. The theory about ecological character displacement accords with the outcome of Fjosne and Gjosæter (1996) that describes 0-group cod as “generalists with the highest niche width of all fish” (Fjosne & Gjosæter, 1996:763). The high niche width enables the individual juveniles to adopt their diet to the availability of prey organisms and to reduce the pressure of competition.
2.6. Valuable habitats

From the pelagic stage, when the juvenile Atlantic cod and saithe feed on zooplankton in the open water, they undergo an ontogenetic shift and settle in the shallow coastal areas. In the shallow water habitats, the diet needs to be adapted to the new environmental conditions, and the juveniles start feeding in the benthic and epibenthic habitats in addition to the pelagic (Hüsey et al., 1997).

The importance of structured habitats such as macro algae and coralline algae (maerl) for the juveniles has been identified in several studies (Keats et al., 1986; Lomond et al., 1989; Borg et al., 1997; De Trouch et al., 2008). The abundance of juveniles in different habitat types has been compared, and the highest densities were always found over structured habitat types such as kelp, eel-grass, and maerl (Gregory, Anderson, & Dalley, 1997; Kamenos et al., 2004a). The most common explanation for the high abundance of juveniles in those habitats is the shelter that the juveniles find between the thalli. The small fish are at high risk of predation while feeding in the pelagic water, and they use the structured habitat to hide from the larger predators (Keats et al., 1986). In addition, larger juveniles that were already feeding on benthic organisms were found in the macro algae and were assumed to utilize the structured habitat for shelter. Assigning the main importance of macro algae to the shelter they provide stands to reason when connecting them to the results of stomach content analysis. According to previous dietary studies, the juveniles continue feeding mainly on pelagic prey organisms after the settlement and continue feeding on the benthic habitat, whereas the macro algae seem to be of lesser importance for foraging (Keats et al, 1986). Despite that, the high densities of juveniles in the macro algae highly indicate that the 0-group use them for shelter and predator avoidance.

*Fucus nodusum* and *Ascophyllum vesiculosus* are very common macro algae in the shallow coastal waters of Iceland and constitute an important, if not the main sheltered habitat for the 0-group juvenile cod and saithe. The macro-algae habitat does not only provide shelter, but are also feeding grounds for the young fish (Keats et al., 1987). Several organisms that inhabit the macro-algae are part of the juveniles’ diet. A study about copepod abundance has shown that some harpacticoid species have specific preferences for single algae species, where some species were highly associated with *Fucus vesiculosus* (De Trouch et al., 2008). Generally, harpacticoid copepods are highly associated with macro-algae turfs.
where they are grazing on sedimentary and epiphytic biofilms (Hicks, 1977; De Trouw et al., 2008). Other prey organisms found in the juvenile stomachs and that were associated with the macro-algae were isopoda of the genus *Idotea* and *Jaera* that again were associated with the species *Fucus vesiculosus* and *Ascophyllum nodosum* (Jansson & Matthiesen, 1971; Gutow, Gimenez, Boos, & Saborowski, 2009). To which extent the juveniles use the macro algae as shelter and to which extent as feeding habitat is not known and would require further research.

Maerl beds form highly biodiverse habitats that are expected to constitute an important feeding ground for the juveniles in shallow waters (Kamenos et al., 2004a). Maerl can be found already in the tidal zone of rocky shores, where it forms a pink cover on stones and provides habitat to diverse flora and fauna (personal observations). From a survey in Ísafjarðardjúp, where bottom samples were taken at depths of 6 to 100 m, it is known that mearl occurs down to a depth of at least 21 m. The most common nodule-forming species in Icelandic waters is *Lithothamnion topiforme* (Karl Gunnarsson, personal communication, February 2016), which can be found in exposed headlands of fjords along the coast, except for the south coast (Hall-Spencer et al., 2010). The importance of maerl for 0-group cod has been investigated by Gotceitas and Brown (1993), who found that the habitat complexity and emergent biota significantly reduced juvenile mortality. Kamenos et al. (2004a) conducted a study about the preferences of feeding habitats of cod, saithe and haddock by comparing the abundance of the gadoids caught over maerl, heavily vegetated rock and gravel. Results have shown that densities of all gadoids were significantly higher over maerl than they were over gravel, which reflects the foraging preference of the juveniles.
3. Methodology

3.1. Study area

The hydrography of Icelandic waters is characterized by two big systems of currents. The Irminger Current, which is fed by the Gulf Stream and carries warm and salt water along the south and west coast towards the northeast, from where the majority of the water masses run westwards toward Greenland. The minority of the Irminger Current mixes with the cold polar waters that hit the Icelandic shelf in the northeast of the island and form an anticyclonic movement of the coastal waters along the north and east coasts (Jespersen, 1940). The intermix of the two currents in the northeast of Iceland cause marked fluctuations in salinity and temperature (Andrzej & Ragnarsson, 2006). The Irminger Current is more vigorous during summer and causes a temperature rise of the coastal waters along the north and east coasts (Jespersen, 1940). This warm period is of great importance for the production of zooplankton and makes the northeast important feeding grounds for juvenile fish and other organisms that feed on zooplankton (Jespersen, 1940).

The biggest fjord in the northwest of Iceland and in the Westfjords is Ísafjarðardjúp, with a length of about 75 km from the mouth to the bottom and a maximum width of about 20 km. The depth is varying from 130 up to 40 m. Along the southern side of Ísafjarðardjúp are nine smaller fjords branching out of the big fjord. The total area of the fjord system of Ísafjarðardjúp is about 786 km² (Hafransóknastofnun, n.d.).
This study was carried out in Hestfjörður, one of the smaller fjords belonging to the fjord system of Ísafjarðardjúp. Hestfjörður is 13 km long, a little over 1 km wide and surrounded by steep mountain sides with hardly any plaine coastal areas (Hafrannsóknastofnun, n.d.). Data about the bathymetry of all Hestfjörður are not available, only for the mouth area, where the greatest depth is about 32 m (Sjómælingum Íkslands, 1989). In order to identify the benthic habitat types, we sent out divers to collect benthic samples on the sampling site. The samples were taken along three transects between the shore and a 20 m contour line, at depths of 18 m, 10 m and 3 m.
The divers also visually evaluated the substrate type, particularly noting the depth of maerl. The samples were only used to identify the distribution of the habitat types. Results showed that the site was characterized by gravel, maerl and vegetation, with *Fucus vesiculosus* and *Ascophyllum nodosum* as the prevailing macro algae species.

### 3.2. Sampling

This study aimed to identify the feeding patterns of juvenile cod and saithe that inhabit the shallow coastal waters. A coastal section in Hestfjörður was chosen as sample site for all samples collected for this study. A beach seine (size: 10.0 x 1.5 m) with a mesh size of 6.0 mm was used to catch juveniles. The sampling time most often coincided with the incoming tide. The beach seine was deployed from the shore and out to a depth of 1.5 m from the water line. On average, 8 to 10 hauls were conducted per sampling day. Each time we deployed the net, the haul was broad back on shore, and cod and saithe were collected and stored in a water tank. Other species found in the net were noted and released into the
sea. Cod and saithe in the water tank were anaesthetized with phenoxyethanol and frozen for storage at –18°C. Sampling took place on 15 days during the period between 22 July and 9 November.

