Master's Thesis

The ecosystem effects of kelp harvesting in the northeast Atlantic

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Kelp forests are highly diverse and productive ecosystems in cold, coastal waters around the world. Kelp forests are important for primary production, coastline protection and providing habitat for many species. The three-dimensional structure of kelp can provide shelter and help the survival of other species living in kelp forests. Kelp has been mechanically harvested for over 50 years with a 5-year harvesting cycle. Previous studies on kelp harvesting show kelp recovery in four years after harvesting, but the recovery of other species inhabiting kelp forests is poorly understood. The Atlantic cod (*Gadus morhua*) and the European lobster (*Homarus gammarus*) are commercially important species that use kelp forests as a habitat. Previous studies have shown that habitat complexity can enhance juvenile fish survival. In the present study we parametrized an allometric trophic network (ATN) model for a northeast Atlantic kelp forest and designed a non-trophic interaction between kelp and juvenile Atlantic cod, and kelp and European lobster. Kelp harvesting was simulated by removing 20% or 80% of kelp biomass at the end of the growth season, and the harvesting events were carried out at 1-, 4-, or 8-year intervals through the harvesting period of 50 years. The biomass changes of kelp, kelp consumers, and the Atlantic cod and the European lobster were explored. We found that kelp biomass recovered with harvesting intervals of 4 and 8 years when 20% or 80% of kelp was removed, but kelp biomass did not recover with either harvesting intensity when kelp was harvested every year. The biomasses of kelp consumers declined, recovered, or increased during the harvesting period, depending on the species. The biomasses of the Atlantic cod age groups 0 and 4+ and the biomass of the European lobster declined with harvesting intervals of 1 and 4 years, and the decline was largest when harvesting intensity was 80%. The non-trophic interaction of kelp cover added to the Atlantic cod and to the European lobster increased the oscillations of the biomasses and the effect of the kelp harvesting on Atlantic cod and European lobster. These results show that the effect of kelp harvesting can impact the wider ecosystem through declining biomass and population fluctuations and indicate that the recovery of kelp associated species may not follow the recovery of kelp.

Susanna Pesari:	Kelppilevän keruun vaikutukset ekosysteemiin koillisella Atlantilla
Pro gradu -tutkielma:	35 s., 2 liitettä (7 s.)
Työn ohjaajat:	Prof. Anna Kuparinen, PhD Pauliina Ahti ja PhD Tommi Perälä
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Kelppilevämetsät ovat erittäin monimuotoisia kylmien rannikkovesien ekosysteemejä. Kelppilevämetsät tarjoavat monia ekosysteemipalveluita: ne esimerkiksi suojaavat rantoja eroosiolta, ovat tärkeitä perustuotannossa ja luovat elinympäristön monille muille lajeille. Kelppilevien kolmiulotteinen rakenne tarjoaa suojaa kelppilevämetsissä eläville lajeille ja auttaa niiden selviytymisessä. Kelppilevää on kerätty mekaanisesti jo yli viidenkymmenen vuoden ajan ja keruu tehdään usein viiden vuoden jaksoissa. Aiemmat tutkimukset kelppilevän keruusta ovat osoittaneet, että kelppileväbiomassa palautuu neljässä vuodessa, mutta keruun vaikutuksia kelppilevämetsän ekosysteemiin on tutkittu vähemmän. Turska (*Gadus morhua*) ja hummeri (*Homarus gammarus*) ovat kaupallisesti tärkeitä lajeja, jotka käyttävät kelppilevämetsiä elinympäristönä. Aiemmat tutkimukset ovat osoittaneet, että elinympäristön moniulotteisuus voi parantaa nuorten kalojen selviytymistä. Tässä tutkimuksessa parametrisoimme allometrisen ekosysteemimallin Koillis-Atlantin kelppilevämetsälle ja tutkimme ei-trofista vuorovaikutusta kelppilevän ja turskan sekä kelppilevän ja hummerin välillä. Kelppilevän keruuta simuloitiin mallissa 1-, 4- tai 8-vuoden välein siten, että kelppileväbiomassaa poistettiin kasvukauden lopussa 20 tai 80 prosenttia kelpin kokonaisbiomassasta. Havaitsimme, että kelppileväbiomassa palautui, kun palautumisaika oli neljä tai kahdeksan vuotta, mutta kelppileväbiomassa ei palautunut, kun keruu tapahtui joka vuosi. Kelpinsyöjien biomassojen muutokset olivat lajikohtaisia. Osa lajien biomassoista väheni, osa palautui ja osa kasvoi. 0- ja 4+-vuotiaan turskan sekä hummerin biomassat vähenivät, kun palautumisaika oli yksi tai neljä vuotta, ja muutos oli suurin, kun kelppiä poistettiin 80% kelpin kokonaisbiomassasta. Kelpin ja turskan sekä kelpin ja hummerin välinen ei-trofinen vuorovaikutus aiheutti turskan ja hummerin biomassojen heilahtelua sekä voimisti kelpin keruun vaikutusta lajeihin. Tulokset osoittavat, että kelppilevien keruulla voi olla vaikutuksia muihin ekosysteemin lajeihin elinympäristön menetyksen ja ravintoverkon dynamiikan muutosten kautta.

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1 INTRODUCTION

Kelp forests are highly diverse and productive underwater ecosystems in temperate coastal waters around the world (Mann 1973). Kelp forests are important for the vast amount of biodiversity they harbour and for the ecosystem services they provide. Kelp forests protect coastlines by reducing wave action (Løvås & Tørum 2001), provide habitat for many different species, including commercial species such as the European lobster (*Homarus gammarus*) and the Atlantic cod (*Gadus morhua*) (Schoenrock et al. 2020), and are harvested for different purposes in biotechnology, food production and pharmaceuticals (Smale et al. 2013). However, globally kelp forests are declining in third of the ecoregions (Krumhansl et al. 2016). Ocean acidification, large storms, overfishing, and kelp harvesting pose a threat to the kelp forest ecosystem and its functioning (Connell & Russell 2010, Byrnes et al. 2011, Steneck et al. 2002, Lorentsen et al. 2010). Kelp harvesting has been carried out mechanically for over 50 years in the northeast Atlantic (Vea & Ask 2011), but no comprehensive studies on the ecosystem scale effects of the harvesting exist.

Kelps are large brown algae, mostly in the order Laminariales, and they inhabit rocky shores in temperate regions. Kelp algae consists of three parts: the holdfast, the stipe, and the lamina (or blades). Kelps are important in primary production, and their ability to attach to a hard substratum with the holdfast facilitates kelp dominance on rocky shores where plants are not able to root (Mann 1982). Nitrogen is a key nutrient for kelp and water turbidity helps nutrient assimilation in kelp making the annual productivity of kelp forests high (Dayton 1985). Kelps are ecosystem engineers modifying and creating habitat structure for many organisms with the three-dimensional form, and they alter physical factors such as light and waterflow on coastal waters. Kelp forests are nurseries for juvenile fish and invertebrates, and important feeding grounds for fish in the northeast Atlantic

(Norderhaug et al. 2005). In the northeast Atlantic the genus *Laminaria* is the dominant kelp forest former.

A study on the Norwegian *Laminaria* kelp forests showed that kelp-derived carbon is important for the near-shore ecosystem and can be a carbon source for different marine animals, including filter feeders (Fredriksen 2003). However, a study on *Macrocystis* kelp forests in California found that benthic herbivores were consuming kelp, but the suspension-feeders are not using kelp derived particulate organic matter but mostly nearshore phytoplankton as food (Page et al. 2008). Mobile invertebrate fauna are important in transporting carbon originating from kelp to higher trophic levels, and large quantities of kelp are exported from the ecosystem by detachment of kelp and drifting (Norderhaug & Christie 2011). Kelp forest fish communities can show inverted biomass pyramids where the higher trophic levels have more biomass than lower trophic levels which could indicate that subsidies from other coastal habitat ecosystems provide higher trophic levels the energy needed to sustain the high biomass (Trebilco et al. 2016). In kelp forest food webs kelp is directly linked to species feeding on kelp and kelp derived carbon, but kelp is also linked to many species indirectly by the habitat kelp forests provide.

While habitat complexity is known to increase prey survival, the survival is likely to be linked to species-specific predator-prey behaviours (Scharf et al. 2006). Lindholm et al. (1999) showed that complex habitat increases juvenile Atlantic cod survival. The mortality of 0-year-old cod on sand habitat was 93.4%, on cobble surface 66.8% and on sponge habitat 32.2%. Beukers & Jones (1998) studied juvenile lemon damselfish (*Pomacentrus moluccensis*) survival on different coral reef habitat complexities and predator densities, and they found that reefs with high-complexity coral with predators supported the same number of damselfish as the reefs with no resident predators, but on low-complexity corals with resident predators the abundance of juvenile damselfish was significantly lower. The kelp forest structure can be related to the sponge and coral habitats regarding their complexity and their benefits for larvae and juvenile fish survival. As kelp

harvesting is usually done mechanically with dredges that decrease the complexity of the seafloor habitat, the effects of kelp harvesting at the ecosystem scale is a concern.

Kelp is harvested both by hand and mechanically. In the northeast Atlantic, mechanical harvesting takes place mostly in Norway and France, and in Ireland the growing demand for seaweed has seen a push for mechanical harvesting (Werner & Kraan 2004). In Norway 160 000 tonnes of *Laminaria hyperborea* is harvested annually (10-15% of standing stock) (Werner & Kraan 2004). Kelp forests in Norway have been harvested mechanically for over 50 years and a 5-year cycle of harvesting (1 year of harvesting and 4 years of recovery) has been regarded as sustainable (Vea & Ask 2011). While research shows that kelp biomass can recover in the 4-year recovery time, the kelp age, size, and the density of kelp recruits were still below pre-harvesting levels (Steen et al. 2016). Additionally, the kelp epiphytes were also below pre-harvesting levels which indicates that further studies on the recovery of kelp-associated species are needed to assess the effects of kelp harvesting on ecosystem functioning.

Lorentsen et al. (2010) studied the foraging effort of the great cormorants (*Phalacrocorax carbo*) in the kelp forests on the coast of Norway and found that the foraging effort was higher in the harvested kelp forests compared to pristine kelp forests. Kelp harvesting decreased the abundance of small fish in the kelp forests which indicates that kelp harvesting can affect species at higher trophic levels and can have a bottom-up effect on the ecosystem. The effect of kelp harvesting can, however, be species or behaviour specific, as a study on European shags (*P. aristotelis*), for instance, found that kelp harvesting did not alter the diving activity of shags (Christensen-Dalsgaard et al. 2020). Christensen-Dalsgaard et al. (2020) did, however, emphasize the need for more fine-scale data to understand the non-trophic interactions and the multitrophic effects of kelp harvesting.

