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The Energy Budget of a Local Jellyfish Proliferation: *Periphylla periphylla* in The Trondheimsfjord, Norway

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Master of Science
Submission date: August 2015
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Acknowledgement

The research reported in this MSc Thesis was conducted at Trondheim Biological Station (TBS), Department of Biology, Norwegian University of Science and Technology (NTNU). The research was a part of the JANUS project funded by The Norwegian Research Council (Project no. 216604).

JANUS has been led by Professor Jennifer Leigh Bailey, NTNU, who was joined by a team of scientists from NTNU and Sintef; Lionel Eisenhauer, Øyvind Knudsen, Yajie Liu, Jarle Mork, and Ulf Båmstedt from The Umeå University, Sweden. The team has offered substantial support in the fulfillment of this Thesis, and I am very thankful for that.

I am particularly indebted to my co-supervisor professor Ulf Båmstedt at the Umeå Marine Sciences Centre in Umeå, Sweden. He offered tremendous professional help in the field work onboard the research vessel as well as in the result analyses. His expertise in marine ecology was available for me at any time throughout the spring semester. The completion of this MSc Thesis rested heavily on his generous support.

My supervisor Jarle Mork, professor at the Department of Biology, NTNU, has been very helpful and supportive. He made sure the connections between all partners were made and held, so I should get all the help I needed. He has been there all the way, showing support both academically and mentally.

I am also grateful for the help from my roommate, Jonas Tøgersen Kjellstadli, considering some of the mathematical calculations, and my sister for correcting grammar and spelling errors.

Finally I want to thank my parents and friends for great support and pep talks whenever it was needed, as well as for bearing over with me, when my craziness got out of hand.

Abstract

Trondheimsfjorden is one of approximately one dozen Norwegian fjords where the crown jellyfish, *Periphylla periphylla* (Scyphozoa, Coronatae) has had massive blooms. It has established large local populations during the last two decades. The population in Trondheimsfjorden is mainly established in three innermost basins. The growth and proliferation have been under close monitoring by regular research vessel cruises done by Trondheim Biological Station (TBS), Department of Biology, Norwegian University of Science and Technology (NTNU).

The Periphylla population seems to have reached a local carrying capacity year 2007. Simultaneously with the increase in the jelly population, local artisanal fisheries for codfishes have suffered from reduced catches. The reduction in catches is caused by clogged nets, fish quality reduction due to burn marks, and longer working hours caused by longer travelling distances and cleaning of nets. Together these factors have resulted in a negative economic development, and reduced the number of fishermen.

This study estimates the economic consequences of the Periphylla bloom in the Trondheimsfjord. A simple ecologic model, public available fisheries statistics from the Norwegian Directorate of Fisheries, and data provided by Yajie Liu, have been applied. The model is based on calculations and estimations of the energy budget (measured in units of carbon), for the growth and maintenance of the current Periphylla population. The calculations include estimates of biomass and density, respiration rates, carbon demand and size distribution of Periphylla in the entire fjord. The economic and ecologic impacts have focused on the inner fjord basins: beyond the shallow sills at Tautra.

The results show a total biomass of Periphylla of 101 466 tons, an average density of $1.83 gm^{-3}$, average production of $2.01\ gCm^{-2}year^{-1}$, and an average carbon turnover rate of 0.0175 per day. The size distribution of the jellies is quite different between the four basins. The distribution are also changing on year to year basis within the basins.

The yearly average possible codfish production, which could have been produced with this carbon budget, is estimated at approximately 70 tons. After the year 2007 when the jelly population assumingly reached the local carrying capacity, this would sum up to an average amount of 600 000 – 900 000 NOK per year, for the fisheries. For the entire period 2007-2015 the total loss is estimated to be 900 000-950 0000 NOK.

Norsk sammendrag

Trondheimsfjorden er en av rundt et dusin norske fjorder hvor kronemaneten *Periphylla periphylla* (Scyphozoa, Coronatae) har hatt masseoppblomstringer. Den har etablert store lokale bestander, i løpet av de to siste tiårene. Trondheimsfjordens bestand har hovedsakelig etablert seg i fjordens indre bassenger. Vekst og utbredelse har vært nøye overvåket ved jevnlig toktvirksomhet utført av Trondhjem Biologiske Stasjon (TBS) ved Institutt for Biologi, NTNU.

Bestandens synes å ha nådd en lokal bæreevne år 2007. Parallelt med økningen i manetbestanden har de tradisjonelle fiskeriene for torskefisk lidd fra redusert fangst. Den reduserte fangsten skyldes tilgrising og tetning av fangstnett og garn, redusert kvalitet på fisken grunnet brennmerker og lengre arbeidsdager, som et resultat av økt vedlikehold for å rense nett, og større reisedistanser. Sammen har disse faktorene negativ økonomisk utvikling, og har redusert antall fiskere i fjorden.

Denne studien estimerer de økonomiske konsekvensene av Periphylla oppblomstringen i Trondheimsfjorden. En enkel økologisk modell basert på offentlig tilgjengelig fiskeristatistikk fra Fiskeridirektoratet, og data fra Yajie Liu, har blitt benyttet. Modellen er basert på kalkulasjoner og estimeringer av energibudsjett (målt i karbon), for vekst og vedvarelse av den nåværende Periphylla bestanden. Beregningene omfatter estimater av biomasse, tetthet, respirasjonsrater, karbonkrav og størrelsesfordeling av Periphylla i hele fjorden. De økonomiske og økologiske konsekvensene har fokusert på de indre fjordbassengene; innenfor den grunne terskelen ved øya Tautra.

Resultatene viser en total Periphylla *b*iomasse på 101 466 tonn, gjennomsnittlig tetthet på 1,83gm^{-3}, gjennomsnittlig produksjon på 2,01 gCm^{-2}år^{-1}, og gjennomsnittlig omsetningshastighet av karbon på 0,0175 per dag. Størrelsesfordelingen er forskjellig i de indre fjordbassengene, og varierte litt over tid innen hvert basseng.

Den gjennomsnittlige mengden torskefisk som kunne vært produsert hvert år med dette karbonbudsjettet, er estimert til omtrent 70 tonn. Etter 2007, det antatte året populasjonen nådde lokalitetens bæreevne, har fiskeriene tapt gjennomsnittlig 600 000-900 000 NOK per år. Totalt økonomiske tap fra år 2000 til 2015 er estimert til 9 000 000 – 9 500 000 NOK.