### 3.3. Stomach content analysis

A total of 107 cod and 233 saithe were caught during the sampling. All cod and saithe were smaller than 13.4 cm, which indicated that all fish were juveniles in the age 0+ group. The length of each fish was measured to the nearest of 1.0 mm, total weight and livers were weighed (wet weight), otoliths were removed in order to determine age determination at a later point and stomachs were preserved in a 10% formaldehyde solution. After seven days, the formaldehyde solution was replaced with a 70% ethanol solution. For further examination, five stomachs from each sampling day and each species were analyzed (chosen at random). The stomach contents of a total of 62 cod and 84 saithe were analyzed.

The stomach contents were emptied into a Petri dish with 70% ethanol solution and analyzed using a modular stereo microscope (Leica MZ6). All prey organisms found in the stomachs were sorted and identified to the lowest possible taxa. Fragments of prey were identified when possible and accounted for the lowest possible number of items. For stomachs that contained more than 100 prey items, four out of 16 random sections were analyzed in the Petri dish and the results were multiplied by four.

To examine changes in diet in relation to juvenile size, the juveniles were divided into size classes based on the total length range for each species. The cod were divided into five size classes (3.0-3.4; 3.5-3.9; 4.0-4.4; 4.5-4.9; >4.9), and the saithe were divided into seven size classes (<4; 4.0-4.9; 5.0-5.9; 6.0-6.9; 7.0-7.9; 8.0-8.9; >8.9). For the purpose of evaluating the foraging habitats of cod and saithe, food items were classified into three categories: pelagic (calanoid copepods, cladocera, cyprid larva, colembola, insects), epibenthic (cyclopoid copepods, gastropoda, acarina, isopods) and benthic (harpacticoid copepods, amphipods, ostracods, chironomidae larvae, polychaeta) (Fjøsne & Gjøsæter, 1996; Hüissy & Tomkiewicz, 1995; Hüissy et al., 1997; Keats & Steele, 1992). Dietary compositions are discussed based on the mean and the percentage of prey numbers.
3.4. Data analysis

3.4.1. Diversity Index

The Shannon-Wiener Index is the most common tool for measuring diversity and niche breadth (Jost, 2006; Krebs, 2014). To examine the diversity index for the numbers of prey organisms by juvenile species, size classes and sampling date, the Shannon-Wiener entropy was calculated using mean values across either sample or size class of the proportions within day for each prey organism (Krebs, 2014). The proportion of diversity was calculated with the following formula:

$$H' = - \sum p_j \log p_j$$

where \( p_j \) is the mean proportion of food category \( j \) in the diets of each species.

3.4.2. Diet overlap

The mean proportions of prey organisms in the diets of the cod and saithe were calculated for sampling days. Mean proportions were used to compare the degree of diet overlap among the species using the simplified Morista’s index (Krebs, 2014). The proportion of diet overlap is calculated with the following formula:

$$C_H = \frac{\sum p_{jc}p_{js}}{\sum (p_{jc}^2 + p_{js}^2)}$$

where \( p_{jc} \) and \( p_{js} \) are the mean proportions of food category \( j \) in the diet of cod \( c \) and saithe \( s \). The values of the index range from 0 (no overlap) to 1 (complete overlap).

3.4.3. Generalized Linear Mixed Model – prey source/feeding habitat

To examine the effects of species (saithe, cod), juvenile size (SD length) and sample date on the occurrence of pelagic, epibenthic and benthic prey items, a Bayesian framework was applied, using Markov chain Monte Carlo (MCMC) methods in the R package MCMCglmm (Hadfield, 2010) for general linear mixed models (GLMM). Three univariate models were run using benthic, epibenthic and pelagic food items as the dependent variables, juvenile species and juvenile length nested within species as fixed effects and sample day as a random effect. All three variables were modeled with a Poisson
distribution with log link and accounting for overdispersion. In all models, non-informative priors (inverse Wishart) were used. All models were run with a burn-in of 10,000 and subsequent 100,000 iterations and a thinning interval of 10. The plots of the traces and posterior distributions were visually inspected, and the autocorrelation between samples was calculated to make sure that the models converged. Autocorrelations were < 0.02 and the effective sample size was ~1,000 for all estimates. The 95% highest posterior densities (HPD) associated with each fixed and random effect were inspected to determine whether they overlapped with zero. A 95% HPD interval contains most of the posterior distribution and is analogous to a confidence interval in the frequentist approach; a 95% HPD that overlaps 0 indicates that the effect does not differ significantly from zero (Hadfield, 2010).
4. Results

4.1. Dietary comparisons

In this study, copepods accounted for more than 50% of the juveniles’ diet for both species (Table 4.1). Beside copepods, cladocera, cyprid larvae, amphipoda and ostracoda are further crustaceans that constitute integral components of the prey spectrum. Furthermore, aquatic insects, including larval stages, gastropoda and annelida that inhabit the shallow coastal areas, were found in the stomachs of juvenile saithe and cod.

Table 4.1 Diet composition of Atlantic cod (Gadus morhua) and saithe (Pollachius virens) described by percentage and mean with standard deviation and standard error

<table>
<thead>
<tr>
<th>Group (phylum or class)</th>
<th>Diet component</th>
<th>Cod</th>
<th>Saithe</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>%  st dev</td>
<td>%  st dev</td>
</tr>
<tr>
<td>Crusatacea</td>
<td>Harpacticoida</td>
<td>25.35  52.0 6.6</td>
<td>20.04 50.4  5.5</td>
</tr>
<tr>
<td></td>
<td>Cyclopoida</td>
<td>22.62  62.1 7.9</td>
<td>8.84  32.1  3.5</td>
</tr>
<tr>
<td></td>
<td>Calanoida</td>
<td>25.27  52.4 6.7</td>
<td>27.05 192.7 21.0</td>
</tr>
<tr>
<td></td>
<td>Copepoda inident.</td>
<td>4.21  10.1 1.3</td>
<td>4.22 14.9  1.6</td>
</tr>
<tr>
<td></td>
<td>Amphipoda</td>
<td>0.43   1.4  0.2</td>
<td>0.89 12.5  1.4</td>
</tr>
<tr>
<td></td>
<td>Ostracoda</td>
<td>0.11   0.8  0.1</td>
<td>0.15  2.3  0.2</td>
</tr>
<tr>
<td></td>
<td>Cladocera</td>
<td>13.18  48.8 6.2</td>
<td>24.52 150.1 16.4</td>
</tr>
<tr>
<td></td>
<td>Isopoda</td>
<td>0.40   4.3  0.5</td>
<td>0.06  0.5  0.1</td>
</tr>
<tr>
<td></td>
<td>Euphausiids</td>
<td>0.02   0.0  0.0</td>
<td>0.74  4.6  0.5</td>
</tr>
<tr>
<td></td>
<td>Cyprid larvae</td>
<td>0.25   1.5  0.2</td>
<td>1.11  4.1  0.5</td>
</tr>
<tr>
<td>Insecta</td>
<td>Chironomidae larva</td>
<td>0.49  1.7  0.2</td>
<td>3.09 18.4  2.0</td>
</tr>
<tr>
<td></td>
<td>Chironomidae adult</td>
<td>0.86  3.8  0.5</td>
<td>2.83 14.4  1.6</td>
</tr>
<tr>
<td></td>
<td>Ceratopogonida</td>
<td>0.00   N/A  N/A</td>
<td>1.16  6.0  0.7</td>
</tr>
<tr>
<td></td>
<td>Nematocera</td>
<td>0.00   N/A  N/A</td>
<td>0.12  5.5  0.6</td>
</tr>
<tr>
<td></td>
<td>Diptera</td>
<td>0.10   0.8  0.1</td>
<td>0.64  8.9  1.0</td>
</tr>
<tr>
<td></td>
<td>Hymenopter</td>
<td>0.00   N/A  N/A</td>
<td>0.14  3.0  2.1</td>
</tr>
</tbody>
</table>
4.2. Diet of Saithe