In this thesis a food web model was used to study the effects of kelp harvesting on the wider kelp forest ecosystem. In addition to the trophic interactions in the food web, a non-trophic interaction between kelp and juvenile (0-year-old) Atlantic cod

(*G. morhua*) and kelp and European lobster (*H. gammarus*) was developed to study the habitat effect on the survival of the two commercially important species in the kelp forest. Northeast Atlantic kelp forests are essential habitats for Atlantic cod and European lobster, and due to their close association with kelp, these species provide a great opportunity to study the non-trophic interaction between habitat and species at higher trophic levels (Bertocci et al. 2015). The research questions were: 1) How does kelp biomass recover after the kelp harvesting? 2) How does kelp harvesting affect the biomasses of kelp consumers? And 3) How does kelp harvesting affect the biomasses of the Atlantic cod and the European lobster through not only the indirect trophic interactions but also through a non-trophic interaction such as the habitat effect of kelp on survival?

2 MATERIALS AND METHODS

2.1 Overview

To study the effects of kelp harvesting at the ecosystem scale, data of the northeast Atlantic kelp forest species were collected from the literature and different kelp harvesting scenarios were simulated with an allometric trophic network (ATN) model. The focus was on a non-trophic interaction between kelp and two commercially important species: the Atlantic cod (*G. morhua*) and the European lobster (*H. gammarus*). The Atlantic cod and the European lobster did not directly feed on kelp but were linked to kelp through other species in the food web (trophic interactions) and by the non-trophic interaction of kelp cover. The final food web consisted of 43 species or groups, and with fish species divided to five age-groups (0-, 1-, 2-, 3-, and 4+ -year-olds) each represented as their own node in the food web, the total number of nodes (guilds) in the food web summed up to 123, and the number of links between guilds (trophic interactions) was 1300. Kelp harvesting was simulated with harvesting intensities of 20% and 80% and harvesting intervals of 1, 4, and 8 years.

2.2 Northeast Atlantic kelp forest food web

The food web used in this thesis consisted of trophic interactions (feeding links) between the northeast Atlantic kelp forest species and non-trophic interactions (habitat effect of kelp cover) between kelp and Atlantic cod and between kelp and European lobster (Figure 1). To construct the kelp forest food web, a species list of invertebrate and fish species from the kelp forests of the west coast of Ireland was used (K. Schoenrock, personal communication, 13.10.2020). Phytoplankton and zooplankton species for the food web were searched from the literature. The invertebrate and fish species list included abundance ranks of Superabundant, Abundant, Common, Frequent, Occasional, and Rare (SACFOR) based on the SACFOR abundance scale which is a unified system for recording the abundance of marine benthic flora and fauna in biological surveys with cover/density scales of super abundant, abundant, common, frequent, occasional, and rare (Hiscock 1996). Invertebrate species (mollusca, crustacea, echinoderms, Actiniaria) with SACFOR abundance of common, abundant, and super abundant were chosen for the food web, and for the fish species also frequent, occasional, and rare species were included.
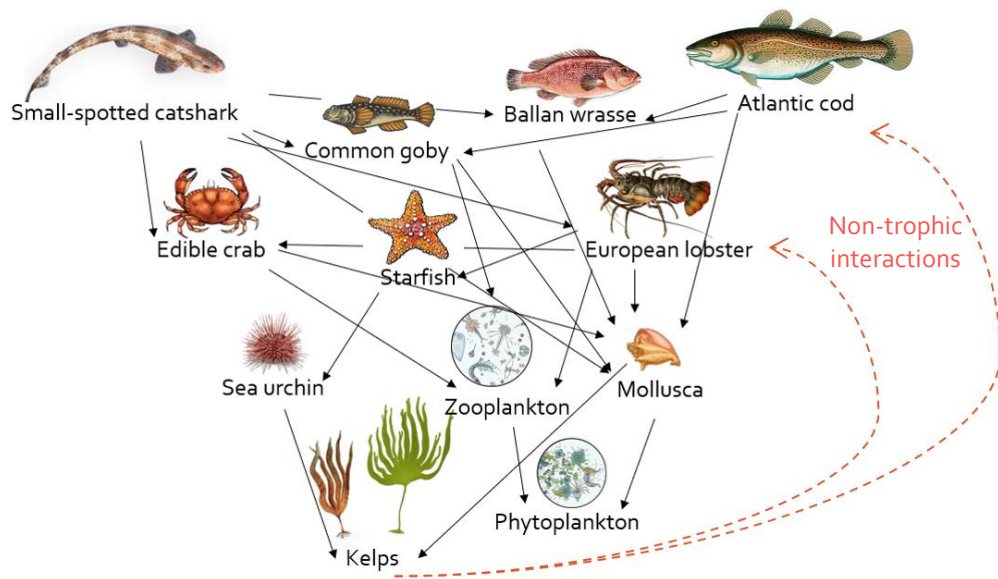
Figure 1. A simplified graph of the northeast Atlantic kelp forest food web. The black arrows represent the trophic links (feeding links) between the species or groups in the food web, and the red dotted arrows represent the non-trophic interactions (habitat effect of the kelp cover) between kelp and the Atlantic cod and the European lobster.

The final species/group list included dissolved organic carbon (DOC), particulate organic carbon (POC), kelp, phytoplankton, zooplankton, invertebrate and fish taxa (Table 1, for detailed fish information see Appendix A). An individual body mass in carbon (µgC) and common prey items for each species were searched from the literature (for all references used see Appendix B). DOC and POC biomasses were calculated by the model. Fish species were separated by age to groups of 0, 1, 2, 3, and 4+ year-olds. Separating different age-stages of fish gives a more realistic model as their body size, and thus their metabolic rate, and feeding links can change with age.

Table 1. The list of species or groups in the northeast Atlantic kelp forest food web. Body masses and prey items are listed for kelp, phytoplankton, zooplankton, and invertebrates. For information on fish species, please see Appendix A. (DOC = dissolved organic carbon, POC = particulate organic carbon, na = not applicable).

Number	Species/group (guilds)	Body mass (µgC)	Prey items (links)
1	DOC	na	na
2	POC	na	na
3	*Laminaria hyperborea*	2.08e+07	na
4	Diatom small	9.24e-04	na
5	Diatom medium	2.31e-03	na
6	Diatom large	7.80e-03	na
7	Dinoflagellate small	1.83e-03	na
8	Dinoflagellate medium	5.78e-03	na
9	Dinoflagellate large	9.21e-03	na
10	Copepoda small	6.37e+01	4-9,
11	Copepoda medium	2.53e+03	4-9,
12	Copepoda large	1.03e+04	4-9,
13	Decapoda larvae	4.14e+01	4-12,
14	Euphausiacea	1.60e+01	4-12,
15	*Palaemon serratus*	7.88e+04	10-14,16,17,
16	*Actinia equina*	3.62e+04	10-14,17,21,22,
17	Mollusca	9.46e+04	3-9,16,
18	Starfish	1.79e+06	17,19,
19	Sea urchin	1.45e+06	2,3,
20	*Cancer pagurus*	1.14e+07	10-13,17,21-23,
21	*Carcinus maenas*	3.83e+06	3,10-13,15,17,20,22,
22	*Pagurus bernhardus*	1.46e+06	3-15,17,20,21,
23	*Homarus gammarus*	1.52e+08	10-13,17-22,
24	*Ctenolabrus rupestris*	{	
25	*Centrolabrus exoletus*		
26	*Symphodus melops*		
27	*Labrus mixtus*	information on fish species	
28	*Labrus bergylta*	see Appendix A	
29	*Pholis gunnellus*		
30	*Platichthys flesus*		
31	*Taurulus bubalis*		
32	*Gobiusculus flavescense*		
33	*Pomatoschistus spp.*		
34	*Thorogobius ephippiatus*		
35	*Gobius niger*		
36	*Gobius paganellus*		
37	*Lipophrys pholis*		
38	*Callionymus lyra*		
39	*Ammodytes tobianus*		
40	*Ciliata mustela*		
41	*Pollachius pollachius*		
42	*Gadus morhua*		
43	*Scyliorhinus canicular*	}	

To estimate the biomass of an individual kelp in µg of carbon, the fresh weight of a 4-year-old *L. hyperborea* was used (M. Pedersen, personal communication, 9.2.2022). The dry weight was calculated with known water content in fresh weight (Rajauria et al. 2021) as follows:

$$dry\ weight = fresh\ weight \times 0.15 \qquad (1)$$

and the carbon content from dry weight was calculated based on Sjøtun et al. (1996) with equation:

$$carbon\ content = dry\ weight \times 0.29 \qquad (2)$$

To describe the phytoplankton groups in the model, diatoms (Oksman et al. 2019) and dinoflagellates (Hinder et al. 2012) were used as reference species. Both groups were divided into three size groups (small, medium, and large). The carbon contents of small, medium, and large diatoms were estimated from the carbon content of *Thalassiosira gravida*, *Thalassiothrix longissima*, and *Rhizosolenia hebetata f. semispina* respectively. The body mass in carbon for these species were extracted from a global diatom database (Leblanc et al. 2012).

The carbon content of dinoflagellates is based on the abundance data of Hinder et al. (2012) so that *Ceratium lineatum* was the reference species for small dinoflagellates, *C. furca*, *C. fusus*, *C. tripos*, *C. macroceros* and *C. longipes,* were the combined average reference for medium dinoflagellates, and *Protoperidium curtipes* was the reference species for large dinoflagellates. The body mass in carbon for these species was extracted from nordicmicroalgae.org. An average carbon content from different-sized cells were used if more than one size was recorded for the species.

The zooplankton species were acquired from Kennington & Rowlands (2006) where zooplankton species and groups were listed by abundance percentages. Zooplankton groups with abundance composition of more than 5% were chosen for the food web and from those groups, species with abundance composition of more than 1% of all zooplankton were taken into consideration and their

individual body masses in carbon were searched from the literature. For *Pseudocalanus elongatus*, *Temora longicornis*, *Acartia clausi,* and *Nyctiphanes couchi,* the body mass in carbon was calculated based on Lindley et al. (1997). The carbon mass of small copepods was based on the species *Calanus helgolandicus* and *Centropages hamatus*, the medium copepods on the species *P. elongatus*, *A. clausi* and *Calanus finmarchicus*, and the large copepods on the species *T. longicornis*. For the decapoda larvae, the *Inachus dorsettensis* was used as a reference species (megalopa stage, Anger 1988) and for the Euphausiacea the reference species was *N. couchi* (Lindley et al. 1999).