Contents

1 Introduction 1

2 Materials and Methods 3

2.1 Study Area 3

2.2 Sampling stations 4

2.3 Vessel and trawling equipment 4

2.4 Estimating basin volumes 4

2.5 VideoTrawl, VideoFrame and filtrated volumes 5

2.6 Carbon requirements of Periphylla - Assumptions and calculations 6

2.6.1 Vertical distribution of abundance and size: 6

2.6.2 Biomass and density: 6

2.6.3 Respiration rates: 7

2.6.4 Carbon demand: 7

2.6.5 Data for comparison 8

2.7 Estimating fish biomass – Assumptions and calculations 8

2.7.1 Model A – Trophic transfers and carbon content 9

2.7.2 Model B – Energy for growth and maintenance 10

2.7.3 Codfish biomass 13

2.8 Economy 13

3 Results 13

3.1 Periphylla biomass estimates 13

3.2 Basin properties and Periphylla size and depth correlation 13

3.3 Periphylla - Size distributions 14

3.4 Periphylla - Production, Carbon demand, Carbon turnover rate and Density 14

3.5 Codfish - Species composition 14

3.6 Codfish – Energy loss – Possible production 15

3.7 Fish prices 15

3.8 Economic loss 15

4 Discussion 15

4.1 Biomass estimates of Periphylla 15

4.1.1 VideoTrawl and VideoFrame - errors 15

4.2 Carbon demand of Periphylla – assumptions 17

4.2.1 Carbon demand and density 17

4.3 Biomass estimates of codfish - assumptions 18

4.4 Available data for economic codfish calculations- assumptions 19

4.4.1 Differences between the fjord basins in ecological and economic impacts 19

4.5 Prospects 20

References 21

APPENDIX 26

1 Introduction

Trondheimsfjorden is one of about a dozen Norwegian fjords where the crown jellyfish, *Periphylla periph*ylla (Scyphozoa, Coronatae, later referred to as Periphylla), has shown massive blooms and established large local populations, during the last two decades. The population in Trondheimsfjorden is mainly established in the three innermost basins (Hetland 2008; Jelmert et al. 2010; Solheim 2012; Yaije et al., 2014).

Most likely, the massive bloom and establishing of the local population in Trondheimsfjorden took place during the first years after year 2000. The population probably reached the local carrying capacity in year 2007 (Borgersen, 2013).

Periphylla has a differentiated menu. The menu is described in Yungbluth and Båmstedt (2001). Copepods, chaetognaths and ostracods were the main prey of Periphylla. Krill, small fish and small individuals of their own species were also found in their stomachs. However, due to "net-capturing-errors" this could not be supported scientifically (Youngbluth, 2001). Other literature sources suggest different prey on Periphyllas' menu as well, but Youngbluth and Blåmstedt (2001) cast some doubt on the validity of these studies.

On the other hand, it is suspected that Periphylla also has fish larvae, fish fry and small squids on the menu (Jelmert et al., 2010).

It has been hypothesized, that Periphylla*s'* vertical migration, is caused by available prey and prey migrations especially krill (Jarms, Tiemann and Båmstedt 2002; Lind 2008; Youngbluth and Båmstedt 2001). The predation behavior is assumed to change depending on which waterlayer they are residing in (Youngbluth and Båmstedt, 2001). Periphylla jellies are tactile predators. They are sensitive to light, and are well adapted to their dark environment (Jarms, Tiemann and Båmstedt, 2002; Sørnes et al. 2008; Sötje, Tieman and Båmstedt 2007). Thus, Periphylla will not be affected by a reduced visibility regime, such as fish, fish larvae and other visual feeders (Eiane et al. 1999; Eiane 2009, Sørnes et al. 2007).

The Periphylla bloom, in Trondheimsfjorden, coincided with a marked decreasing trend in the abundance of cod (Yajie et al., 2014). However, a cause-effect relationship has not been established, and it cannot be excluded that both phenomenon have a common cause. It could be possible that e.g. a general temperature rise in the fjord, over the last decades, are to be blamed (Milzer et al. 2013a, 2013b; Tiller et al., 2014A, 2014B).

Nevertheless, Periphyllas' assumed predation on fish larvae and fry, as well as a prey-competition interaction with fish larvae on zooplankton (with copepods as keystone species) (Vadstein, 2009), might hinder the recruitment of several commercially important species, like cod and saithe (Jelmert et al., 2010).

Except for a sessile sea anemone (Isotealia antarctica), Periphylla has no natural predator in the Norwegian fjords. Its recruitment is also very efficient (Jarms et al. 1999; Jelmert et al. 2010). Thus, it is not surprising that there might be, or already have been, changes in the top predator hegemony in several Norwegian fjord ecosystems due to the Periphylla proliferations (Jelmert et al. 2010).

For the traditional commercial fisheries in the inner Trondheimsfjord, many undesirable effects of the Periphylla proliferation have been reported (Tiller et al., 2014b). One of them are large volumes of Periphylla caught in the fishing nets instead of commercial fish. Cleaning nets after catches of jellyfish is another undesired consequence. Cleaning nets are expensive considering the time spent, and it is also dangerous. Several incidents with burning caused by jelly slime in the eyes have been reported. The quality and price of the fish are also reduced due to red coloring and burn marks on fish skin. To avoid such problems, fishermen have had to find new fishing grounds that are not yet affected by the jellyfish (Tiller et al., 2014a). This leads to increased fuel costs and time loss.

Mass deaths of Periphylla have occurred. The jellies sink to the bottom and creates oxygen depletion in the decomposing process. This has created unfavorable conditions for fish and other animals in the marine fauna (Purcell 2007; Tiller et al. 2014a, 2014b).

Fish stocks are known to fluctuate naturally. These fluctuations are primarily caused by annual variability in the strength of incoming year classes. The recruitment variation is usually explained by the "match-mismatch"-hypothesis. Marin fish larvae, unlike Periphylla, are visual feeders and need to be close (0.7-1.0 body lengths) to its prey to localize it. Thus, copepod eggs and other non-motile food have been found in their stomachs. The perceptive distance of fish larvae increases with prey size linearly. Typical food of most marine fish larvae are copepods ranging from eggs and naupliar, to copepodites and full grown adult copepods. The prey selection is size dominated, and the feeding menu changes as the fish grows (Hunter, 1980). In Atlantic waters, the key species *Calanus finmarchicus* (later referred to as just Calanus), is the most abundant herbivorous copepod (Tande, 1991). According to Yungbluth and Båmstedt (2001), it may be the main prey item of Periphylla.

This Thesis has focused on the ecological and economic cost of the bloom and persistence of Periphylla in the inner Trondheimsfjord, from its start in the year 2000 until today (2015). The main focus has been on the possible costs of predation on, and competition with, commercial fish species in the gadoid family. Specifically, the traditionally commercially species in the cod family, with traditions in artisanal fisheries in the inner parts of the fjord have been subject to monitoring during the jelly proliferation.

2 Materials and Methods

2.1 Study Area

Trondheimsfjorden is situated in the central part of Norway. It is the third longest and seventh deepest Norwegian fjord. It is 126 km long and 630 m deep. Total volume is 235 km3. The fjord has three main basins; Ytterfjorden, Midtfjorden and Beitstadfjorden. There are sills at Agdenes, Tautra and Skarsundet (See APPENDIX 1).