The main diet of 0-group saithe were copepods (55.89%), whereas calanoid (27.05%) and harpacticoid copepods (20.04%) were distinctly more abundant than cyclopoid copepods (8.84%) (Table 4.1). Other prey organisms represented with high numbers were cladocera (24.53%), insects (8.25%) and gastropoda (2.1%). Insects (Chironomidae, Certopogonidae, Nematocera, Diptera, Hymentoptera and Colembola) were most abundant during August (Figure 4.1). The numerous appearances of chironomidae larva (77.5%) was outstanding on the first sampling day (22 July). The combined numbers of calanoid copepods and cladocera comprised the highest proportion of food items in the second half of September. Harpacticoid copepods, euphausiids and gastropoda comprised the main diet in October and November.
Figure 4.1 Composition of prey organisms found in the stomach contents of 0-group saithe: percentage of organisms per sampling day

4.3. Diet of Cod

The diet of 0-group cod consisted of 73.14% of copepods; 25.35% of them harpacticoid copepods, 25.27% calanoid copepods and 22.62% cyclopoid copepods (Table 4.1). Further important prey organisms were cladocera (13.18%), insects (1.47%), acarina (1.19%) and gastropoda (0.55%). The proportion of copepod orders varied with time (Figure 4.2). The numbers of harpacticoid copepod were highest in August, whereas big proportions of calanoid copepoda were found in September, and cyclopoid together with harpacticoid copepods were the main dietary components from mid-October on. Cladocera were a continuous part of the diet until late October and could even constitute the main proportion of food items.
Figure 4.2 Composition of prey organisms found in the stomach contents of 0-group Atlantic cod for each sampling day

Nematoda were found in the juveniles’ stomachs, but they were not considered to be food items. They account as endoparasites (Højgaard, 1999) and were not further discussed in this study.

### 4.4. Size of the juveniles

Analysis of the size frequency over time showed a consistent increase in the length distribution of 0-group saithe (Figure 4.3) and indicates that growth occurred throughout the study time. The first saithe was caught on 7 July with a mean length of 3.7 cm. The highest value for the mean length was reached on 3 November, with a mean length of 9.7 cm. The minimum length of individual saithe was 2.9 cm (22 Jul), and the maximum was 13.4 cm (03 Nov).

Cod was caught for the first time on 17 August. The mean length for each sampling did not exhibit a continuous increase over time. The length distribution until mid-September varied from 3.3 to 3.9 cm and from mid-September until November from 4.1 to 5.0 cm. The minimum length of individual cod was 3.0 cm (1 Sept) and maximum was 6.2 cm (20 Oct).
4.5. **Size dependent feeding pattern**

The proportion of copepods in the diet of 0-group cod was higher than 75% at all size classes. In the size classes 3 to 4.9 cm cyclopoida determined the lowest proportion within the copepods. In the diet of cod larger than 4.9 cm the proportion of cyclopoida constituted 69% of the copepods. The amount of prey organisms beside copepods and cladocera decreased with increasing size of the juveniles.

The smallest size class of saithe was mainly feeding on insects and harpacticoid copepods. The proportion of insects decreased with increasing size of the juvenile saithe. The proportion of copepods varied between the size classes of saithe and seemed to be low whenever the proportion of cladocera in the diet is high. Only the bigger juveniles fed on Euphausiids.

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*Figure 4.3 Mean length of the 0-group cod and saithe for each sampling day*
Figure 4.4 Proportion of prey items for each size class of 0-group cod

Figure 4.5 Proportion of prey items for each size class of 0-group saithe
4.6. Mean number of prey items

The mean number of prey items increased over time up to a maximum amount, from where the numbers gradually decrease again (Figure 4.6). The maximum mean of prey items for saithe was found in the stomachs from mid-September (16 Oct), at 625 items per fish. For cod, the maximum numbers of prey items occurred on 20 October with an amount of 190 prey items per fish.

![Figure 4.6 Mean number of prey items of 0-group cod and saithe for each sampling day](image)

4.7. Diversity of the diet

The Shannon-Wiener measure revealed an overall higher diversity index in the diet of saithe than in the diet of cod (Table 4.2). For saithe, the species diversity of the prey organisms showed little variation between sampling days for the time from late August until mid-September (18 Aug to 14 Sep; Figure 4.8). For the subsequent samples, the values of the diversity index exhibited high variations with high differences between sampling days.
Figure 4.7 Shannon-Wiener Diversity Index calculated for the prey organisms found in the stomach content of 0-group cod and saithe.

Table 4.2 Shannon-Wiener Index for the mean diet composition of Atlantic cod and saithe for each sampling day:

<table>
<thead>
<tr>
<th>Date</th>
<th>Cod</th>
<th>Saithe</th>
</tr>
</thead>
<tbody>
<tr>
<td>22 Jul</td>
<td>0.89</td>
<td></td>
</tr>
<tr>
<td>17 Aug</td>
<td>0.76</td>
<td>1.87</td>
</tr>
<tr>
<td>18 Aug</td>
<td>1.32</td>
<td>1.39</td>
</tr>
<tr>
<td>25 Aug</td>
<td>1.34</td>
<td>1.40</td>
</tr>
<tr>
<td>26 Aug</td>
<td>1.21</td>
<td>1.57</td>
</tr>
<tr>
<td>01 Sep</td>
<td>1.33</td>
<td>1.40</td>
</tr>
<tr>
<td>14 Sep</td>
<td>1.60</td>
<td>1.47</td>
</tr>
<tr>
<td>16 Sep</td>
<td>0.69</td>
<td></td>
</tr>
<tr>
<td>17 Sep</td>
<td>1.03</td>
<td>1.40</td>
</tr>
<tr>
<td>25 Sep</td>
<td>1.14</td>
<td>0.64</td>
</tr>
<tr>
<td>02 Oct</td>
<td>0.98</td>
<td></td>
</tr>
</tbody>
</table>
The diversity index for the size classes decreased with increasing length apart from size class 8.0 – 8.9 cm, where the index reached its highest value of all classes of saithe (Table 4.3). For cod, the diversity index was higher during the first half of sampling (until 14 September) compared to the second half until 9 November. A negligible small variation was indicated by the index for the size classes of cod.

Table 4.3 Shannon-Wiener Index for the mean diet composition of Atlantic cod and saithe for each size class

<table>
<thead>
<tr>
<th>Cod size class</th>
<th>value</th>
<th>Saithe size class</th>
<th>value</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.0-3.4</td>
<td>1.35</td>
<td>&lt;4</td>
<td>1.69</td>
</tr>
<tr>
<td>3.5-3.9</td>
<td>1.34</td>
<td>4.0-4.9</td>
<td>1.75</td>
</tr>
<tr>
<td>4.0-4.4</td>
<td>1.58</td>
<td>5.0-5.9</td>
<td>1.61</td>
</tr>
<tr>
<td>4.5-4.9</td>
<td>1.52</td>
<td>6.0-6.9</td>
<td>1.29</td>
</tr>
<tr>
<td>&gt;4.9</td>
<td>1.23</td>
<td>7.0-7.9</td>
<td>1.20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>8.0-8.9</td>
<td>1.92</td>
</tr>
<tr>
<td></td>
<td></td>
<td>&gt;8.9</td>
<td>1.33</td>
</tr>
</tbody>
</table>