The individual body mass in carbon and the prey species for invertebrates were recorded for nine species or groups (*Palaemon serratus*, *Actinia equina*, *Cancer pagurus*, *Carcinus maenas*, *Pagurus bernhardus*, *H. gammarus,* and groups mollusca, starfish, and sea urchin). The reference species for mollusca were *Calliostoma zizyphinum* and *Hinia reticulata*, for starfish the reference species was *Asterias rubens*, and for sea urchin the reference species was *Echinus esculentus*. For starfish only species *A. rubens* was used as a reference due to lack of data on other starfish species, and for sea urchin *E. esculentus* was used as it was the most abundant species. Literature searches were conducted for all the 20 fish species in the model for average lengths and prey species for the different age classes. The length for the 0-year-old fish was calculated to be an average of 1cm and the length of a 1-year-old fish. The food web model calculated the weight of the fish based on the length using the length-weight equation of Ricker (1975):

$$W = a \times L^b \tag{3}$$

where W = fresh weight in grams and L = length in cm. The coefficients a and b in the equation for each fish species were found from literature and fishbase.org. The dry weight is calculated based on the fresh weight following Murray & Burt (2001):

$$\text{dry weight} = \text{fresh weight} \times 0.2 \tag{4}$$

and from that the carbon content is calculated based on Blaxter (1989) with an equation:

$$\text{carbon content} = \text{dry weight} \times 0.53 \qquad (5)$$

The carbon content of fish is about 10% of the fresh weight of the fish.

2.3 ATN model

The allometric trophic network (ATN) model was used to study the effects of kelp harvesting on the northeast Atlantic kelp forest ecosystem. The ATN model was developed by Brose et al. (2006) and further developed by Kuparinen et al. (2016) and Bland et al. (2019) to include the structure of fish life-history. The ATN model is based on the metabolic theory of ecology which states that most biological activities are determined by metabolic rates (Brown et al. 2004). Here the model was parametrized for a northeast Atlantic kelp forest. The constructed food web contained 123 guilds and 1300 links in total. A non-trophic interaction was added to the model to explore the survival benefit of the protection provided by the kelp habitat to larvae and juvenile (0-year-old) Atlantic cod and European lobster.

The ATN model is based on ordinary differential equations which describe the changes in the carbon densities in the food web. The model calculates how carbon transfers between the different species or groups in the food web through predator-prey or consumer-resource interactions. The biomass unit is $\mu gC/m^3$. The equations for producers (6), consumers (7) and detritus (8) are based on Boit et al. 2012, Kuparinen et al. 2016, and Brose et al. 2006.

$$\frac{dB_i}{dt'} = \overbrace{r_i B_i G_i(\mathbf{B})(1 - s_i)}^{\text{gain from producer growth}} - \sum_j \frac{\overbrace{x_j y_{ji} B_j F_{ji}(\mathbf{B})}^{\text{loss to consumer } j}}{e_{ji}} \qquad (6)$$

$$\frac{dB_i}{dt'} = -\overbrace{f_m x_i B_i}^{\text{maintenace loss}} + \overbrace{f_a x_i B_i \sum_j y_{ij} F_{ij}(\mathbf{B})}^{\text{gain from resources } (j)} - \sum_j \frac{\overbrace{x_j y_{ji} B_j F_{ji}(\mathbf{B})}^{\text{loss to consumer } j}}{e_{ji}} \qquad (7)$$

$$\frac{dD}{dt'} = \sum_i \sum_j \left[\frac{\overbrace{x_i y_{ij} B_i F_{ij}(\boldsymbol{B})}^{\text{ingestion of resource } j \text{ by consumer } i}}{e_{ij}} \cdot \frac{\overbrace{}^{\text{egestion}}}{(1 - e_{ij})} \right] + \sum_i \overbrace{r_i B_i G_i(\boldsymbol{B}) s_i}^{\text{exudation by producer } i} - \sum_j \frac{\overbrace{x_j y_{ji} B_j F_{ji}(\boldsymbol{B})}^{\text{loss to detritivore } j}}{e_{ji}} \quad (8)$$

In the equations, $\boldsymbol{B}$ = vector of all biomasses, B_i = biomass of species or group i, r_i = intrinsic growth rate of species or group i, $G_i(\boldsymbol{B}) = {}^{[1 - (\sum_{j=producers} c_{ij} B_j)/K]}$ is the limiting factor in the producer's logistic growth model, which includes producer competition coefficients c_{ij} and carrying capacity coefficient K of phytoplankton or kelp, s_i = fraction of exudation, x_i = mass-specific metabolic rate of consumer i based on allometric scaling, y_{ij} = maximum consumption rate scaling factor of species or group i feeding on species or group j, e_{ij} = assimilation efficiency describing the fraction of ingested biomass that is actually assimilated, f_m = maintenance respiration coefficient, f_a = fraction of assimilated carbon used for production of consumers' biomass. $F_{ij}(\boldsymbol{B})$ is the consumers' normalized functional response and for this thesis we modified the equation to include the effect of kelp habitat to lower the success of predation and this non-trophic interaction is described in detail in section 2.3.1.

Fish species were divided into five age groups. The larvae and juvenile fish (age groups 0 and 1) have the same equation as consumers (7) but adult fish (age groups 2, 3, and 4+) allocate portion of the biomass to reproduction with the following equation (9) based on Uusi-Heikkilä et al. (2022):

$$\dot{B}_i^+ = \begin{cases} P_i I_i \cdot \dfrac{g_i^2}{2\ell_i}, & g_i < \ell_i \\[2mm] P_i I_i \cdot \left(g_i - \dfrac{1}{2}\ell_i \right), & g_i \geq \ell_i \end{cases} \quad (9)$$

where $\dot{B}_i^+$ = the rate of biomass allocation to reproduction by adult fish guild i during the growth season, the consumption gains $g_i = f_a x_i B_i \sum_j y_{ij} F_{ij}(\boldsymbol{B})$ and the maintenance losses $\ell_i = f_m x_i B_i$ determine the biomass allocation, P_i = the proportion of mature biomass in adult fish guild i, and I_i = the parameter controlling how much gets invested into reproduction. The proportion of mature

biomass in age groups 2, 3, and 4+ are 5%, 50%, and 95%, and the investment parameter values are 10%, 15%, and 20%. To form the equation for adult fish (10), the reproduction equation (9) is added for the adult fish to the consumer equation (7) as follows:

$$\frac{dB_i}{dt'} = - \overbrace{f_m x_i B_i}^{maintenace\ loss} + \overbrace{f_a x_i B_i \sum_j y_{ij} F_{ij}(\mathbf{B})}^{gain\ from\ resources\ (j)} - \sum_j \overbrace{\frac{x_j y_{ji} B_j F_{ji}(\mathbf{B})}{e_{ji}}}^{loss\ to\ consumer\ j} - \dot{B}_i^+ \qquad (10)$$

After each growth season, the reproduction biomass of year Y $B_{Y,i}^+(t^{end})$ is allocated to the initial larvae (age group 0) biomass for the next growth season by the adult fish guild i. The equation for the initial biomass of larvae in year $Y+1$ is then the sum of reproduction biomass produced by all adult fish group of the species:

$$B_{Y+1,i}(0) = \sum_{a=2}^{4} B_{Y,i+2a}^+(t^{end}) \qquad (11)$$

The initial biomass of age groups 1, 2, and 3 for the year $Y+1$ is the biomass of the previous age group at the end of the growth season Y.

$$B_{Y+1,i}(0) = B_{Y,i-2}(t^{end}) \qquad (12)$$

The age group 4+ consist of fish ages of 4-year-olds and older, and the initial biomass for the group 4+ for the year $Y+1$ is the sum of the biomass of the previous age group and the biomass of the group 4+ at the end of the growth season Y.

$$(13)$$

$$B_{Y+1,i}(t^{init}) = B_{Y,i}(t^{end}) + B_{Y,i-2}(t^{end})$$

2.3.1 Non-trophic interaction of kelp cover

A habitat interaction was added between kelp and a 0-year-old Atlantic cod, and between kelp and the European lobster. The Atlantic cod or the European lobster did not have a direct trophic link to the kelp (i.e., they did not feed on kelp). The non-trophic interaction of the habitat effect of kelp cover was implemented into

the model by modifying the commonly used Holling type III – Beddington – deAngelis –hybrid functional response as follows:

$$F_{i,j}(\mathbf{B}(t)) = \frac{\omega_{i,j}\,(C_{i,j}(\mathbf{B}(t))B_j(t))^q}{B0_{i,j}^q + d_{i,j}B0_{i,j}^q B_i(t) + \sum_{k \in \mathcal{J}_i^{\mathrm{prey}}} \omega_{i,k}\,(C_{i,k}(\mathbf{B}(t))B_k(t))^q} \qquad (14)$$

where $\omega_{i,j}$ = relative prey preference of consumer species i feeding on resource species j, q = 1.2 which forms a relatively stable functional response intermediate between the Holling Type-II and Type-III functional responses, $B0_{i,j}$ = half saturation constant of resource species j at which consumer species i achieves half of its maximum feeding rate on species j, $d_{i,j}$ = coefficient of feeding interference, and B_K = kelp biomass. Here the term $C_{i,j}$ captures the proportion of prey j available for consumption by predator i, and is given by:

$$C_{i,j}(\mathbf{B}(t)) = \overbrace{(1 - P_j(\mathbf{B}(t)))}^{\text{proportion of unprotected prey } j} + \overbrace{(1 - c_{i,j})P_j(\mathbf{B}(t))}^{\text{proportion of prey } j \text{ partially protected by kelp}} \qquad (15)$$

where $c_{i,j} \in [0, 1]$ = protection level offered by habitat for prey j from predator i. For the interspecies kelp competition, we assume that it is related to the inverse of the kelp utilization coefficient, so that those species with improved kelp utilization (and hence smaller λ-value) have a competitive edge. Then, of the kelp utilized by all prey with the non-trophic interaction (here 0-year-old Atlantic cod and European lobster), the species j occupies a fraction $q_j(\mathbf{B}(t)) := \lambda_j^{-1}B_j(t)/\sum_{k \in \mathcal{J}_K} \lambda_k^{-1}B_k(t)$. Here λ_j = coefficient of kelp utilisation by prey species j, and J_K = set of indices for the functional guilds utilizing kelp for habitat protection. Note that competition applies only when the total kelp biomass is fully utilized by the non-trophic interaction prey, $\sum_{k \in \mathcal{J}_K} \lambda_k B_k(t) \geq B_K(t)$, otherwise the kelp can accommodate all non-trophic interaction prey biomass.

To calculate the proportion P_j of prey species' j biomass under the protection of kelp, we first calculate how much of the utilized kelp biomass is associated with the biomass of species j. This is achieved by multiplying the total kelp biomass with the fraction of kelp utilized by species j, and finally multiplying with the

inverse of the utilization efficiency to transform the kelp biomass into that of the prey: $\lambda_j^{-1}q_j(\mathbf{B}(t))B_K$. Then, we compare this with the total biomass of species j:

$$\frac{\lambda_j^{-1}q_j(\mathbf{B}(t))B_K}{B_j(t)} = \frac{\lambda_j^{-2}B_K(t)}{\sum_{k\in\mathcal{J}_K}\lambda_k^{-1}B_k(t)} = \frac{B_K(t)}{\lambda_j B_j(t)}\frac{1}{\sum\limits_{k\neq j}\lambda_k B_k(t)} \tag{16}$$

This results in

$$P_j(\mathbf{B}(t)) = \begin{cases} 1 & \text{if } \sum_{k\in\mathcal{J}_K}\lambda_k B_k(t) < B_K(t) \quad \text{and} \quad j\in\mathcal{J}_K \\ \frac{B_K(t)}{\lambda_j B_j(t)}\frac{1}{\sum\limits_{k\neq j}\lambda_k B_k(t)} & \text{if } \sum_{k\in\mathcal{J}_K}\lambda_k B_k(t) \geq B_K(t) \quad \text{and} \quad j\in\mathcal{J}_K \\ 0 & \text{if } j\notin\mathcal{J}_K \end{cases} \tag{17}$$

The biomass dynamics of kelp is

$$\dot{B}_K(t) = r_{\text{kelp}}B_K(t)\left(1 - \frac{B_K(t)}{K_{\text{kelp}}}\right)(1 - s_{\text{kelp}}) \tag{18}$$

where r_{kelp} = intrinsic growth rate of kelp, s_{kelp} = fraction of exudation, and K_{kelp} = carrying capacity coefficient of kelp.