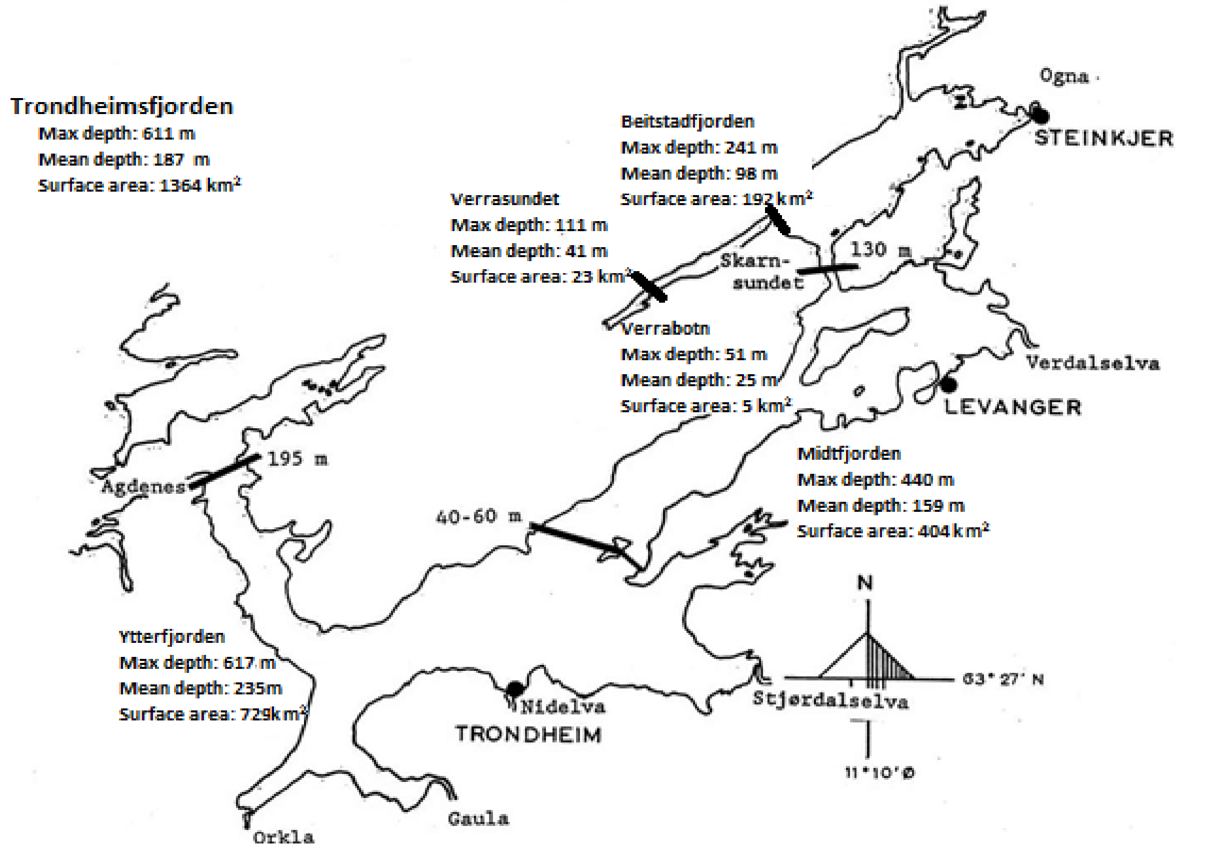

Figure 2.1.1. Map of Trondheimsfjorden with sills (black solid bars) separating the basins and sidearms. Values of max and mean depth, as well as surface area, are presented. Adopted from Bakken et al. (2000), with modifications.).

Beitstadfjorden has two narrow sidearms; Verrasundet with Verrabotn south-westwards and Hjellebotn to the north-east (Fig. 2.1.1.) (Bakken,

2000).

The open connection between the Trondheimsfjord and the Norwegian coast allows for estuarine circulation. The circulations renews bottom water in the fjord twice a year. It supplies current-transported pelagic organisms. The mixing forces are driven partly by estuarine circulation by several large rivers. The circulation is also driven by wind, tidal forces, and density driven mixing due to differences in salinity and temperature (Bakken et al., 2000).

2.2 Sampling stations

Sampling station 1-4 were approximately the same as in Hetland (2008) and Solheim (2012). In the present investigation, two new stations were included; station 5 and 6. Coordinates for sampling, date and time are given in Table 2.2.1.

2.3 Vessel and trawling equipment

The research vessel "Gunnerus" of NTNU, was used for video sampling in three previous studies (Borgersen 2014; Hetland 2008; Solheim 2012) as well as in the present.

2.4 Estimating basin volumes

The volume of Beitstadfjorden, Verrabotn, Verrasundet, Ytterfjorden and Midtfjorden was estimated at 10m intervals. The estimations were based on maps from "Sjøkartverket" (the Norwegian Hydrographic Service) with 25m horizontal resolution (some interpolation was done in the outermost parts of the basins). Desired depth intervals were calculated by adding

Table 2.2.1. Periphylla Periphylla sampling locations. Date, time and GPS-coodrinates for sample collection with VideoTrawl and VideoFrame

Location	**Date**	**Time**		**GPS –coordinates**	
		Down	**Up**	**Down**	**Up**
Verrabotn	19.6.2014.	10:00	10:09	N 63°49,045 E 10°38,140	N 63°49,300 E 10°38,758
Verrasundet	19.06.2014.	13:20	13:42	N 63°51,112 E 10°44,126	N 63°51,274 E 10°44,992
Beitstadfjorden	17.06.2014.	16:50	17:15	N 63°56,204 E 11°04,563	N 63°56,685 E 11°04,985
Midtfjorden	16.06.2014.	18:20	18:50	N 63°44,829 E 11°04,061	N 63°45,185 E 11°07,220
Ytterfjorden	16.06.2014.	13.05.	Not recorded	N 63°27,987 E 09°57,385	N 63°28,8204 E 09°55,933

the volume of the 10 m intervals (See APPENDIX 1 for volume and maps).

2.5 VideoTrawl, VideoFrame and filtrated volumes

As in previous surveys (Borgersen 2013; Hetland 2008; Solheim 2012), a Light Weight VideoTrawl (referred to as LVPP in previous master theses) designed by Ulf Båmstedt, was used to estimate the vertical distribution, biomass and abundance of Periphylla. The VideoTrawl is a rigid aluminum frame with a video camera, a SAIV CTD, and a transponder for contact with the RV attached (Fig. 2.5.1.). A net was attached in front of the frame to increase the filtered volume. The instrument was towed like a trawl (Fig. 2.5.2.). It recorded a depth profile continuously throughout the dive. Timers on the LVPP and RV transponder log were synchronized. The dive profile videos were analyzed frame by frame using various in-house computer software (Ulf Båmstedt). The picture was frozen every time a medusa appeared. Manual measuring of the coronal diameter (CD) was performed on screen.