4.8. Dietary overlap

Calculations of the Morisita’s overlap index revealed high values for the diets of cod and saithe during August and September (Table 4.4). All values for this period were higher than 0.55, and 4 of 12 values were higher than 0.9. The index for the diets in October and November dropped down to values between 0.16 to 0.47 and indicated a lower diet overlap between cod and saithe later in the season.
Table 4.4 Simplified Morisita’s index of dietary overlap between Atlantic cod and saithe for each sampling day

<table>
<thead>
<tr>
<th>day</th>
<th>Overlap</th>
</tr>
</thead>
<tbody>
<tr>
<td>17 Aug</td>
<td>0.74</td>
</tr>
<tr>
<td>18 Aug</td>
<td>0.92</td>
</tr>
<tr>
<td>25 Aug</td>
<td>0.98</td>
</tr>
<tr>
<td>26 Aug</td>
<td>0.56</td>
</tr>
<tr>
<td>01 Sep</td>
<td>0.96</td>
</tr>
<tr>
<td>14 Sep</td>
<td>0.79</td>
</tr>
<tr>
<td>17 Sep</td>
<td>0.93</td>
</tr>
<tr>
<td>25 Sep</td>
<td>0.87</td>
</tr>
<tr>
<td>09 Oct</td>
<td>0.20</td>
</tr>
<tr>
<td>20 Oct</td>
<td>0.47</td>
</tr>
<tr>
<td>03 Nov</td>
<td>0.19</td>
</tr>
<tr>
<td>09 Nov</td>
<td>0.16</td>
</tr>
</tbody>
</table>

### 4.9. Foraging habitat

The foraging habitat of 0-group saithe was classified according to the habitat of the prey species found in the stomach content of the juveniles (i.e. pelagic, epibenthic or benthic). Measured as a percentage of total food items, cod was feeding mainly on benthic organisms and saithe fed largely on pelagic organisms (Figure 4.4; Figure 4.5). The juveniles of both species exhibited similar feeding patterns during most of the study time, where the diet in the beginning of August consisted mainly of benthic organisms. From then on, the proportion of benthic and pelagic prey items gradually shifted until the diet mainly contained pelagic organisms in the end of September. In October, benthic and epibenthic organisms became the main food source for cod and saithe again. In November, saithe primarily fed in the pelagic zone, whereas cod remained in the benthic and epibenthic habitat.
Figure 4.8 Proportion of foraging habitats of 0-group cod for each sampling day

Figure 4.9 Proportion of foraging habitats of 0-group saithe for each sampling day
The generalized linear mixed model analysis (Table A2) showed that the number of epibenthic and benthic, but not pelagic, prey items differed significantly between species (Table 4.5). Benthic and epibenthic organisms constituted the main diet of cod (64%), but represented only 33.8% of the prey organisms of saithe. Larger saithe juveniles had consumed fewer epibenthic and benthic prey items than had smaller saithe juveniles. Juvenile size did not affect the number of prey items in any of the three prey categories for juvenile cod.

Table 4.5 Results of a generalized linear mixed model (MCMCglmm, Hardfield 2010) using benthic, epibenthic and pelagic food items as the dependent variables, juvenile species and juvenile length nested within species as fixed effects and sample day as a random effect.

<table>
<thead>
<tr>
<th></th>
<th>POSTERIOR MODE</th>
<th>95% HPD INTERVAL</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>lower</td>
</tr>
<tr>
<td><strong>Random effects</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between day variation</td>
<td>0.012</td>
<td>0.000</td>
</tr>
<tr>
<td>Within day variation</td>
<td>2.148</td>
<td>1.560</td>
</tr>
<tr>
<td><strong>Fixed effects</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Model intercept</td>
<td>0.273</td>
<td>-2.735</td>
</tr>
<tr>
<td>Between species</td>
<td>3.835</td>
<td>0.811</td>
</tr>
<tr>
<td>Length of cod</td>
<td>0.580</td>
<td>-0.138</td>
</tr>
<tr>
<td>Length of saithe</td>
<td>-0.312</td>
<td>-0.546</td>
</tr>
<tr>
<td><strong>Random effects</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between day variation</td>
<td>0.174</td>
<td>0.001</td>
</tr>
<tr>
<td>Within day variation</td>
<td>0.998</td>
<td>0.755</td>
</tr>
<tr>
<td><strong>Fixed effects</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Model intercept</td>
<td>1.433</td>
<td>-0.110</td>
</tr>
<tr>
<td>Between species</td>
<td>3.436</td>
<td>1.627</td>
</tr>
<tr>
<td>Length of cod</td>
<td>0.294</td>
<td>-0.110</td>
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</tr>
<tr>
<td>Length of saithe</td>
<td>-0.339</td>
<td>-0.471</td>
</tr>
</tbody>
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**Random effects**

<p>| | | | |</p>
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<tbody>
<tr>
<td>Between day variation</td>
<td>0.733</td>
<td>0.249</td>
<td>2.427</td>
</tr>
<tr>
<td>Within day variation</td>
<td>1.553</td>
<td>1.205</td>
<td>2.117</td>
</tr>
</tbody>
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**Fixed effects**

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<tbody>
<tr>
<td>Model intercept</td>
<td>5.407</td>
<td>2.523</td>
<td>7.045</td>
</tr>
<tr>
<td>Between species</td>
<td>-0.999</td>
<td>-3.123</td>
<td>1.277</td>
</tr>
<tr>
<td>Length of cod</td>
<td>-0.605</td>
<td>-1.030</td>
<td>0.021</td>
</tr>
<tr>
<td>Length of saithe</td>
<td>-0.119</td>
<td>-0.297</td>
<td>0.076</td>
</tr>
</tbody>
</table>

There was significant variation in prey categories between sampling days, although for both epibenthic and benthic prey items the effect size is low and marginally significant (Table 4.5). There was high, and significant, variation within sampling days, signaling that individuals within each sampling differed in how much they foraged in epibenthic, benthic and pelagic niches.
5. Discussion

The results of this study show that the diet of Atlantic cod and saithe 0+ juveniles in shallow coastal waters consists of highly variable prey organisms from benthic, epibenthic and pelagic habitats. This implies that both species have a wide foraging niche that allows them to utilize different resources according to the geographical and temporal abundance of prey. The flexibility in their foraging indicates that juveniles of both species are highly opportunistic feeders, which, in turn, may enable them to mitigate competition for food among species as well as among individual juveniles.

5.1. Stomach content analysis

5.1.1. General patterns of prey species and comparisons to previous studies

In the current study, copepods accounted for more than 50% of the juveniles’ diet. That number is in line with the results of several previous studies that referred to copepods as the major resource of food for both juvenile cod and saithe (Rangeley & Kramer, 1995; Bromley et al, 1997; Hüssey et al. 1997). Especially the order of calanoid copepods has been found to constitute prevailing amounts of prey organisms in studies across the North Atlantic (Nedreaas, 1987; Lomond et al., 1998; Heath & Lough, 2005) with Calanus finmarchicus, Pseudocalanus spp., Arcarita spp., and Temora spp. as the most abundant species for juvenile cod in Icelandic waters (Thorisson, 1998). The calanoid species identified in this study were Temora longicornis, Acartia longiremis and C. finmarchicus, and although they constituted a significant proportion of the diet, they did not constitute the majority of prey items (Table A1; Table 4.1). The specific importance of C. finmarchicus for the juvenile gadoids, as described in previous studies (Nedraas, 1987; Bromley et al, 1997; Heath & Lough, 2005), might therefore be applicable only to the juveniles inhabiting the pelagic zone, which is the habitat of C. finmarchicus (Gislasson et al., 2014). The results of the current study, however, have shown that the diet of 0-group cod and saithe in shallow coastal waters consists of highly variable organisms, where C. finmarchicus plays a subsidiary role. In particular I identified high numbers of harpacticoid
and cyclopoid copepods as a crucial part of the juveniles’ diet. Most studies on the diet of juvenile cod and saithe in the North Atlantic have been conducted outside of Iceland. The only studies that investigated the feeding ecology of 0-group cod were conducted by Thorisson (1989) and Pálsson (1980 and 1983). Only a single study has investigated the diet of juvenile saithe in 1980, whereas the number of samples was low (213 stomach analyses for saithe with a size from 18 to 105 cm) and the author recommended that the results be regarded as preliminary (Pálsson, 1983).