2.4 Simulation design and carrying capacity estimation

Six different kelp harvesting scenarios were simulated on MATLAB Version 9.4 (R2018a). First, a 500-year burn-in period was run to find an ecologically stable state for the food web. This was then followed by a 50-year period of kelp harvesting where depending on the harvesting intensity, 20% or 80% of kelp biomass was removed at the end of the growth season, with harvesting intervals of 1, 4 and 8 years. After the harvesting period, simulations were continued for another 50 years for the ecosystem to reach a stable state again. The model removed kelp in single action which meant that the recovery time in the harvesting period was the same as the harvesting interval, in other words recovery time after each harvesting event was 1, 4, or 8 years. In the 5-year-cycle of kelp harvesting the recovery time is 4 years, and 1 and 8 years were chosen to explore the effect of the harvesting when the recovery time would be shorter or longer.

Estimation of carrying capacity of kelp forest is needed for the model, but data on kelp forest carrying capacity is lacking. Carrying capacity in the model is not the same as annual productivity which for kelp is estimated 340-1000 gC/m² (Smale et al. 2020, Pedersen et al. 2012) and for phytoplankton 73 gC/m² (Skogen et al. 2007). A 1 000 000 µgC/m³ carrying capacity was chosen for both kelp and phytoplankton for the simulations. This is based on a similar work in Lake Constance where the annual phytoplankton productivity is estimated to be 300 gC/m² (Tilzer & Beese 1988) and where the ATN model carrying capacity for phytoplankton was set to 540 000 gC/m3. Since the kelp productivity in the northeast Atlantic is estimated to be higher (up to 1000 gC/m²) we chose a higher carrying capacity for both kelp and phytoplankton.

3 RESULTS

3.1 Kelp biomass

The kelp harvesting had an effect on kelp biomass in the kelp forest ecosystem. There were similar patterns in the change of kelp biomass at harvesting intensities of 20% and 80% but the magnitude of the change was larger when 80% of kelp was removed (Figure 2). When kelp was harvested every year, the kelp biomass remained at a substantially lower level for the whole harvesting period: at harvesting intensity of 20% the kelp biomass declined by almost 30% compared to the pre-harvesting level and at intensity of 80% the kelp biomass declined by almost 90% compared to the pre-harvesting level. However, when kelp was harvested every 4 or 8 years, the kelp biomass recovered to the pre-harvesting state after each harvesting event, and in the case of the 8-year recovery time, the kelp biomass exceeded the pre-harvesting level after each harvesting event (increase of almost 10%). After the 50-year harvesting period the kelp biomass reverted to the pre-harvesting biomass level. At harvesting intensity of 80% and

harvesting interval of 1 year, the kelp first increased over 50% over the pre-harvesting biomass level before recovering to the pre-harvesting biomass level.
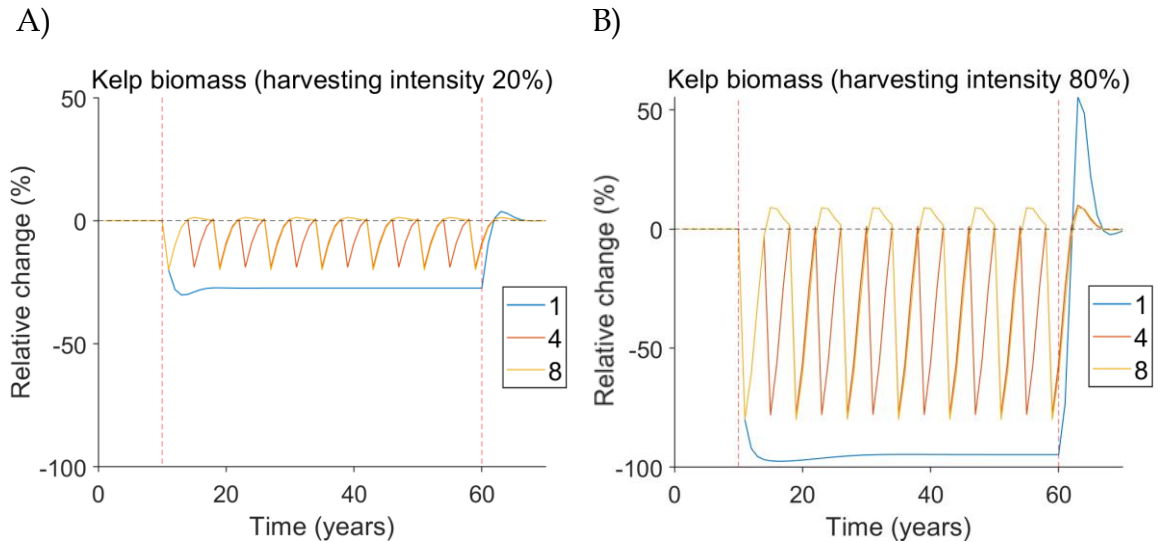
A)

B)

Figure 2. The relative change of the kelp biomass at harvesting intensities of A) 20% and B) 80%, with kelp harvesting intervals of 1, 4 and 8 years. The black dotted line represents the pre-harvesting biomass level of kelp, and the harvesting period of 50 years is displayed between the red dotted lines.

3.2 Kelp consumers

In this food web model, the kelp consumers were mollusca, sea urchin, green shore crab (*C. maenas*), and common hermit crab (*P. bernhardus*). The patterns of the biomass changes of the kelp consumers were similar at both kelp harvesting intensities of 20% and 80%, but at harvesting intensity of 80% the relative changes were bigger than at 20% (Figure 3). Between the kelp consumers, the relative biomass changes were different. The biomass of mollusca declined when kelp was harvested every year: at harvesting intensity of 20% the biomass was 3% lower compared to the pre-harvesting biomass, and at harvesting intensity of 80% the biomass was almost 20% lower compared to the pre-harvesting biomass. With harvesting intervals of 4 and 8 years, the biomass of mollusca oscillated but recovered after each harvesting event beyond the pre-harvesting biomass at both kelp harvesting intensities.
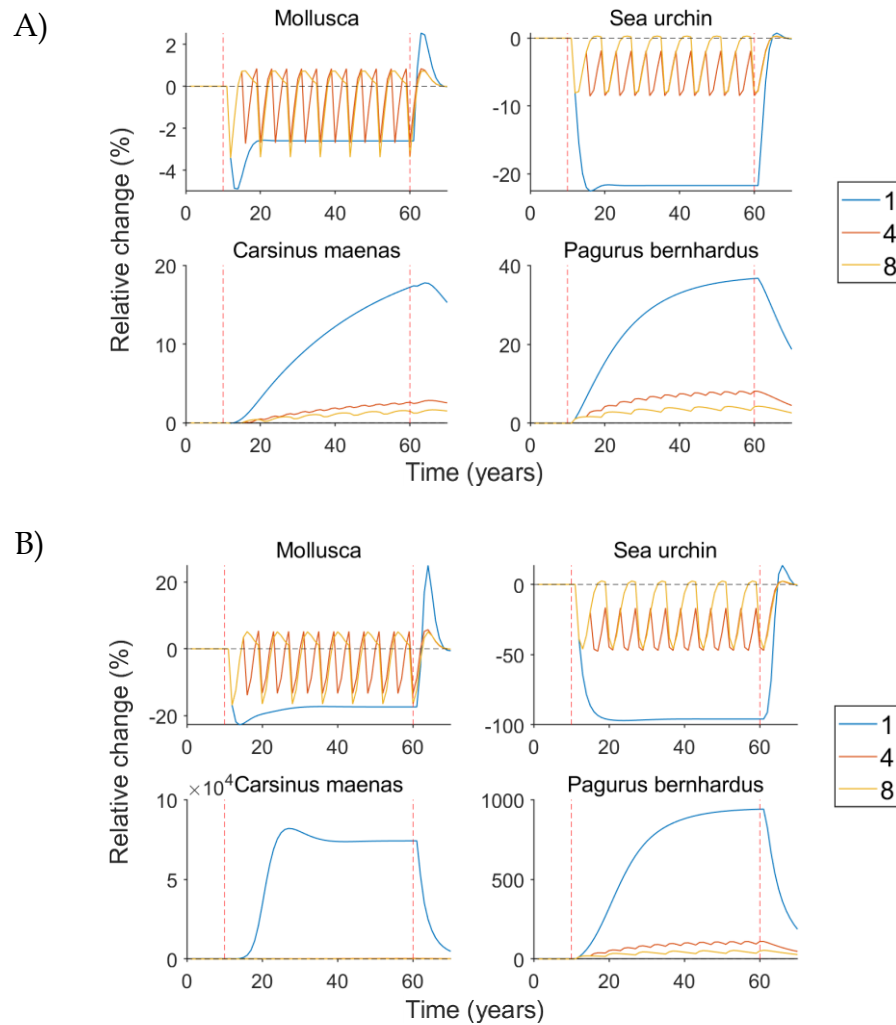
Figure 3. The effect of kelp harvesting on the relative biomass of invertebrate consumers feeding on kelp with kelp harvesting intensities of A) 20% and B) 80% and with harvesting intervals of 1, 4, and 8 years. The kelp harvesting period is shown between the red dotted lines and the black line represents the biomass before harvesting. (Note that the y-axis scales are different in each subplot)

The biomass of sea urchin declined with harvesting intervals of 1 and 4 years at both harvesting intensities of 20% and 80% (Figure 3). When kelp was harvested every year, the sea urchin biomass was over 20% lower than the pre-harvesting biomass at harvesting intensity of 20%, and with harvesting intensity of 80%, the sea urchin biomass was over 90% lower than the pre-harvesting biomass. When the harvesting interval was 4 years, the sea urchin biomass was 3% lower than pre-harvesting biomass at harvesting intensity of 20%, and at harvesting intensity of 80% the biomass was almost 15% lower than the pre-harvesting biomass. When

kelp harvesting interval was 8 years, the sea urchin biomass recovered at both harvesting intensities.