The other instrument, a VideoFrame, built like the VideoTrawl, but without a collecting net, was used for some of the sampling. Lacking a collecting net, this instrument had a smaller opening area ($1.13 m^2$ vs. $3,24 m^2$) and thus a smaller filtered water volume. Both instruments were lowered and hauled describing U-like haul profiles through the water masses.

The water volume, filtrated by the VideoTrawl, was calculated using

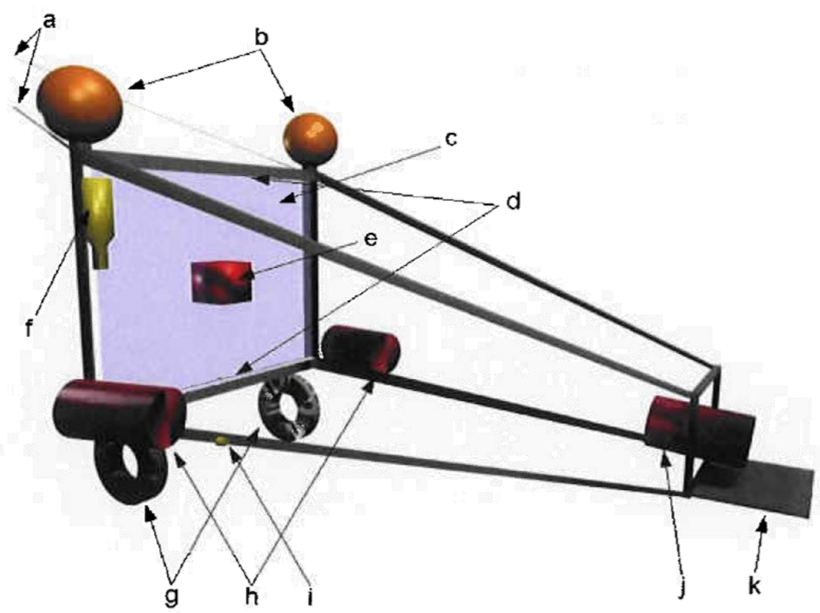

Figure2.5.1. Schematic description of LVPP that shows the most important features. a=towing cables, b=floatation buoys, c=opening, d=directional light, e=illustrative medusa in the opening, f=transponder, g=steel weight, h=battery packs, i=CTD, j=aluminum casing for video camera, k=stabilizing fin. Adopted from Hetland (2008).

Pythagoras theorem in three steps (see Figure 2.5.2. for visual explanation).

When the maximum depth (b), the corresponding use of wire (a) and trawling distance (d) are known, the total trawling distance for the VideoTrawl (f+a) can be calculated. Multiplying the trawling distance for the VideoTrawl by its opening area gives us the total filtrated volume.

Filtrated volumes (e; grey area) were calculated by applying the properties of similar triangles.

Water volume filtrated by the VideoFrame was easily calculated by multiplying the opening aria with the maximum depth. Knowing the speed of the vertical lowering and hauling, the volume filtrated in each depth interval could be calculated.

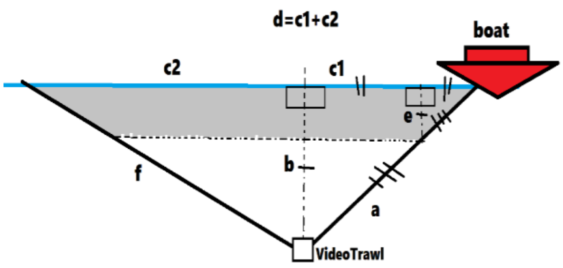

Figure 2.5.2. Visual explanation of how to calculate filtrated water volume.

2.6 Carbon requirements of Periphylla - assumptions and calculations

2.6.1 Vertical distribution of abundance and size:

The topography of the basins affects their volume. Thus, the abundance, size and vertical distribution cannot be expected to be equally distributed in all water layers. Due to this, information of the vertical distribution, abundance and size of the medusa were needed to calculate the total biomass of Periphylla in the fjord. The fjord basins were divided into small intervals of 10 m each. Estimations were done in each interval. The estimated biomass, in each interval, was multiplied by the volume of the desired depth interval. Intervals were added together to get the total biomass estimate of Periphylla in the fjord.

2.6.2 Biomass and density:

A regression based on the correlation between coronal diameter (CD) and wet weight (WW) was used to estimate the Periphylla biomass. The regression presented below (Eq.1.) The regression is based on unpublished data in the EU project EUROGEL, and generously provided by Ulf Båmstedt:

$$WW = 0.2269 \times CD^{3.2753} \quad \text{Eq. 1}$$

The wet weight (WW) is measured in gram (g), and coronal diameter (CD) is measured in cm (R^2 for the regression is 0.9681). Applying Eq.1. the wet weight for each medusa in each dive was calculated for the different depth intervals. These wet weight estimates were divided by the filtrated volume in the corresponding depth interval. Further it was multiplied by the volume of the depth interval. These biomass estimates were added to get the biomass of the fjord basin.

2.6.3 Respiration rates:

Gelatinous zooplankton show significant lower dry weight-specific rates than non-gelatinous zooplankton and fish (Schneider, 1992). Due to this, carbon has been chosen as a body mass unit for calculations and estimations of respiration. This has been done in previous studies considering gelatinous zooplankton (Bakken 2000; Cetta et al. 1986; Larson 1987; Schneider 1992; Youngbluth and Båmstedt 2001).

To estimate the respiration rate of Periphylla, the carbon content of each individual was needed. It was calculated by applying an average carbon content of 0.571 % ± 0.051 % of WW (with 95% confidence interval). This information was provided by Ulf Båmstedt, based on results in the EUROGEL project.

The carbon weight of each individual was calculated and used to estimate the mean respiration rate in each basin, by applying equation 2 (below). The mean respiration rate of the total population was calculated from these estimates.

$$ln(RR) = 2.201 - 0.411 \times ln(C) \qquad Eq.\ 2$$

Carbon weight (C) is measured in mg and the oxygen consumption, the respiration rate (RR), is measured in µL O2 mg $C^{-1}h^{-1}$.

2.6.4 Carbon demand:

Carbon demand (Carbon utilized per unit time), based on oxygen consumption (Respiration rates (RR)), was calculated for each individual by equations from Harris et al. (2000).

$$RR \times \frac{12}{22.4} \times RQ = C_{utilized} \qquad Eq.\ 3$$

RR is measured in ml oxygen per hour. $\frac{12}{22.4}$ is the weight of carbon in 1 mole of carbon dioxide. RQ is the respiratory quotient. $C_{utilized}$ is carbon utilized in mg per hour (Harris et al., 2000).