Another order of crustaceans that constituted a high proportion of the stomach content was cladocera, with the genera *Evadne* and *Podon* being frequently found, although their relative ratios fluctuated across the sampling period. Juveniles fed on cladocera throughout the sample period; however, I could not identify any patterns in their abundance over time, which is in concordance with the results of Jespersen (1940), who described high fluctuations in the abundance of cladocera, which “sometimes constitute a considerable part of the plankton” (Jespersen, 1940: 36). Other crustacean of lesser importance for the juveniles’ diet were cyprid larvae, amphipoda, ostracoda and isopoda. Aquatic insects, mainly in the juvenile stages living in the benthos, were also important prey organisms for both juvenile species. The adult stages of insects, mainly diptera, which can be found at the water surface, were only found in the stomachs of saithe. Furthermore, molluscs and polychaeta that inhabit the epiphytic and benthic were found in the stomachs of both juvenile saithe and cod.

Previous studies on the diet of juvenile cod in Icelandic waters identified fish larvae, mainly capelin, euphausiids and copepods as the most important prey species (Pálsson, 1980; Thorisson, 1989). According to Thorisson (1989), cod juveniles started feeding on fish larvae as soon as they had reached a size of 2.5 cm in July and continued throughout August and September. In the current study, fish remains were found in neither cod nor saithe stomachs. Euphausiids only became important for saithe in late October, when the juveniles had reached a length of 7.0 cm (Figure 4.1; Figure 4.3). A possible explanation for the difference in the juvenile cod diet reported in the current study and by Thorisson (1989) and Pálsson (1980) might be the sampling depth. Most other studies on the diet of juvenile cod that have been conducted on juveniles sampled in deeper water, sometimes down to 200 m (Thorisson, 1989; Pálsson, 1980). In contrast, the sampling for the current study was conducted at depths between 0 to 1.5 m. The invertebrate fauna, species
abundance and thereby the potential prey species are likely to differ in relation to water depth. That might also explain the high proportions of harpacticoid and cyclopoid copepods that inhabit the benthic and epibenthic habitats that comprise most of the shallow coastal waters.

The quantity and composition of zooplankton in Icelandic waters undergo high seasonal fluctuations, and great differences in zooplankton composition have been revealed along the coasts of the country (Jespersen, 1940). The dependence of Icelandic cod juveniles on zooplankton has been previously shown in a study by Astthorsson et al. (1994), who identified a significant correlation between the abundance of 0-group cod and the biomass of zooplankton in Icelandic waters. In the current study, the composition of prey items of cod and saithe mostly follows similar patterns during the sampling period (Figure 4.1; Figure 4.2). Those patterns might reflect the fluctuation of the zooplankton and thus, the fluctuation of prey abundance. The general pattern of stomach contents across the sampling period, which is characterized by concomitant fluctuations in Atlantic cod and saithe, considerable diversity and different species (albeit similar groups) as reported in previous studies, collectively indicates high flexibility in the juvenile feeding habits.

5.1.2. Feeding pattern during the transition stage

Previous studies about the general feeding patterns of 0-group cod after settlement describe the decrease of pelagic prey organisms in the juveniles’ diet and the growing importance of benthic habitats as feeding grounds after settlement. The results of the current study contrast this pattern. The stomach content analysis revealed that juveniles underwent a gradual shift from the benthic towards the pelagic habitat (Figure 4.4; Figure 4.5). Interpreting this pattern, the low sample size and limited geographical distribution should be kept in mind. However, taking results of previous studies that describe the juveniles’ behavior and connecting them to the Icelandic environment might explain the habitat shift observed in this study. The Arctic light conditions, with midnight sun during the summer, might be one explanatory factor for the feeding patterns observed in the current study.

Juveniles have been observed to follow diurnal feeding rhythms, a mechanism to reduce the predation risk (Grant & Brown, 1998). During the day, the juveniles hide in the sheltered macro algae habitats, which they leave to feed in the pelagic environment between dusk and dawn. Assuming that the juveniles need the dark to feed in the pelagic
waters, the conditions in Iceland with 24 hour daylight during the summer months would not allow the juveniles to leave the sheltered habitat. As a consequence, they would feed on the available prey in the protected area, mainly benthic and epibenthic organisms. During the autumn and, thus, during the sampling time, the darkness increased and with this the possibility for the fish to gradually leave the macro algae and feed in the pelagic environment. This gradual shift in the juveniles’ diet from the benthic towards the pelagic habitat displays the feeding pattern observed in this study. The light conditions might explain the contrasting feeding patterns after settlement in the current study, but these are speculations and are mentioned here only to motivate further study. Another factor of the feeding patterns observed in the current study is the overall small size of cod juveniles, as will be further discussed below.

5.1.3. Size dependent feeding pattern and habitat utilization

The diet analysis revealed that the juveniles of both species fed in all three habitats (benthic, epibenthic and pelagic), and most types of prey organisms were utilized by both species. Results of the generalized linear mixed model, however, showed a significant variation in the proportions of prey organisms, which indicate that the juveniles are utilizing the habitats to a variable extent (Table 4.5). Benthic and epibenthic organisms constituted the main diet of cod (64%), but represented only 33.8% of the prey organisms of saithe, which was mainly feeding in the pelagic habitat (66.2%). Furthermore, some prey organisms have been found in the stomach content of either saithe or cod. Adult stages of insects and euphausiids are mainly consumed by saithe, whereas cod is feeding in higher percentages on copepods. Insects are found in surface near waters and euphausiids in the pelagic, while copepods (harpacticoids and cyclopoids) remain in the benthic and bentho-pelagic habitats. The different proportions and types of prey organisms indicate that the foraging niches of cod and saithe are not identical, which might be an adaptation that makes a co-existence of the two species in the same environment possible.

With both species feeding in all three habitat types, the question arises, why there are differences in the composition of prey items at all? An explanation for that might be physical limitations, such as the size. During the phase when insects constitute high proportions in the diet of saithe, juvenile saithe are about 1.5 cm longer than cod, where during the end of the study time, when saithe starts feeding on euphausiids, the difference
in size between the two species is up to 5 cm. Lomond et al. (1989) suggested that different feeding preferences are determined by the mouth opening and thus the ability of larger juveniles to feed on larger prey items. Insects and shrimp have both higher body volume compared to other prey items in the same sample. The ability to feed on larger prey organisms broadens the range of prey organisms and thus diversifies the prey spectrum of 0-group saithe.