The biomasses of the green shore crab (*C. maenas*) and the common hermit crab (*P. bernhardus*) were highest when kelp was harvested every year at both harvesting intensities of 20% and 80% (Figure 3). At harvesting intensity of 20% the biomass of the green shore crab was 18% higher compared to the pre-harvesting biomass, and the biomass of the common hermit crab was almost 40% higher compared to the pre-harvesting biomass. At harvesting intensity of 80%, the biomasses of both crab species were remarkably higher than the pre-harvesting biomasses: the green shore crab over 10 000% higher, and the common hermit crab almost 1 000% higher. When the harvesting interval was 4 or 8 years, the biomasses of the green shore crab and the common hermit crab increased but not as much as it did at the 1-year harvesting intensity.

The diets of the kelp consumers were examined for the 4-year harvesting interval scenario. The diet items were consumed at different proportions and the diets were measured as the biomass gained from the consumption of the resource species. Small changes were detected when the pre-harvesting consumption gains of kelp consumers were compared to consumption gains during the harvesting period (Figure 4). At 20% harvesting intensity the changes between consumption gains before and during kelp harvesting were smaller than at harvesting intensity of 80%. For all kelp consumer species, the kelp consumption decreased during the harvesting period and the consumption of the other diet items increased. For the sea urchin the change in the consumption gains between the pre-harvesting and the harvesting period was very small (< 1%).
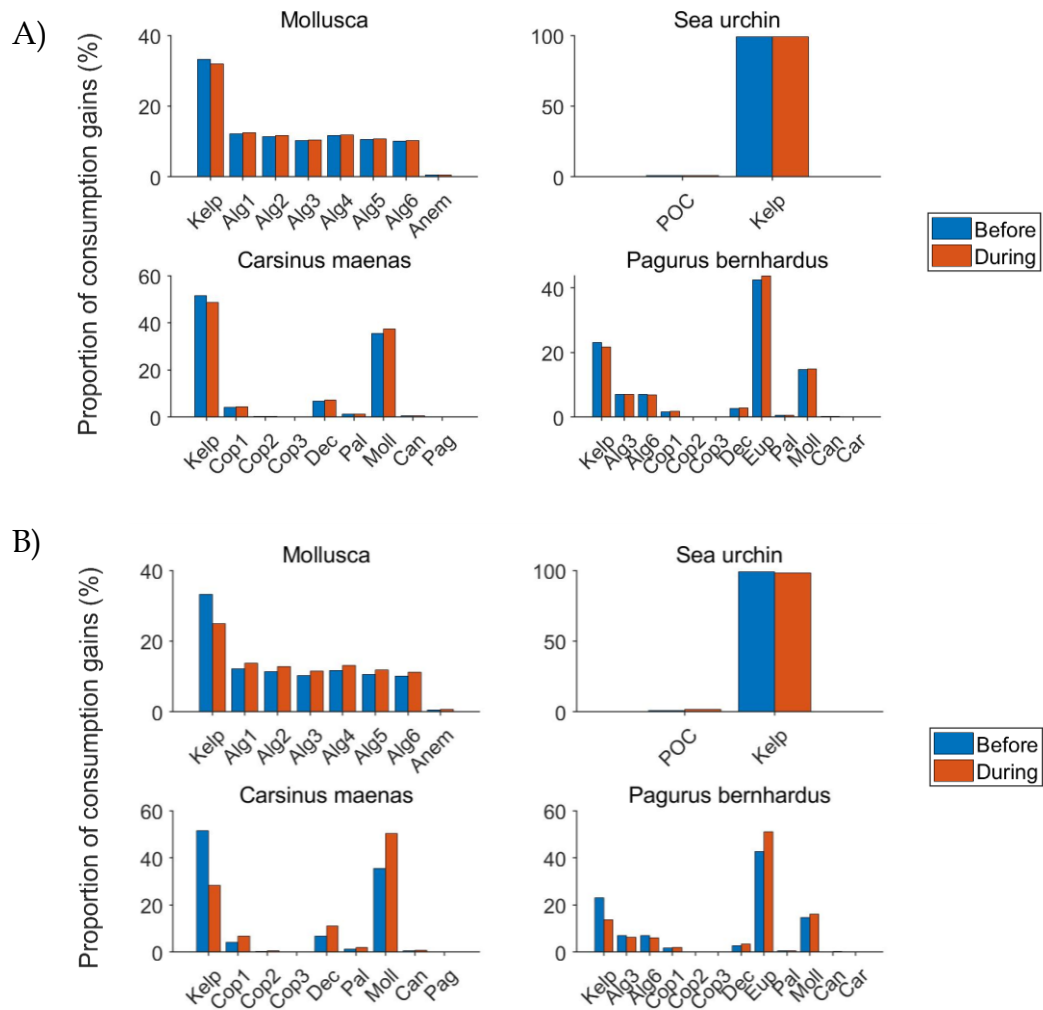
Figure 4. The proportion of consumption gains of different diet items of kelp consumers at kelp harvesting intensities of A) 20% and B) 80% and harvesting interval of 4 years. The blue bars represent the consumption gains before harvesting period and the red bars represent the consumption gains during the 50-year kelp harvesting period. (POC = particulate organic carbon, Alg1 = diatom small, Alg2 = diatom medium, Alg3 = diatom large, Alg4 = dinoflagellate small, Alg5 = dinoflagellate medium, Alg6 = dinoflagellate large, Cop1 = copepoda small, Cop2 = copepoda medium, Cop3 = copepoda large, Dec = decapoda larvae, Eup = Euphasiacea, Pal = *Palaemon serratus*, Moll = mollusca, Anem = *Actinia equina*, Can = *Cancer pagurus*, Car = *Carsinus maenas*, Pag = *Pagurus bernhardus*) (Note that the y-axis scales are different in each subplot)

3.3 Non-trophic interaction

3.3.1 Atlantic cod

The relative changes of biomass in the different age groups of Atlantic cod were small at kelp harvesting intensity of 20%, but at harvesting intensity of 80% the changes were larger (Figure 5). The biggest biomass changes in the Atlantic cod were in the age groups of 0 and 4+ with harvesting intervals of 1 and 4 years. When kelp was harvested every year, the biomass of the age group 0 at harvesting intensity of 20% was 6% lower compared to the pre-harvesting biomass level, and at harvesting intensity of 80% the biomass was almost 30% lower compared to the pre-harvesting biomass. The biomass of the age group 4+ was almost 3% lower compared to the pre-harvesting biomass at harvesting intensity of 20%, and 15% lower compared to the pre-harvesting biomass at the harvesting intensity of 80%. When kelp harvesting interval was 4 years, the biomass of age group 0 was 1% lower compared to the pre-harvesting level at harvesting intensity of 20%, and almost 10% lower compared to the pre-harvesting level at harvesting intensity of 80%. The biomass of the age group 4+ was almost 1% lower compared to the pre-harvesting biomass at harvesting intensity of 20%, and almost 5% lower compared to the pre-harvesting biomass at harvesting intensity of 80%. With kelp harvesting interval of 8 years, the biomasses of both age groups recovered to pre-harvesting state at both harvesting intensities. The biomasses of both age groups oscillated when kelp harvesting interval was 4 or 8 years.

The Atlantic cod age groups 1, 2, and 3 recovered when harvesting interval was 4 or 8 years at both harvesting intensities of 20% and 80%, but the biomass oscillated during the harvesting period. When kelp was harvested every year, the biomass of the age group 1 was just under the pre-harvest level at harvesting intensity of 20%, but at harvesting intensity of 80% the biomass was approximately 5% lower compared to the pre-harvesting biomass level. The biomasses of the age groups 2 and 3 declined at both harvesting intensities when kelp was harvested every year.

At harvesting intensity of 20%, the biomasses of age groups 2 and 3 were about 1% lower compared to the pre-harvesting biomass, and at harvesting intensity of 80%, the biomasses were almost 10% lower compared to the pre-harvesting biomasses.

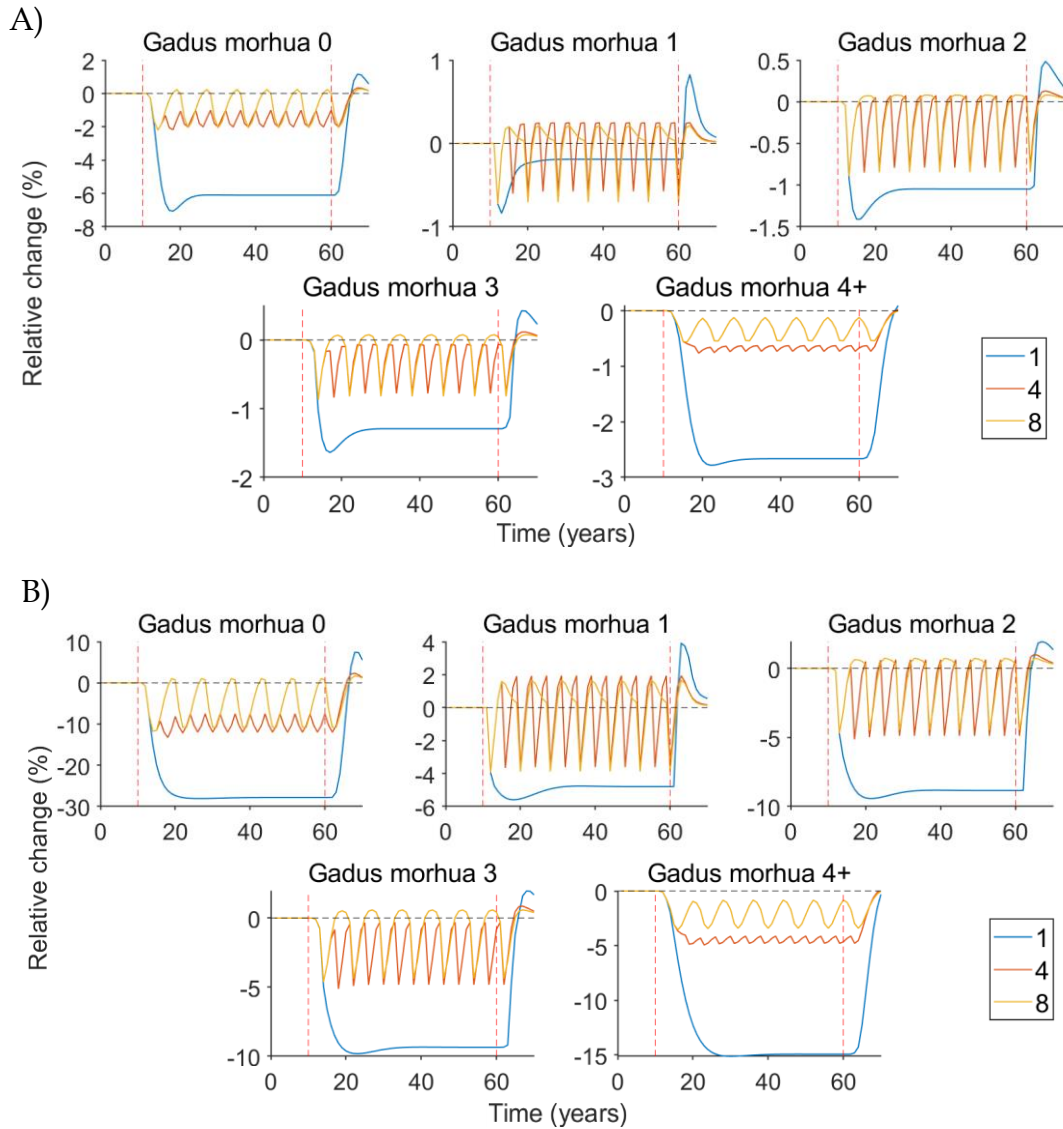Figure 5. The effect of kelp harvesting on the Atlantic cod (*Gadus morhua*) for age groups of 0, 1, 2, 3, and 4+ year-olds. Kelp harvesting intensities were A) 20% and B) 80%, and harvesting intervals were 1, 4, and 8 years. The black dotted line represents the biomass before harvesting and the harvesting period of 50 years is between the red dotted lines. (Note that the y-axis scale varies between the subplots)