Yearly carbon demand per square meter, in the different basins, was calculated. This was done by estimating the average carbon demand in each water interval. The carbon demand was further multiplied by the corresponding volume of the desired water interval, before it was summed. Finally, the carbon demand was divided by the total area of the basin and multiply by 365.

According to Parsons (1973), an RQ of 0.8 was applied, as in accordance with previous studies (Purcell 2010; Youngbluth and Båmstedt 2001).

An assimilation efficiency of 90% was assumed, according to previous published studies in the field (Conover 1978; Parsons 1973; Purcell 1983; Youngbluth and Båmstedt 2001).

2.6.5 Data for comparison

Biomass estimates from the year 2007 were taken from Hetland (2008). Estimates from 2010 and 2011 were taken from Borgersen (2013).

2.7 Estimating fish biomass – assumptions and calculations

To estimate the fish biomass that could have been produced by the energy consumed by Periphylla, two simple models have been applied. Both models; A and B, are based on basic ecology. The respiratory demands of the Periphylla population was converted to yearly production. Further this was converted to the amount of prey consumed. Calanus was used as a model species for prey consumed. The amount of Calanus that is consumed is converted to fish biomass. This is done in six steps in each model. The last steps; the fifth and sixth step, differs in the two models. Model A is based on

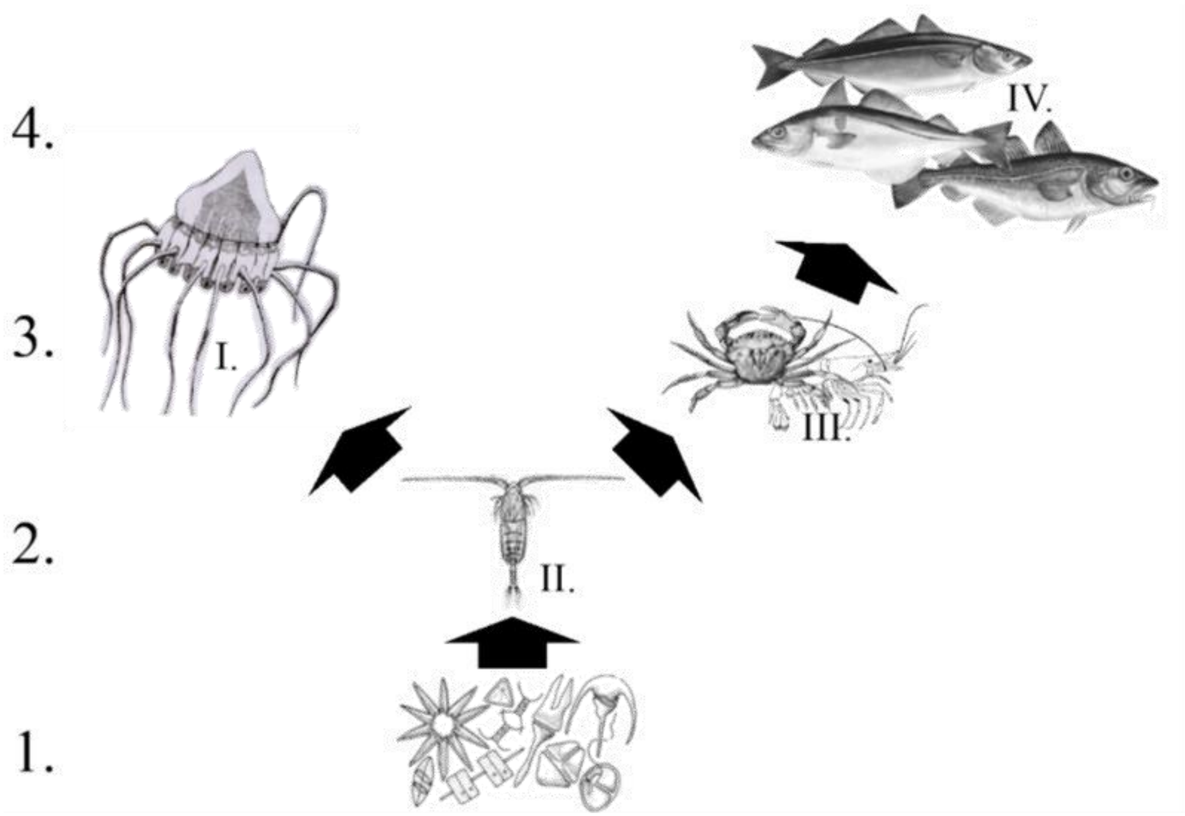

Figure 2.6.5.1. Shows the simplified food web between Periphylla periphylla, Calanus finmarchicus and codfish. Numbers to the left represent the trophic level, roman numbers represent the first four steps in the models. Picture collage made from adopted pictures from: .Emerton (1882), Sars (1901), Svendsen (2013), unknown-a (nd), unknown-b(nd), unknown-c(nd).

"classic energy transfers" with general ecologic assumptions (elaborated in section 2.7.1.). Model B is based on the same assumptions as model A, but it includes energy demands for maintenance and growth of cod in particular (elaborated in section 2.7.2.).

To estimate the possible production of fish biomass in the previous years (2000-2013), a simple linear regression was applied. It is assumed close to zero Periphylla year 2000 (see section 1.2.), and a final biomass of 101 466 tons in 2007. As mentioned earlier, it is assumed that the population had reached its' carrying capacity year 2007.

2.7.1 Model A – Trophic transfers and carbon content

Since Model A (and Model B) is based on general ecologic assumptions about trophic transfers, a short theoretical will be presented. The assumptions that are made will be explained.

2.7.1.1 Trophic levels and transfers

A trophic level of an organism can be explained as its position in a food web, or food chain. This position is relative to other organisms, in the same community, which it preys on or is eaten by. This Thesis has its focus on Calanus, Periphylla and codfishes (See Figure 2.7.1.1. for trophic level interactions).

Trophic efficiency is the efficiency of the energy transfer from one trophic level to another. The efficiency is roughly 10 %, according to Lindeman's "law" (Chapman, 1992). The "law" is actually not a law, and Lindeman was cautious not to suggest extrapolations from one community to another. The "law" does however state that the efficiency increases as one go to lower trophic levels in a food chain or web. Exceptions exist (Lindeman, 1942).

Data for calculating exact trophic efficiency was not available for Periphylla and codfishes. Thus, the 10% rule, has been applied as done in previous studies, when better estimates were absent (Irigoien et al. 2014; Pauly and Christensen 1995; Lindeman 1942; Odum 1957; Rand 1998).