This study identified a significant variation between the size distribution of juvenile saithe and the epibenthic and benthic habitat they were feeding in, respectively. During the whole study time, saithe and cod were feeding in all three habitats and therefore all size classes could be found feeding in the benthic and epibenthic habitat. Several studies consistently report of size-dependent feeding patterns of juvenile cod (Bergstad et al., 1987; Thorisson, 1989) and saithe (Rangeley & Kramer, 1995). The overall dietary pattern resulting from those studies suggests that the stomachs of the smaller juveniles contained high numbers of small prey organisms, whereas the stomach contents of the larger juveniles consisted of fewer, but bigger prey items. The change in the diet from smaller to bigger prey items occurred when saithe reached a length of 7 cm. From then on, the diet contained high amounts of euphausiids (Figure 4.5), which possess a distinct higher body volume compared to the other prey organisms investigated. No effects of size on the number of benthic, epibenthic or pelagic food items were determined for cod. The low size range of cod (3.0–6.2 cm) compared to saithe (2.9–13.4 cm) might be the reason that potential effects of changing size on the diet of juvenile cod remained unrevealed in this study.

According to the higher proportions of benthic and epibenthic organisms found in the stomachs of cod (Figure 4.4) assists with a study on diet during the settlement stage of 0-group cod. According to that, cod continue to feed on pelagic prey after settlement and before shifting to benthic prey (Lomond et al., 1998). The stomach content of cod with a size between 4.0 and 5.9 cm contained 98% pelagic prey items, whereas cod with a size between 6.0 and 10.0 cm contained 39% of pelagic prey items. Cod that were bigger than 10 cm contained 13% of pelagic prey items. Comparing the size classes from the present study (3.0–6.2 cm) to those results, cod would have been just about to change their diet to include more benthic items.
5.1.4. Intra- and interspecific trophic competition

Competition is defined as “the demand, typically at the same time, of more than one organism for the same resources of the environment in excess of immediate supply.” (Larkin, 1956). This definition, however, describes a wide range of animal interrelations. Within my study, I focus on competition for food within and between 0-group saithe and cod. The results of the stomach content analysis were used to investigate the potential for trophic competition primarily through examination of diet overlap, but also through interpretation of prey diversity.

The spawning time of saithe in Icelandic waters is several weeks earlier than the spawning time of Atlantic cod, so that by the time that juveniles of both species settle in the same environment, the saithe juveniles are at a more advanced developmental stage and considerably larger (Jónsson, 1996). Bromley (1997) suggests that 0-groups from early spawning events enter a simple food web and, thus, will be less subject to predatory pressure but also less exposed to competition for food. Fish species commonly undergo ontogenetic niche shifts where larger prey items are incorporated as the juveniles grow (Lomond et al., 1998). Fast growth, and the consequent incorporation of more varied and larger prey items, has often been found to be an instrumental factor in intra-cohort competition of fish (Svanbäck & Bolnick, 2006). The considerable size difference between the juvenile cod and saithe in the current study may therefore be expected to act to diversify the overall prey spectrum and thereby reduce competition. Nevertheless, calculations of the Morisita’s overlap index resulted in values close to 1, which revealed a very high overlap in the diet of 0-group cod and saithe at the sampling site. The index values were calculated for each sampling day, which means that regardless of the high divergence in the size of the juveniles from the two species, they were utilizing the same resources at the same time (Table 4.4). High values for most sampling days demonstrate that cod and saithe are feeding for high proportions on the same groups of organisms and indicate that there is a large potential for resource competition among 0-group cod and saithe. A drop in the values of the overlap index during the end of the sampling time implies that competition decreases during the end of October and November. During this time, cod is mainly feeding on benthic and epibenthic organisms while saithe starts feeding on shrimp, a prey organism that had not previously appeared in the diet (Figure 4.1; Figure 4.2). Diversifying the diet and feeding on different prey organisms lead to less overlap in
the diet and consequently to a decrease of competition. The period of pre- and early benthic settlement (Tupper & Boutilier, 1995) of juvenile cod, which coincides with the current sampling period, is therefore likely to reflect a crucial time in the survival of 0-group juveniles when competition between the two species is potentially high. This period may therefore be particularly vulnerable to fluctuations or changes in prey abundance.

A generally higher diversity in the diet of saithe compared to the diet of cod is indicated by the Shannon–Wiener index. The physical ability of larger fish to feed on a wider prey spectrum due to a bigger mouth gap has been explained in above. Saithe have been of a bigger size throughout the study, which allows them to feed on larger organisms and therefore have higher diversity in their diet compared to cod. With a wider prey spectrum, saithe can feed on organisms that are unavailable to cod and therefore reduce intraspecific competition. The physical ability to feed on larger prey items also allows the juvenile saithe to react more flexibly to environmental changes that affect the availability of prey organisms.

Results of the current study also identified several characteristics and feeding habits of the juveniles that may mitigate competition to some extent. The wide and generalist foraging niche, as indicated by Fjøsne and Gjøsæter (1996) and Mattson (1990) and Link and Garrison (2002), is likely to allow the juveniles to utilize different resources as they become available. Moreover, the significant variation in the feeding habitat on sampling days (Figure 5.1; Figure 5.2) suggests that individual juveniles foraged on different prey items. Individual specialization is thought to mitigate trophic competition within species or foraging groups and allow coexistence of larger foraging groups (Bolnick et al. 2003; Svanbäck & Bolnick, 2006). Juveniles may therefore decrease inter- and intraspecific competition by individual specialization.
Figure 5.1 Proportion of foraging habitat utilize by individual 0-group cod on three sampling days.

Figure 5.2 Proportion of foraging habitat utilize by individual 0-group saithe on three sampling days.
Potential competition that occurs between saithe and cod might be affected by several factors that interfere in the complex ecosystems of the coastal areas. Identifying all factors and analyzing their consequences is beyond the scope of the current study. The content of our haul during field work, however, showed that the shallow coastal area was inhabited by more fish species than just cod and saithe. Other species caught were *Myoxocephalus scorpius*, *Cyclopterus lumpus*, *Pholis gunnellus* and *Pleuronectes platessa*. Other fish species occupying the same habitat might affect competition and have an impact on the variations in the foraging behavior identified in this study, but there is no information available that substantiates any further discussion.

5.2. Habitat destruction and consequences for the juveniles

One question that I was aiming to answer with my study is the importance of the habitat types for the juvenile fish after the settlement. The importance of maerl and kelp as feeding grounds and a refuge for juvenile cod and saithe has already been identified in previous studies, and their results are described in the literature review. The juveniles that were sampled for this study were caught in an area with maerl and kelp as the prevailing vegetation types, and results from the stomach content analysis have shown that the fish were feeding on benthic and epibenthic organisms to a considerable amount. Those two factors highly indicate that the juveniles inhabit the macro-algae habitat and maerl and utilize them as feeding grounds. Furthermore, the juveniles were identified to be generalized/opportunistic feeders, which allows them to adjust to different environmental conditions and react flexibly to fluctuations in the prey availability. Nevertheless, the juveniles require few essential conditions in their nursery grounds that cannot be replaced. The majority of previous studies that have investigated the habitats of 0-group cod and saithe identified that the juveniles occurred in areas with, firstly, a habitat to feed in and, secondly, a habitat to find shelter (Borg et al., 1997; Keats et al., 1987; Keats & Steele, 1992; Kamenos et al., 2004a). Those two characteristics are provided by maerl and kelp, two structured habitats that provide shelter for the juveniles to hide from predation and also provide feeding grounds, especially maerl, which exhibit a high species diversity.