3.3.2 European lobster

The relative changes in the biomass of the European lobster showed similar patterns at both harvesting intensities (Figure 6). When kelp was harvested every year, the European lobster biomass remained at a lower level compared to pre-harvesting biomass: at harvesting intensity of 20% the biomass was over 20% less than in the pre-harvesting state, and at harvesting intensity of 80% the biomass was over 80% less than in the pre-harvesting state. When kelp harvesting interval was 4 years, the European lobster biomass was 5% lower compared to the pre-harvesting biomass at kelp harvesting intensity of 20%, and over 30% lower compared to the pre-harvesting biomass at kelp harvesting intensity of 80%. When kelp harvesting interval was 8 years, the biomass of the European lobster recovered at harvesting intensity of 20%, but at harvesting intensity of 80%, the biomass was approximately 5% lower compared to the pre-harvesting biomass. The biomasses oscillated in the harvesting period when the harvesting interval was 4 or 8 years.
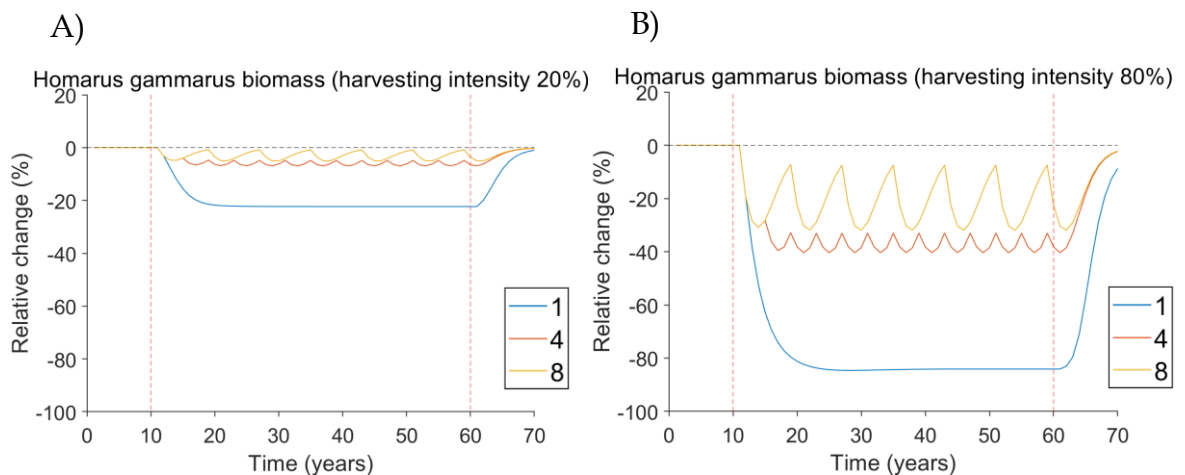

Figure 6. The effect of kelp harvesting on European lobster (*Homarus gammarus*) biomass when A) 20% and B) 80% of kelp is removed at each harvesting event. Harvesting intervals of the harvesting events were 1, 4, and 8 years and the harvesting period of 50 years is between the red dotted lines. The black line represents the European lobster biomass before harvesting.

3.3.3 Kelp cover effect

The effect of the non-trophic interaction between kelp and European lobster and kelp and 0-year-old Atlantic cod was further tested for scenario where kelp harvesting intensity was 80% and harvesting interval was 4 years. The response of biomasses to kelp harvesting was tested with and without the non-trophic interaction (kelp cover). The effect of kelp harvesting to European lobster was over 10% larger when the kelp cover was included (Figure 7). The oscillation of the relative biomass of the European lobster was also larger when the kelp cover was included.
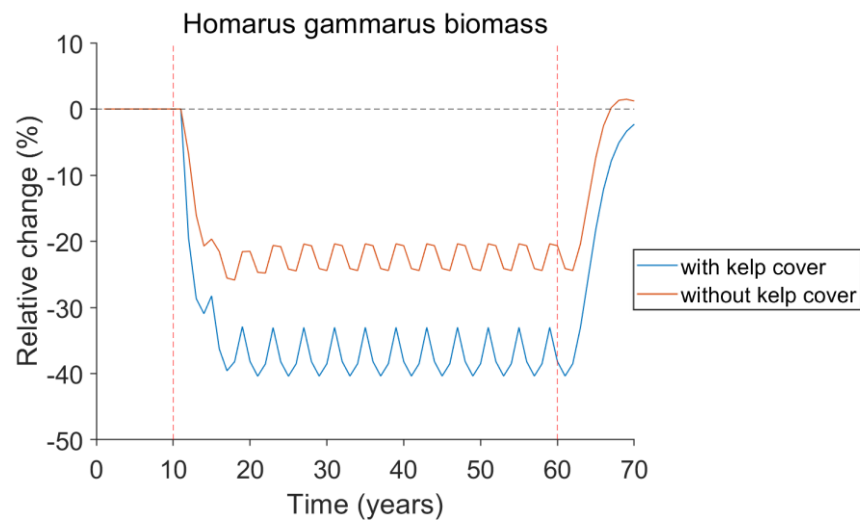
Figure 7. The effect of kelp cover on European lobster (*Homarus gammarus*) with kelp harvesting intensity of 80% and harvesting interval of 4 years. The blue line represents the relative biomass change with the non-trophic interaction, and the red line represents the relative biomass change without the non-trophic interaction. The black dotted line is the European lobster biomass before harvesting. The kelp harvesting period of 50 years is marked between the red dotted lines.

The effect of the non-trophic interaction (kelp cover) on Atlantic cod age group 0 was very small: there was not much difference in the effect of kelp harvesting whether the kelp cover was included or not (Figure 8). However, the non-trophic interaction added to the age group 0 is expressed in the subsequent age groups (1, 2, 3, and 4+) where the biomasses showed greater oscillation when the kelp cover was included (Figure 8). The oscillation was the largest in age groups 1, 2, and 3,

and from those the greatest oscillation amplitude was in age group 1 (ranging from 2% to -4% of relative biomass change).

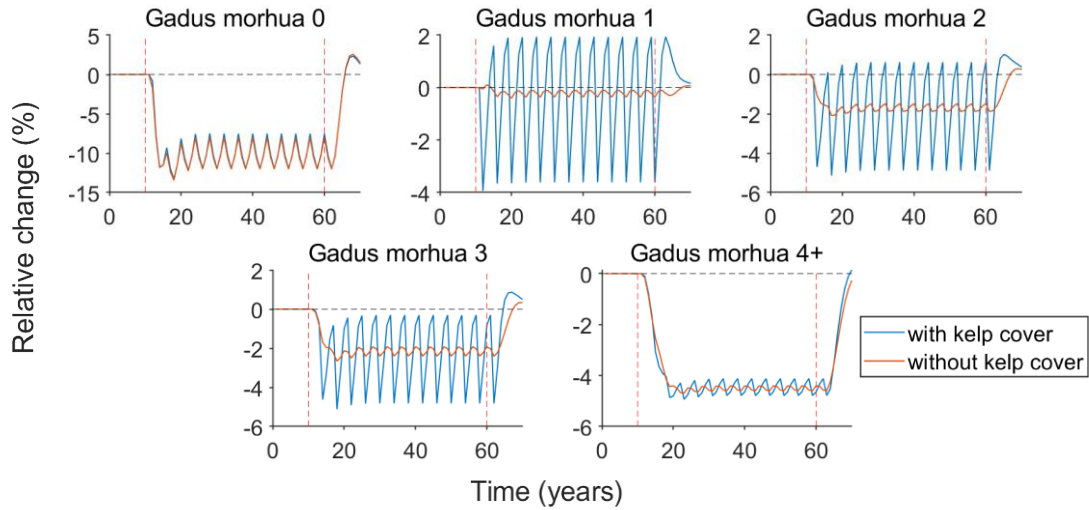Figure 8. The effect of kelp cover on juvenile Atlantic cod (*Gadus morhua* 0) and cascading effects on age groups 1, 2, 3, and 4+ at kelp harvesting intensity of 80% and harvesting interval of 4 years. The blue line represents the relative biomass change with the non-trophic interaction, and the red line represents the relative biomass change without the non-trophic interaction. The black dotted line is the biomass of Atlantic cod before harvesting and the dotted red lines represent the kelp harvesting period of 50 years. (Note that the y-axis scales varies between the subplots)

4 DISCUSSION

The aim of this thesis was to construct a northeast Atlantic kelp forest food web to study the ecosystem scale effects of kelp harvesting, and to implement a non-trophic interaction to the allometric trophic network (ATN) model to study the effect of kelp cover on Atlantic cod and European lobster. The results showed that including the non-trophic interaction increased the biomass oscillations and the effect of kelp harvesting on the Atlantic cod and the European lobster, and that kelp harvesting had multitrophic effects to the kelp forest ecosystem.

The non-trophic interaction was introduced between kelp and juvenile (0-year-old) Atlantic cod and between kelp and European lobster as a survival benefit

provided by kelp cover on the species. The effect of the kelp cover on the Atlantic cod age group 0 was very small, but the kelp cover effect cascaded to subsequent age groups as larger oscillations of the relative biomasses in the kelp harvesting period. In the age groups 1, 2, and 3, the biomass oscillation was much larger when the kelp cover was included, which indicates that the habitat effect on the species survival is not limited only to the juveniles, but it has a greater effect on the species. Including the kelp cover effect on the European lobster increased the oscillation of the biomass of the European lobster in the harvesting period and increased the effect of the kelp harvesting over 10%, suggesting that the kelp cover effect has an important role when studying how kelp harvesting may affect the wider ecosystem.