As argued in section 2.6.4. the assimilation efficiency of Calanus and Periphylla, was set to 90 %.

Carnivore fish generally have an assimilation efficiency of 80 % due to the carbon content of their diet (Brafield 1985; Brett and Groves 1979). Thus, an assimilation efficiency of 80% for codfish-species has been applied.

For crustaceans, and "other" animals on trophic level three, assimilation efficiency was set to 80 %. This seems reasonable according to studies of different crustacean species (Lasker 1966; Moriarty and Barclay 1981; Urabe and Watanbe 1991).

2.7.1.2 Carbon content of fish

It is hard to find exact values of dry weight and carbon content of the selected fish species. An estimated value based on previous studies of other fish-species has been made, since variation between different species are small (Harris et al. 1986; Huang et al. 2012; Sterner and George 2000; Tanner et al. 2000). A dry weight of 20% has been applied in this study, and a carbon content of 50% of the dry weight.

2.7.1.3 Model A – step by step

I. Production of Periphylla, $P_{Periphylla}$, is calculated (from 2.6.).

II. $P_{Periphylla}$ is divided by the ecologic efficiency of Periphylla, $E_{Periphylla}$, and assimilation efficiency of Periphylla, $AE_{periphylla}$, to get the Calanus production. $P_{Calanus}=P_{Periphylla}\div(E_{Periphylla}\times AE_{periphylla})$

III. $P_{Calanus}$ is multiplied by its ecologic efficiency and assimilation efficiency to get the production on trophic level 3. $P_{Crustaceans}=P_{Calanus} \times E_{Calanus} \times AE_{Calanus}$.

IV. $P_{Crustaceans}$ is multiplied by its ecologic efficiency and assimilation efficiency to get the production of whole level 4, including codfish. $P_{Fish}=P_{Crustaceans} \times E_{Crustaceans}\times AE_{Crustaceans}$.

V. Total available Carbon, Tot.C., is calculated by multiplying P_{Fish} with the total area of the fjord basins in question.
Tot.C.=$P_{Fish} \times$ Area

VI. Tot.C. is finally divided by the amount of Carbon in one kg fish, which gives the possible production of fish that could have been produced.

2.7.2 Model B – Energy for growth and maintenance

This model have applied the same assumptions as Model A in step I-IV. Step five and six have a few more assumptions which will be reviewed in the following.

2.7.2.1 Temperature preferences for growth for codfish

According to Jobling (1981) the preferred temperature for fish is a good indicator for the optimum temperature for growth. Thus optimum temperature for growth roughly equals the “preference temperatures”. Some species are known to have slightly higher temperature optimum for growth than its “preference temperatures” (Jobling, 1983).

The temperature preference range for some of the selected commercial codfish species, lies between 1 and 10°C (Bøhle 1974; Coutant 1977; Mergardt and Temming 1997; Cargnelli et al. 1999).

Considering the above, and the average temperature of the fjord (Bakken 2000; Sakshaug and Tangen 2000), there have been used a constant temperature-factor of 7 degrees in the following model (Model B).

2.7.2.2 Converting energy to mass of carbon

The regression used for calculations in Model B (below) has KJ as energy unit. It has been converted to mass of carbon consumed. This has been done by applying Eq.3., and by including conversion factors for consumption of one liter oxygen per kcal (easily converted from KJ) spent. These factors are 4.68, 4.76 and 5.05 for lipids, proteins and carbohydrates respectively (Harris et al., 2000). Calanus is chosen as the model prey item. Although this is not strictly correct, it is close to the truth (Bromley et al. 1997). This has been done because the contents of Calanus is known, considering lipids, proteins and carbohydrates. Another reason was that one of the key species in the fjord is Calanus. Calanus is also a large part of the codfish diet in the early stages of life. Calanus consists of 50% lipids, 30% proteins and 13% carbohydrates (Harris et al. 2000; Tokle and Sakshaug 2000). The remaining 7% were set to zero amount of energy.

2.7.2.3 Energy (Carbon) demand to produce a certain amount of fish

To estimate how much fish biomass that could be made from the available carbon on trophic level three (step 4 in Model A and B), it was necessary to combine the growth rate and energy consumption (feeding intake) of fish.

Equations from Jobling (1983), were applied to calculate the energy consumption for both maintenance and growth. The equation below applies for a weight-specific growth rate for a large amount of fish species.

$$ln(G) = a - 0.4ln(W) \qquad \text{Eq. 4}$$

W stands for weight in gram, *a* is a desired parameter like saturation or salinity and G is growth rate in percentage per day (Jobling, 1983).

Jobling (1983) provided an equation that included temperature (factor a), and specified it for cod (*Gadus morhua*):

$$ln(G) = (0.206 + 0.297T - 0.000538T^3) - 0.441 \times ln(W) \qquad \text{Eq. 5}$$

Where T is measured in °C, and G and W as explained above (Jobling, 1983). This equation was applied for all codfish species. The temperature T, was set to 7 degrees.

The argumentation for this assumption is the same as in section 2.7.2.1.

To estimate the energy needed to produce a certain amount of fish, a regression for energy absorption according to weight were applied:

$$ln(FI) = (0.104T - 0.000112T^3 - 1.500) + 0.802 \times ln(W) \qquad Eq.\ 6$$

Where FI, feeding intake, is measured in KJ day^{-1}, and T and W is as presented above (Jobling, 1988).

An integral, including equation 5 and 6, were made to estimate the amount of energy needed to grow a fish to a certain weight. It is measured in in KJ. The integral includes the effects of sea temperature and weight of fish on growth rate.

$$FI_{tot} = \int_0^{T_{max}} FI(W(T))dT \qquad Eq.\ 7$$

When solved, one gets the following equation for the estimate of energy consumption:

$$FI_{tot} = \frac{c}{a} \times \frac{1}{d-b}\left[W_{max}^{d-b} - W_0^{d-b}\right] \qquad Eq.\ 8$$

Where *c* is the temperature variable from Eq.6.. *d* is the weight factor from Eq.6.. *a* is the weight variable from Eq.5. divided by 100, and *b* is the weight factor from Eq.5.

W_0 and W_{max} are the start – and final weight of the fish measured in gram (g) and FI_{tot} are the total feeding intake measured in KJ.

After calculating the energy consumption (FI_{tot}), Eq. 3. from section 2.6.3. was applied to convert the amount of oxygen spent per KJ (or kcal) to mass of carbon consumed. Finally the assimilation efficiency was included.

Since exact size distribution of the codfish populations was unknown, it was not possible to calculate the exact energy requirements of the populations. To simplify, size distributions and weight-length correlations of previous studies of codfish were applied. Most codfish in the studied populations were in the size interval 40-60cm with a corresponding weight of 1.5-3.5 kg (Jobling 1988; Witherell and Ianelli 1997). Thus, Model B has a standard start-weight of 2 kg.