Bottom classification data from Gregory et al. (1997) in Placentia Bay, Newfoundland, determined that “the amount of suitable habitat for juveniles cod was a small portion of
that available” (Gregory et al., 1997: 3). Little information is available about the distribution of habitat types around Iceland. Despite that, habitats that can be assumed to be important nursery grounds for commercially important fish species are currently exploited. Especially for maerl, which is characterized to be a non-renewable resource, the habitat destruction in combination with the lack of information about the habitat distribution causes the risk that juveniles lose an important nursery habitat. A change in the condition or availability of a substratum type is considered to directly affect the survival of fishes (Johnsson, 2006; Elliot, Ahti, Heath, Turrell, & Bailey, 2016). Johnsson (2006) identified that the mortality decreased with an increase in structured habitats and pointed out that a shortage in the refuge space can affect the survival of the juveniles.

In the literature review, I described some of the key industries that are increasingly exploiting habitats of importance for the juvenile stages of cod and saithe. The juveniles inhabiting the shallow waters are feeding in high proportions in the benthic habitats. The high species diversity occurring on maerl suggests that the calcareous algae might be a feeding habitat of high value for the juveniles, and its degradation is thought to be impacting gadoid stocks (Kamenos, Moore, & Hall-Spencer, 2004b). According to Hall-Spencer (2010), the habitat removal has major effects on the species occurring on maerl, and consequently, a habitat loss would lead to a decrease in the available prey organisms and food would become a limiting factor in the juveniles’ environment.

Besides maerl mining, harvesting seaweed is one of the growing industries in Iceland that exploit marine resources that provide valuable habitats for the juvenile fish. The value of macro-algae relies on their role as feeding grounds as well as on the shelter they provide (Keats et al. 1986). With the loss of this habitat, juvenile fish will be more exposed to predation, and this will reduce the chances of survival for the juvenile gadoids (Gotceitas et al. 1995).

### 5.3. Size dependent trophic vulnerability

With this study, I identified the potential for high competition between and within 0-group cod and saithe in shallow coastal waters. Specifically, the two species have a very high niche overlap and exhibit a nearly identical prey spectrum at the onset of the benthic settlement of 0-group cod. Further reduction of the available habitats, and thereby a decrease in the available prey organisms as a consequence of habitat destruction, is likely
to increase the competition between and within the juvenile cod and saithe. Competition benefits those individuals that fit best to the particular conditions. Previous studies identified the competitive advantage of juveniles of bigger sizes and of those that settle early in the shallow waters (Ólafsdottir et al., 2015). Specifically for trophic interactions, larger juveniles seem to have an advantage towards other fish with similar prey spectrum as described above. Consequently, those juveniles that arrive later in the shallow waters or/and with a smaller body size have a competitive disadvantage in trophic interactions and therefore are most vulnerable to habitat degradation and its consequences. The reduction of the habitat in addition to the existing competition would decrease the probability of survival for juveniles of a small body size and that settle late in the shallow waters. This could in particular have dire consequences for 0-group cod, as saithe juveniles are significantly larger at this time.

5.4. Conservation management on valuable habitats

Looking at the post-settlement stage of the juveniles as a bottle neck, the destruction of important nursery habitats would tighten the opening and thus decrease the number of juveniles that survive this critical stage. Conservation measures would be needed to prevent the habitats from further destruction. After identifying the trophic vulnerability of the juveniles and the importance of their nursery habitats, I will discuss potential conservation measures that would protect the habitats, enhance the survival of the juveniles and, by extension, of the adult fish stocks.

In the literature review, I identified a high number of actual and potential threats on the juvenile fish and their environment. A management plan that would address all those impacts, including climate change and the various types of pollution, would by far extend the scope of a comprehensible management plan. Nevertheless, it is important to keep the various potential effects of climate change and other large-scale anthropogenic impacts in mind, as they increase the need for immediate precautionary actions with the goals of conservation and ecosystem based management.

5.4.1. Legal background in Iceland

Few fisheries regulations that approach the protection of juvenile fish or their habitat can be found in the Icelandic legislation. One regulation that protects valuable habitats such as
nursery grounds mandates the closure of specific areas to fishing activities. The closure can be set either temporarily or permanently, and the restriction can ban, for example, specific fishing gear or extend to a total ban of fishing activity. The designated areas are listed in the Act No. 79/1997 on Fishing in Iceland’s Exclusive Fishing Zone, and the decision to enact this measure for a specific area is made by the minister of fisheries in consultation with the Marine Research Institute (Art 9). Further protective regulations dictate a minimum size of the fish that may be caught. Here, specific rules for areas and fishing gear are in place that often apply only for a specific period of the year. Legal compliance is controlled by inspectors commissioned by the Ministry of Fisheries that go aboard fishing vessels and check on the fishing practices of the vessels (Art 10).

5.4.2. Incorporating international guidelines on maerl protection

The EU Habitat Directive introduced conservation regulations that oblige all member states to implement management measures for maerl beds. The measures mainly assist the conservation by protecting the maerl beds from physical damage, which applies for maerl mining and the employment of destructive fishing gear on the sea bottom (Hall-Spencer, 2010). Those regulations do impede the extraction of maerl. However, using France as an example, such regulations do not completely inhibit the commercial exploitation of maerl (92/43/EEC 1992). On the other hand, the EU regulations and OSPAR recommendations can also encourage the countries to go one step ahead and implement their own legislation concerning the protection of maerl. A role model for this case is the UK, which incorporated some maerl forming species in their Biodiversity Action Plan (UK BAP) (BRIG, 2007) and stopped granting extraction licenses (Hall-Spencer, 2010).

Using the existing regulations as a guideline and implementing an extended legislation that includes a prohibition of maerl mining and a ban of harmful fishing practice on maerl, would be the first protective measurements for maerl beds in Iceland and a first step to protect the nursery grounds of cod and saithe.

Further conservation measurements might be orientated towards the EU recommendations that encourage the states “to apply the precautionary approach and an ecosystem approach in adopting and implementing conservation and management measures […] protecting habitats of specific concern” (A/RES/61/105 2006: 14). In their conservation status, macro algae habitats are of minor concern despite the shelter and feeding grounds that they
provide for the juvenile fish. Literature research has shown that little is known about the value of macro algae as nursery habitats for fish in Iceland. However, given that various studies have proven the importance of macro algae, I would highly recommend following the precautionary approach in macro algae conservation. A special focus should be set on areas where macro algae and maerl occur in close proximity. Therefore, following the EU recommendations that calls upon states “to take action immediately, individually [...] and consistent with the precautionary approach and ecosystem approaches, to [...] protect vulnerable marine ecosystems” (A/RES/61/105 2006: 14), a legislation in Iceland that prohibits harvesting the macro algae in combined habitats, where both macro-algae and maerl occur, would be a crucial step for the protection of the nursery grounds of juvenile cod and saithe.

**5.4.3. Regulations to diminish the effects of aquaculture on maerl**

Protecting the surrounding sites of natural interest including seabeds with special characteristics and of scientific value is highly recommended by the Icelandic Nature Conservation Act no. 44/1999 Art. 54. The increasing number of aquaculture installations in the Westfjords and their destructive effects on the maerl beds demands for an immediate regulation to prevent their harmful impacts. Hall-Spencer et al. (2006) identified that the effects of fish farms on maerl are traceable up to a radius of 100 m around the sea cages. Following this state of knowledge, the future locations of the net pens would have to be outside a minimum distance of at least 100 m away from the edge of occurring maerl beds. Those safety zones would need to be designated on maps and incorporated into the licensing processes when new areas for fish farms are planned.