Food web models are usually based on consumption of resources (e.g., consumer-resource and predator-prey interactions) and this basic unit is known to be oscillatory. Oscillations in populations can be caused by for example resource-limitations, competition, or predation (Kuno 1987), but here we demonstrated that non-trophic interactions (such as habitat effect) in food webs can create or increase biomass oscillations in nature. In this study, the biomasses of the species in the food web oscillated through the trophic links in the food web originating from the changes in kelp biomass caused by the kelp harvesting, but the habitat effect of kelp cover (non-trophic interaction) for the Atlantic cod and the European lobster caused greater oscillations in the biomasses of these species and this indicates that the habitat effect of kelp cover could affect the biomass changes in the food web. Habitat complexity has been shown to increase species survival (Beukers & Jones 1998, Lindholm et al. 1999, Scharf et al. 2006), and when studying the effects of lowering the complexity of habitat in a food web (e.g., kelp harvesting in kelp forest ecosystem), there might be a need to include the habitat effect on food web models so that the results are representative of the natural dynamics.

The results of the kelp harvesting showed that the kelp biomass recovered when the recovery time after kelp harvesting was 4 or 8 years, but not when kelp was harvested every year. These results align with the studies supporting the existing

5-year cycle of kelp harvesting with a 4-year recovery time (Vea & Ask 2011, Steen et al. 2016). Here the kelp biomass was simulated for a 4-year-old kelp (*L. hyperborea*). The growth rate and fertility of *L. hyperborea* increases with age (Kain & Jones 1975, Sjøtun & Fredriksen 1995). In this model, the kelp age-structure was not included, and to examine the long-term effects of kelp harvesting on kelp biomass and recovery, it could be interesting in the future to implement the growth rates and fertilities of different ages of kelp to the model.

The species feeding directly on kelp had different responses to kelp harvesting, but the oscillation patterns caused by the kelp harvesting on kelp biomass were reflected through the trophic links on the species or groups in the food web. The biomass of the sea urchin declined almost 15% when the recovery time after kelp harvesting was 4 years and the amount of kelp biomass removed in each harvesting event was 80%. The sea urchin biomass declined also when 20% of the kelp biomass was removed, but the decline was smaller (3%). The sea urchin was the most dependent on kelp in its diet of the kelp consumers, and in the kelp harvesting period the sea urchin did not shift from kelp food resource to other resources for replacement and therefore the biomass of the sea urchin followed the biomass changes of kelp but at a slower rate not being able to recover in the 4-year harvesting interval.

The biomass of mollusca recovered when the recovery time between kelp harvesting events was 4 years. Mollusca are filter feeders and had other food resources in the diet in addition to kelp, and when kelp biomass decreased, mollusca could shift from kelp resource to phytoplankton resource and recover after each kelp harvesting event. Also, mollusca had many predator species in the food web, some of which decreased in biomass during the harvesting period, which could have facilitated in part the recovery of the biomass of mollusca if the predation pressure on mollusca was lower during the harvesting period. These results on kelp consumers support previous studies (e.g., Steen et al. 2016) that more research on the kelp-associated species is needed when the effects of kelp harvesting are examined.

The initial biomasses of the green shore crab and the common hermit crab were very low: < 1 µgC/m³ and < 10 µgC/m³ respectively. The low initial biomasses explain the considerable relative increase of the biomasses of the two crabs in the harvesting period and may introduce uncertainty to the results of these two species. The increase of the biomasses of the green shore crab and the common hermit crab in the harvesting period indicate that some species could retain higher biomass level when kelp is harvested. This could be caused by increase in prey biomass or decrease in biomass of the predatory species, and for the green shore crab and the common hermit crab the decrease of the biomass of the predatory species European lobster could be the main reason for the biomass increase in the kelp harvesting period.

The effect of kelp harvesting on the Atlantic cod was greatest in the age group 0 and the age group 4+ measured in average biomass decline. When the recovery time between the kelp harvesting events was 4 years, the biomasses of the age groups 0 ang 4+ did not recover to the pre-harvesting state: the biomasses of the age groups declined about 1% at harvesting intensity of 20%, and at 80% harvesting intensity the decline was 10% and 5% respectively. The change in the biomass of the age group 0 was caused by the changes in the trophic links since including the non-trophic interaction of kelp cover had only a very small effect on the biomass. The biomass of the age group 4+, however, was affected by both the trophic links and the non-trophic interaction added to the 0-year-olds. It seems that the very small effect of kelp cover on the biomass of the 0-year-olds did influence the biomasses of the consequent age groups and ultimately the age group of 4+-year-olds. The kelp harvesting affected the Atlantic cod biomass through the biomass changes of the prey species and through the decrease of the kelp cover provided for the age group 0. This shows the cascading effect of the kelp harvesting through the food web, and the cascading effect of a non-trophic interaction through the life-stages of the species.

The European lobster biomass decreased when the recovery time was 4 years by 5% at harvesting intensity of 20% and by over 30% at harvesting intensity of 80%.

The kelp harvesting effect on the European lobster came from the trophic links (feeding links) of other species than kelp and the non-trophic interaction of the kelp cover. The non-trophic interaction had a large effect on the decline of the European lobster biomass during the kelp harvesting period, and this supports studies showing that complex habitats can affect the survival of the species (Beukers & Jones 1998, Lindholm et al. 1999). Kelp forests are complex habitats and the changes in the kelp biomass can affect the survival of other species directly through the kelp biomass changes cascading through the trophic levels and indirectly through the kelp cover effect.

The kelp harvesting caused biomass oscillation in the kelp and this oscillation cascaded through the food web to higher trophic levels. Fishing can cause or increase population oscillations (Kuparinen et al. 2016, Uusi-Heikkilä et al. 2022), and here we show that harvesting of the producers (here kelp) can have similar effects and the harvesting can create oscillation patterns that affect the whole food web. Oscillations of the biomass or populations in the food web could destabilize the ecosystem and could lead to loss in the resilience of the ecosystem (Scheffer et al. 2001). Also, the effect of the oscillation could be seen as evolutionary, and for fish this could show as a change in asymptotic length when the oscillation wavelength is shorter than the lifespan of the species (Ahti et al. 2022). The results of this thesis showed that not all species in the kelp forest ecosystem recovered in the 5-year kelp harvesting cycle, supporting studies where the concern of multitrophic effects of kelp harvesting has been raised (Lorentsen et al. 2010, Steen et al. 2016, Christensen-Dalsgaard et al. 2020), and that kelp harvesting could create biomass oscillations to the species in the food web through trophic links and through the habitat effect of kelp cover.

The kelp harvesting intensities in this study were 20% and 80%. In Norway the annual removal of kelp biomass is 10-15% of the standing stock and in France 30% (Werner & Kraan 2004). The patterns of relative biomass changes in species were similar in both harvesting intensities of 20% and 80%. However, the harvesting intensity affected the magnitude of change in the relative biomass of species. The

80% harvesting intensity caused bigger changes in relative biomass than 20% harvesting intensity. As kelp is removed also naturally from the ecosystem (Norderhaug & Christie 2011), the local effect of kelp harvesting effort can be much higher than the mechanistic removal of 10-30% reported from Norway and France, and for example, with 4-year harvesting interval and 80% harvesting intensity, the biomass of the European lobster decreased over 30% which is considerably less than the pre-harvesting biomass. If the kelp removal locally is 80%, it could have a drastic effect on species living in the kelp forest. In this model, other causes of biomass loss (e.g., human exploitation of other species in the ecosystem) were not accounted for, so the realised decrease can be even greater for species living in kelp forest habitat.

To study the ecosystem scale effects of kelp harvesting the high complexity of the food web was purposeful, however, the interpretation of the results of biomass changes of the guilds was intricate due to the extensive number of feeding links between guilds. Also, a simpler food web could bring forth the effect of the non-trophic interaction more clearly. Furthermore, there were some species that were not represented accurately, such as the green shore crab and the common hermit crab. To tackle this problem, the food web construction could have been started with a few species and when adding new species, the functioning of the food web could have been checked and modified at small steps.

In model parametrization, the kelp and phytoplankton carrying capacities were noted to have a great effect on the magnitude of the relative changes of species biomasses in the northeast Atlantic kelp forest food web. For example, when the carrying capacity of kelp was kept at 1 000 000 µgC/m^3 and phytoplankton carrying capacity was lowered to 200 000 µgC/m^3, the change in species relative biomasses was larger compared to the simulation scenario with both kelp and phytoplankton carrying capacity at 1 000 000 µgC/m^3. Additionally, some species were not able to fully recover as they had in the 4-year harvesting interval (e.g., kelp, mollusca). When phytoplankton carrying capacity was raised to 5 000 000 µgC/m^3, and kelp carrying capacity kept at 1 000 000 µgC/m^3, the change in

species biomasses were smaller than in the original scenario of the same carrying capacities of 1 000 000 μgC/m³ for both kelp and phytoplankton. For example, the change in the biomass of the European lobster was 10% less when the phytoplankton carrying capacity was higher than the carrying capacity of kelp. The reversed reactions to relative changes in biomasses were observed when phytoplankton carrying capacity was kelp at 1 000 000 μgC/m³, and kelp carrying capacity was decreased to 200 000 μgC/m³ or increased to 5 000 000 μgC/m³. These results of carrying capacity alterations showed that kelp-phytoplankton carrying capacity relationship has an effect on the results and the carrying capacities for kelp and phytoplankton in kelp forest ecosystem should be studied more to have reliable results considering the ecosystem effects of kelp harvesting and to produce reliable ecosystem models for kelp forest ecosystem and its functioning.

5 CONCLUSIONS

The results of this thesis showed that the 5-year cycle of kelp harvesting can have effects on species in the kelp forest ecosystem on different trophic levels. In this study the biomass of kelp recovered as in previous studies, but there were some species in the kelp forest ecosystem that did not recover, adding to the concern raised about the multitrophic effects of kelp harvesting. Furthermore, the non-trophic interaction of kelp cover added on the Atlantic cod and European lobster increased the oscillations caused by the kelp harvesting and with European lobster increased the decline in biomass in the kelp harvesting period. This shows that non-trophic interactions can be important factors to be accounted for when food web models are used to study changes in the ecosystems. Also, this thesis brought forward the effect of the carrying capacity in food web models. When modelling ecosystems with more than one group of producers (here kelp and phytoplankton) the relationship between the carrying capacities of the producers have great effect

on the results. Future studies on kelp forest ecosystem modelling should focus firstly on determining the carrying capacities of kelp and phytoplankton.

Overall, here we extended the ATN model to include a non-trophic interaction between species in the food web and suggested that non-trophic interactions could be included on food web models to have more realistic representations of the natural dynamics. Here we also emphasize the need for more studies on the ecosystem scale effects of kelp harvesting. Kelp forest ecosystems harbour vast number of species, including commercially important species, and the need to manage kelp harvesting sustainably from the ecosystem perspective is crucial to ensure the existence of the species-rich kelp forests in the future.

ACKNOWLEDGEMENTS

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APPENDIX A

Fish species information for the ecosystem model. Constants **a** and **b** are for equation $W = a \times L^b$, where W= fresh weight in grams and L=length in cm.