2.7.2.4 Model B – step by step

Equal to Model A in step I.-IV.

V. $P_{Crustaceans}$ is multiplied by the area of the fjord basins in question to get the total available carbon for fish production.
   Tot.C $= P_{Crustaceans} \times$ Area.

VI. Tot.C. is then divided by the energy demand for producing 1 kg fish biomass during one year (see 2.7.2.3.), which gives you the possible production of codfish.

2.7.3 Codfish biomass estimates

Model A and B do not estimate the possible production of codfish alone. They estimate the possible production for the whole trophic level (level 4). To deal with this, data kindly provided by Yajie Liu; expert in bioeconomics, environmental and energy economics have been applied, as well as public available data from the Norwegian Directorate of Fisheries. This information was kindly provided by Yajie Liu, expert in bioeconomics, environmental and energy economics. The data includes catch statistics and economic values (price in NOK/kg) from year 2000 to 2012, for the whole of Trøndelag and for Sør-Trondelag

By comparing species compositions of the total catch in different years, estimates of the proportion of codfish in the fjord, have been made. This was done by assuming that the total catch is representable for the actual species composition, and by assuming that the species composition in entire Sør-Trøndelag is equal to the composition in the Trondheimsfjord.

2.8 Economy

Fish prices and composition of codfish species varied considerably throughout the given time span (2000-2012). Thus, the average fish price for each species, and the species composition of codfish in Trøndelag, have been used to calculate the economic impact for the fishermen. The economic impact was measured in NOK/kg. It is calculated on the basis of what the fishermen could sell the hypothetical production of codfish for.

3 Results

3.1 Periphylla biomass estimates

Biomass estimates of Periphylla, year 2014, showed a large increase from previous estimates (year 2007, 2010 and 2011) in all basins. Estimates in Beitstadfjorden were more than five times as high as the previous highest estimate in 2007 (63998 v.s. 11291 tons). Estimates in Midtfjorden (36951 tons) and Ytterfjorden (41498 tons) were also quite high, however data for comparison do not exist. The estimates for Verrabotn (278 tons) and Verrasundet (239 tons) were the smallest, but still much larger than estimates from 2010 (57 tons and 164 tons, respectively). See Table 2.1. in APPENDIX 2. for details.

3.2 Fjord basin properties and Periphylla size and depth distribution

Depth and volume increased in the different basins in the following order: Verrabotn, Verrasundet, Beitstadfjorden, Midtfjorden, Ytterfjorden. The topography differed both within and between basins. (See Figure

1.1.-1.6. and Table 1.1.-1.5. in APPENDEIX 1. for details).

Periphylla abundance increased with increasing depth (See Figure 5.1.-5.5. in APPENDIX 5.). The main part of the Periphylla population in Verrabotn resides in the water interval of 35-45 m. In Verrasundet: 80-100m, in Beitstadfjorden; 150-225 m, in Midtfjorden; 250-350m and in Ytterfjorden; 275-400m. Thus, Periphylla resides in approximately 60-80% of the total depth in all basins, when samples were taken, during daytime. (See Table 3.1. in APPENDIX 3.)

3.3 Periphylla - size distributions

The size distribution of Periphylla appears to be dynamic. In the present materials it varies between basins as well as between years within each basin. The main trend was that Ytterfjorden and Midtfjorden have a majority of small and medium sized individuals (2-4 cm and 4-6 cm). Beitstadfjorden was dominated by small and large sized individuals (2-4cm and 10-12cm). Verrasundet and Verrabotn had mainly medium sized individuals (8-10cm). See Figure 7.1.-7.4. in APPENDIX 7 for details.

No correlation between size (CD) and depth was found (See Figure 4.1.-4.5. in APPENDIX 4.).

3.4 Periphylla - production, carbon demand, carbon turnover rate and density

Estimates of production, carbon demand, carbon turnover rate and density of Periphylla, vary between each basin. Variations are due to differences on the total biomass and the size distribution in each basin.

On average, there was an average production of 2.01 $gCm^{-2}year^{-1}$, an average carbon demand of 0.07 $mgCm^{-3}$, an average carbon turnover rate of 0.0175 per day and an average density of 1.83gm^{-3}. Specific values for each basin can be read from Table 6.1. in APPENDIX 6.

3.5 Codfish - species composition

There was a large increase in tons of fish harvested from 2000-2012 in Sør-Trøndelag (Figure 8.1. in APPENDIX 8.) It was also noticeable that the proportion and amount of codfish in the total catch was changing on year to year basis. It had a large increase year 2006. The proportion of codfish seemed stable from year 2009 to 2012 (Figure 8.3. in APPENDIX 8.).

There was some variation in species composition within the codfish-group. Cod and saithe were the species that always dominated, while hake was always harvested in the smallest amounts (see

Figure 8.2 and 8.3. in APPENDIX 8. For details).

3.6 Codfish – Energy loss – Possible production

Based on the energy consumption of Periphylla from 2000-2012, the models predict a possible codfish production of approximately 70 tons per year.

According to the models, the possible production was increasing from 2000-2006 and decreasing from 2006-2012. The production was approximately stable in the years 2009-2012; just above 50 tons per year (see Figure 9.1. in APPENDIX 9).

3.7 Fish prices

Commercial prices for codfishes are determined by national and international markets. They are volatile both between species, and over time within species. For the conditions on which this study is based, the average price for all the codfishes was 8.5 NOK per kg. For the selected species in this study; cod, haddock, saithe, pollack and hake, the prices were on average 11.7, 7.7, 4.7, 9.5, 20.0 NOK kg^{-1}, respectively, during the selected period (2000-2012). See Figure 10.1. in APPENDIX 10 for details.

3.8 Economic loss

The average economic loss per year after 2007 was estimated at 600 000-900 000 NOK. After that year, observations of winterly Periphylla mass deaths (Solheim 2012) indicated that the Periphylla population in the inner fjord had reached the environments' carrying capacity. For the entire period 2000-2012, an overall average loss of 600 000–650 000 NOK per year, was estimated.

The total economic loss from 2000-2012 was 8 000 000-9 000 000 NOK. If further loss is assumed to be equal to losses in 2009-2012, the total loss from 2000 to 2015 would be 9 000 000-9 500 000 NOK. See Figure 11.1.-11.2. in APPENDIX 11. for details.

4 Discussion

4.1 Biomass estimates of *Periphylla*

4.1.1 VideoTrawl and VideoFrame - errors

Estimates of the coronal diameter (CD) of Periphylla specimens, from the video film, were done by on-screen measurements and an in-house computer program (by Ulf Båmstedt). Due to the various angles of Periphylla when passing through the frame, different light levels as well as relatively low camera resolution, it was difficult to get very accurate measurements. Due to this, medusa smaller than 2 cm were not detected. Medusa with CD larger than 14cm were set to 14cm. It is acknowledged that to some degree, these procedures have affected the biomass and carbon demand conservatively.