**5.5. Feasibility and Implementation**

The prerequisite for all management measures suggested is the availability of data about the habitat distributions, which would require mapping of the coastal waters around Iceland. Of all potential difficulties that might arise with implementing the conservation approaches suggested, the lack of available data about the habitat distributions seemed to be the most formidable obstacle. Mapping of the seafloor has been conducted in scattered areas around the country, but most bottom characteristics of the seafloor within the EEZ are unknown (Hjalti Karlsson, personal communication, June 2016). For the area in Ísafjarðardjúp where the present study has been conducted, for example, there are no data
about sea floor habitat distribution available (Cristian Gallo, personal communication, May 2016). To obtain the needed data would require the deployment of highly specialized equipment. For effective protection, mapping around Iceland and thus of a large area would be needed, which is extremely expensive and time consuming. Using a multibeam system to scan the seafloor provides a detailed map about bathymetry combined with the distribution of sediment types. The results of the seabed survey do not only benefit science, but also the fisheries, since the knowledge of the maps increase fishing efficiency (Garcia & Ragnarsson, 2007). To designate the maerl habitats would require a complete mapping around the country. The implementation of such a large scale project became first realistic in 2015, when the Icelandic government bestowed the financing of a bottom survey for Icelandic waters on the 50th anniversary of the Marine Research Institute (Hafrannsóknastofnun, 2016). This survey would provide the required sea floor data for implementing the conservation regulations.

The shallow coastal areas where maerl can be found are of little importance for the Icelandic fisheries. The only fishing gear that is implemented in those areas are scallop dredges and, rarely, the Danish seine (Garcia & Ragnarsson, 2007). After the collapse of the scallop stocks in 2003, scallop dredging has played a negligible role for Icelandic fisheries (Garcia & Ragnarsson, 2007). Therefore, the shallow coastal waters are of marginal importance for the fisheries as such, since most fishing gears are deployed in deeper waters. Consequently, the suggested conservation measure on the valuable habitats hardly affects fisheries. No interference with the areas of interest of the fisheries, an industry with high economic impact, might facilitate the implementation of the habitat regulations. Even more, since the conservation measurements are expected to enhance the growth and survival of the juvenile fish of economic value and are likely to be beneficial for the fisheries.

Establishing a minimum distance of 100 meters between the maerl beds and the fish farms might interfere with the plans of aquaculture companies. This areal restrictions for the placement of aquacultures might become even a bigger matter of concern, since local companies in the Westfjords applied for governmental licenses to multiply the amount of farmed fish and consequently will require larger areas for a higher numbers of fish cages. The legal framework that might be applicable for the protection of habitats against the impacts of aquaculture is the regulation No. 48/1994 on pollution control. The regulation
provides a legal framework to protect waters against pollution, especially for areas that are vulnerable towards the impacts of fish farms (Jonsson, 2000).

The coastal waters around Iceland are divided into two juridictional areas. The waters from the low-water mark out to 115m are under the the legislation of the local government and can be utilized by the landowners (“Netlög”, Jarðalög nr. 81/2004). Waters beyond the 115 m line are under governmental jurisdiction. The discussed habitats maerl and kelp can be mainly found close to the coast; however, in shallow fjords, those habitats also occur further out than 115 m. For the protection of the habitat that occur in both areas, a legislation that applies to the whole marine environment would be needed to prevent conflicts between the different areas of jurisdiction. The Nature Conservation Act no. 44/1999 applies to Icelandic territorial waters and exclusive economic zone and therefore provides a suitable legislative framework for the protection of the discussed habitats.

5.6. Further recommendations on future research

There has been limited research on the foraging behavior of juvenile Atlantic cod and saithe in Iceland, and knowledge about the feeding grounds and habitat distribution is based mostly on studies conducted on the east coast of North America, in the Baltic and in the northeast Atlantic. More basic research on the juveniles’ stomach contents is needed, and this requires a high sampling size and a good species knowledge of the prey organisms (possibly down to the species level) to gain a better understanding of the feeding patterns and diet overlap.

Saithe and cod were the main, but not the only, fish species that were caught during the sampling. Investigating the feeding habits of other species that share the habitat with 0-group cod and saithe would provide a more complete picture about the actual food competition between juvenile fish species.

The information about the abundance and distribution of the prey organisms found in the stomach content of the juveniles was obtained from previous studies about feeding ecology and about the Icelandic ecosystem. For future research investigating the feeding patterns of juveniles, I recommend the sampling of each habitat type and of different depths to know about the detailed distribution of the prey organisms in the habitats and over the time period investigated. Allocating the prey organisms to a specific habitat would enable the
researcher to obtain precise information about the juveniles’ migration patterns from the pelagic to benthic environments during the early settlement.

Understanding the early-life dynamics and recruitment processes would require the implementation of long-term studies on early-life stages of cod and saithe. Annual fluctuations in the ecosystem and their effects on the early life stage of cod and saithe requires an ongoing sampling that would last for several years. In addition, stretching out the research not only in time, but also in space by comparing different sampling sites would provide a broader understanding for the juveniles feeding behavior and habitat dependency.
6. Conclusion

Despite the great importance of cod and saithe for the fisheries in Iceland, little research has been investigated the early life stages of those two fish species. With this study, I analysed the feeding pattern of 0-group cod and saithe and connect them to species interaction. The results showed a high dietary overlap between 0-group cod and saithe from which I inferred that food competition among those two species is highly likely to occur. The juvenile habitats that were sampled for this study consisted mainly of maerl and macro algae, habitat types that have been identified by previous studies to be highly valuable nursery ground. The current distribution of those habitats in the Westfjords is at an unknown stage, but habitat exploitation and destruction due to anthropogenic impacts constitute an increasing threat to the juvenile habitats. The wide range of prey organisms indicates that juveniles of both species are opportunistic feeders, which gives them the ability to adopt to various changes in their environment. A further reduction of the available habitats and a decrease in the available prey organisms as a consequence of habitat destruction, however, is likely to increase the competition between and within the juvenile cod and saithe. The available food determines the growth and survival of the early life stages of cod and saithe (Fjøsne & Gjøsæter, 1996) and therefore, an ongoing loss of their habitats will eventually lead to a decrease in the population of juvenile cod and saithe. With this study, I identified the need for conservation measurements to protect valuable nursery habitats and suggest regulations for anthropogenic impacts occurring in the Westfjords, mainly caused by resource extraction and fish farming. Creating a legal framework for the protection of maerl beds within Icelandic waters by following existing international guidelines on habitat protection would be a first step to incorporate the early life stages of fish into ecosystem management. One crucial requirement for the implementation of the suggested management measures is to accomplish a seafloor mapping around Iceland and thereby obtain baseline information to locate valuable habitats. Future studies should incorporate long-term studies to understand the conditions and behaviour that control and regulate recruitment during the early life stages of Atlantic cod and saithe.
References


Appendix

Table A1 Calanoid Copepods from 7 stomach contents were analyzed down to species level by Teresa Sofia Giesta da Silva.

<table>
<thead>
<tr>
<th>Sample ID</th>
<th>Temora longicornis</th>
<th>Calanus finmarchicus</th>
<th>Acartia longiremis</th>
<th>Acartia spp.</th>
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</thead>
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<td></td>
<td></td>
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</table>

Table A2 The R-code for the generalized linear mixed model (MCMCglmm, Hardfield 2010). The code was calculated for “benthic diet”.

```r
MCMCglmmBenthic <- MCMCglmm(benthicdiet ~ species + species:length, 
  random= ~ sampleday, 
  data=data,family="poisson",pr=TRUE, 
  nitt=100000,thin=10,burnin=10000, 
  prior=prior1, 
  verbose=FALSE)
```