Number	Species	length (cm)	a	b	Prey items (links)
24	Ctenolabrus rupestris 0	4,5	0.01230	3.000	10-13,
25	Ctenolabrus rupestris 1	7,9	0.01230	3.000	10-13,
26	Ctenolabrus rupestris 2	9,5	0.01230	3.000	14,15,17,20-22,
27	Ctenolabrus rupestris 3	11,3	0.01230	3.000	14,15,17,20-22,
28	Ctenolabrus rupestris 4+	12,9	0.01230	3.000	14,15,17,20-22,
29	Centrolabrus exoletus 0	5,3	0.0047	3.230	10-13,
30	Centrolabrus exoletus 1	9,5	0.0047	3.230	10-13,
31	Centrolabrus exoletus 2	11,5	0.0047	3.230	14,15,17,20-23,
32	Centrolabrus exoletus 3	12,3	0.0047	3.230	14,15,17,20-23,
33	Centrolabrus exoletus 4+	13,3	0.0047	3.230	14,15,17,20-23,
34	Symphodus melops 0	5,1	0.0056	3.180	10-13,
35	Symphodus melops 1	9,1	0.0056	3.180	10-13,
36	Symphodus melops 2	12,9	0.0056	3.180	15,17,20-22,
37	Symphodus melops 3	14,9	0.0056	3.180	15,17,20-22,
38	Symphodus melops 4+	18,6	0.0056	3.180	15,17,20-22,
39	Labrus mixtus 0	4,7	0.00480	3.318	10-13,
40	Labrus mixtus 1	8,4	0.00480	3.318	10-15,17,20-22,
41	Labrus mixtus 2	11,9	0.00480	3.318	14,15,17,18,20-23,
42	Labrus mixtus 3	14,3	0.00480	3.318	14,15,17,18,20-23,
43	Labrus mixtus 4+	17,8	0.00480	3.318	14,15,17,18,20-23,
44	Labrus bergylta 0	4,7	0.01190	3.115	10-13,
45	Labrus bergylta 1	8,4	0.01190	3.115	10-13,
46	Labrus bergylta 2	13	0.01190	3.115	13-15,17,20-23,
47	Labrus bergylta 3	16,1	0.01190	3.115	15,17,20-23,
48	Labrus bergylta 4+	21,9	0.01190	3.115	15,17,20-23,
49	Pholis gunnellus 0	4,3	0.00430	3.018	10-13,
50	Pholis gunnellus 1	7,6	0.00430	3.018	10-13,
51	Pholis gunnellus 2	9,7	0.00430	3.018	13-15,17,20-22,24,29,34,39,44,49,54,59,64,69,74,79,84,89,94,99,104,109,114,
52	Pholis gunnellus 3	12,2	0.00430	3.018	13-15,17,20-22,24,29,34,39,44,49,54,59,64,69,74,79,84,89,94,99,104,109,114,
53	Pholis gunnellus 4+	17,7	0.00430	3.018	13-15,17,20-22,24,29,34,39,44,49,54,59,64,69,74,79,84,89,94,99,104,109,114,
54	Platichthys flesus 0	4,2	0.00980	3.024	10-13,
55	Platichthys flesus 1	7,4	0.00980	3.024	10-13,17,54,
56	Platichthys flesus 2	15	0.00980	3.024	10-13,15,17,54,55,69-73,79,80,84,85
57	Platichthys flesus 3	21,9	0.00980	3.024	15,17,20-22,49-52,54-56,69-73,79-82,84-87,99-102,
58	Platichthys flesus 4+	30,1	0.00980	3.024	15,17,20-22,51-53,56,57,71-73,81-83,86-88,101-103
59	Taurulus bubalis 0	1,5	0.01540	3.000	10-13,
60	Taurulus bubalis 1	1,9	0.01540	3.000	10-14,
61	Taurulus bubalis 2	7	0.01540	3.000	10-15,17,64,65,69,79,74-75
62	Taurulus bubalis 3	12	0.01540	3.000	14,15,17,20-22,64-67,69-77,79-82,84-87,94-97,
63	Taurulus bubalis 4+	16,7	0.01540	3.000	14,15,17,20-22,66-68,71-73,76-78,81-83,86-88,96-98,
64	Gobiusculus flavescense 0	2	0.00603	3.090	10-12,
65	Gobiusculus flavescense 1	3	0.00603	3.090	10-13,
66	Gobiusculus flavescense 2	5,5	0.00603	3.090	10-13,
67	Gobiusculus flavescense 3	5,5	0.00603	3.090	10-13,
68	Gobiusculus flavescense 4	5,5	0.00603	3.090	10-13,
69	Pomatoschistus spp. 0	1,8	0.00750	3.180	10-12,
70	Pomatoschistus spp. 1	2,5	0.00750	3.180	10-13,
71	Pomatoschistus spp. 2	4	0.00750	3.180	10-13,
72	Pomatoschistus spp. 3	4	0.00750	3.180	10-13,
73	Pomatoschistus spp. 4	4	0.00750	3.180	10-13,
74	Thorogobius ephippiatus	2	0.0075	3.180	10-12,
75	Thorogobius ephippiatus	3	0.0075	3.180	10-13,
76	Thorogobius ephippiatus	4,5	0.0075	3.180	10-13,15,17,
77	Thorogobius ephippiatus	6	0.0075	3.180	10-13,15,17,
78	Thorogobius ephippiatus	8	0.0075	3.180	10-13,15,17,

Number	Species/group	length (cm)	a	b	Prey items (links)
79	Gobius niger 0	1	0.0110	3.030	10-12,
80	Gobius niger 1	5,6	0.0110	3.030	10-13,79,84,
81	Gobius niger 2	9	0.0110	3.030	10-13,15,17,69,70,79,80,84,85,89,90,
82	Gobius niger 3	10,9	0.0110	3.030	10-13,15,17,21,69-73,79-81,84-86,89-91,
83	Gobius niger 4	10,9	0.0110	3.030	10-13,15,17,21,69-73,79-81,84-86,89-91,
84	Gobius paganellus 0	2	0.0112	3.100	10-12,
85	Gobius paganellus 1	3	0.0112	3.100	10-13,
86	Gobius paganellus 2	6	0.0112	3.100	10-13,15,34,
87	Gobius paganellus 3	7,5	0.0112	3.100	10-13,15,21,22,34,
88	Gobius paganellus 4+	10,5	0.0112	3.100	10-13,15,21,22,34,
89	Lipophrys pholis 0	4,5	0.00930	3.000	10-12,
90	Lipophrys pholis 1	7,9	0.00930	3.000	10-13,15,79,
91	Lipophrys pholis 2	10,9	0.00930	3.000	15,17,79,80,
92	Lipophrys pholis 3	12,3	0.00930	3.000	15,17,79-81,
93	Lipophrys pholis 4+	14,7	0.00930	3.000	15,17,79-83,
94	Callionymus lyra 0	6	0.02040	2.578	10-13,
95	Callionymus lyra 1	11	0.02040	2.578	10-13,
96	Callionymus lyra 2	17	0.02040	2.578	13,15,21,22,
97	Callionymus lyra 3	19	0.02040	2.578	13,15,20-22,
98	Callionymus lyra 4	21	0.02040	2.578	13,15,20-22,
99	Ammodytes tobianus 0	3	0.00630	2.693	4-12,
100	Ammodytes tobianus 1	4,9	0.00630	2.693	4-12,14,99,
101	Ammodytes tobianus 2	13	0.00630	2.693	10-15,17,99,100,
102	Ammodytes tobianus 3	17	0.00630	2.693	10-15,17,100,101,
103	Ammodytes tobianus 4	19,5	0.00630	2.693	10-15,17,101,102,
104	Ciliata mustela 0	6,8	0.00520	3.169	10-13,
105	Ciliata mustela 1	12,5	0.00520	3.169	13-15,17,18,21,
106	Ciliata mustela 2	18,5	0.00520	3.169	13-15,17,18,21,64-88,
107	Ciliata mustela 3	25	0.00520	3.169	13-15,17,18,21,64-88,
108	Ciliata mustela 4	25	0.00520	3.169	13-15,17,18,21,64-88,
109	Pollachius pollachius 0	11,5	0.01070	2.966	10-15,
110	Pollachius pollachius 1	22	0.01070	2.966	14,15,17,20-22,39-42,44-47,64-73,79-88,94-98,109,114,
111	Pollachius pollachius 2	35	0.01070	2.966	14,15,17,20-22,39-48,64-73,79-88,94-98,109,110,114,115,
112	Pollachius pollachius 3	40	0.01070	2.966	14,15,17,20-22,40-43,45-48,65-68,70-73,80-83,85-88,95-98,100-103,109-111,114,115,
113	Pollachius pollachius 4+	50,5	0.01070	2.966	14,15,17,20-22,40-43,45-48,65-68,70-73,80-83,85-88,95-98,100-103,110-112,114-116,
114	Gadus morhua 0	11,9	0.00650	3.098	10-15,
115	Gadus morhua 1	22,7	0.00650	3.098	10-15,17,18,20,22,23,70-73,79-83,89-93,94-98,104-106,109,110,114,
116	Gadus morhua 2	44,6	0.00650	3.098	10-15,17,18,20,22,23,49-58,69-73,79-110,119,120,
117	Gadus morhua 3	64,9	0.00650	3.098	10-15,17,18,20,22,23,50-53,55-58,80-83,85-88,90-93,95-98,100-103,105-111,119-121,
118	Gadus morhua 4+	87,05	0.00650	3.098	10-15,17,18,20,22,23,51-53,56-58,81-83,91-93,96-103,106-108,110-112,120,121,
119	Scyliorhinus canicular 0	10	0.00210	3.128	10-15,17,
120	Scyliorhinus canicular 1	15	0.00210	3.128	13-15,17,20-23,
121	Scyliorhinus canicular 2	22,5	0.00210	3.128	13-15,17,20-23,50-58,64-88,94-97,99-102,119,120,
122	Scyliorhinus canicular 3	32,5	0.00210	3.128	13-15,17,20-23,50-53,55-58,64-88,95-98,100-103,119-121,
123	Scyliorhinus canicular 4+	62,5	0.00210	3.128	13-15,17,20-23,50-53,55-58,65-68,70-73,75-78,80-83,85-88,95-98,100-103,120-122,

APPENDIX B

All literature references utilized to find carbon masses and prey items for the species in the northeast Atlantic kelp forest food web.

KELP:

Pedersen, M.F., Nejrup, L.B., Fredriksen, S., Christie, H. & Norderhaug, K.M. 2012. Effects of wave exposure on population structure, demography, biomass and productivity of the kelp *Laminaria hyperborea*. *Marine Ecology Progress Series*, 451: 45-60.

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PHYTOPLANKTON:

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ZOOPLANKTON:

Anger, K. 1988. Growth and elemental composition (C, N, H) in *Inachus dorsettensis* (Decapoda: Majidae) larvae reared in the laboratory. *Marine Biology*, 99: 255-260.

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