The method for estimating Periphylla size (the CD, and from CD to biomass) by filtration of known water volumes and capturing the individuals on film, is probably the best existing method (Ulf Båmstedt pers. comm.). There was no significant correlation between size and depth (Figure 4.1.-4.5. in APPENDIX 4). However, correlations between abundance and depth were found (Figure 5.1.-5.5. in APPENDIX 5), and it was found acceptable to divide the basis into depth intervals, each with average sized individuals, for calculation of the total biomass (Table 3.1. in APPENDIX 3).

In line with previous findings in the Trondheimsfjord (Solheim 2011), there was no significant correlation between Periphylla size and depth in this study. In other studies such correlations were found, potentially explained by a behavioural mechanism of the small specimens, i.e. seeking to the deep water. Such behaviour would help counteract misplacement by advection as well as predation by their larger relatives higher in the water column (Ulf Båmstedt pers. comm.). It is noted, however, that the present detection limit of CD=2 cm would tend to mask an actual size-depth correlation in the present materials.

4.1.1.1 Biomass estimates in Verrabotn and Verrasundet

In Verrabotn and Verrasundet the accuracy of the biomass estimates are regarded as reasonable, considering normal population fluctuations in small habitats, and the sources of errors discussed in section 4.1.1 above.

Figures 7.1. and 7.2. in APPENDIX 7. show variable Periphylla size distribution from one year to another. This variation has an effect on the present estimates of possible production of codfish by inducing different carbon demands (See Table 6.1. APPENDIX 6.). The observed variation in size distribution could probably be explained by cyclic variations due to mass deaths, recruitment variability and advection, availability of food and other common environmental variables. The Periphylla stock in these two shallow basins is probably occasionally and variably recruited by export from a mother population in the nearby basin Beistadfjorden (Hetland 2008; Solheim 2011; Borgersen 2014).

4.1.1.2 Biomass estimates in Beitstadfjorden

A comparison of the biomass estimates from 2007, 2010, 2011 with the new estimates in 2014 (See Table 2.1. in

APPENDIX 2.) reveals a substantial increase in the Periphylla biomass in Beitstadfjorden. Possible causes of this result include both the error sources discussed above (4.1.1. and 4.1.2.) and normal environmental variables as mentioned in 4.1.2.1. From the size distribution in different years (Figure 7.4. in APPENDIX 7.) there seems to be large annual differences in the recruitment. This would support explanations involving mass deaths (Solheim 2011) and normally occurring marine food web variability.

4.1.1.3 Biomass estimates in Midtfjorden and Ytterfjorden and the total Trondheimsfjord

For Midtfjorden and Ytterfjorden, there were no previous biomass estimates for comparison. These two fjord basins have much larger depths than the three innermost ones. Thus, in these two basins, Periphylla was distributed well above the bottom, but still at depths not commonly used by net-gear fisheries for codfishes. Due to this, the jelly proliferation has not affected the bottom-net fishery noticeably in these basins. Nor has it been accentuated as a major problem, or concern, for fisheries in previous scientific investigations. The majority of individuals in these two basins were small and thus not readily catchable in net gear or bottom trawl. Nevertheless, the total Periphylla biomass estimated for these two basins was substantial (30 000 – 40 000 tons) (see Figure, 7.1. in APPENDIX 7).

Due to the inter-basin differences in the composition of size classes, it was found necessary to calculate the total biomass and its corresponding respiratory demand~~s~~ for each population in the different basins. They were summed in order to estimate the total Periphylla biomass, and production, of the Trondheimsfjord (elaborated in 4.2.1.).

4.2 Carbon demand of Periphylla – assumptions

Estimation of carbon demand of Periphylla was based on calculations of CD, and some assumptions and educated guessing, about AE and RQ. Thus, errors of CD estimates (as explained in section 4.1.1.) would affect the estimated carbon demand as well as the assumed values of AE and RQ. The carbon demand estimates utilized a regression based on individual Periphylla basal metabolism. Therefore, those estimates are conservative. Actual growth rates and energy demands of Periphylla at different stages in their life cycle are not to be found in the scientific literature.

4.2.1 Carbon demand and density

Large Periphylla individuals have lower respiration rates per gram than small individuals. This is seen from the non-linearity of the respiration-regression (Eq. 2). This fact explains that despite a much lower density of Periphylla in Ytterfjorden than in Verrasundet, the respiration (in $mgCm^{-3}$) for the two locations was equal (Table 6.1. APPENDIX 6). The size distribution in Ytterfjorden consisted mainly of small individuals while in Verrasundet, the individuals were large (Figure 7.1 APPENDIX 7).

Consequently, the energy cost of a blooming or growing population *of a given size* of Periphylla, will be much larger than what is needed to maintain an already established and stable population. This applies even when the energy needed for growth is not included. It is thus possible that the ecological consequences would actually be larger when a population is blooming, than in an already established and relatively stable population.

If there are cyclic variations due to mass deaths, this would induce cyclic differences in energy consumption as well. This would affect the remaining fauna and flora correspondingly, and in turn he economic consequences of Periphyllas' presence.

4.3 Biomass estimates of codfish - assumptions

Both models, A and B, assume that the assimilation efficiency and energy transfer efficiency, carbon content and dry weight of all codfish species are equal. The values for these variables are based on previous studies and may, or may not, be correct. This will affect the estimates in some way.

None of the models consider mortality rates, predation or competition between and within fish species. Thus, the estimated possible fish production, in this study, is probably overestimated, but to an unknown extent. The applied food web is also quite simple and includes only a few key species (see Figure 2.7.1.7.). These assumptions and simplifications will affect the estimates which thus should be regarded as approximations.

Model B has some simplifying assumptions considering temperature preferences and growth of codfish species. These assumptions are not very precise, and this has affected the estimates. An example is that the temperature in the fjord is assumed constant. As can be seen from equation 7: when the temperature increases, less energy is needed to produce a fish of a certain size. Theory states that growth is more effective close to the preferred temperature. This temperature varies slightly between the cod fish species involved, and this will affect the estimates to some degree.

For Model B, it is noted that Jobling (1983, 1988) stressed the fact that the regressions for feeding intake and growth rate were made under the conditions where the fish were fed either to satiation or in excess.

They were also kept in favorable conditions, which assumingly promoted maximum growth rates. This would lead to overestimates of the production of codfish. Also, most of the fish used in Joblings' experiments did not exceed 2 kg. According to Jobling, extrapolating the estimates for larger fish should be done with caution. The average start weight of fish in Model B (2 kg) was chosen by considering growth of codfish in different studies (Gulland et al.1992; Witherell 1997). This choice appears as a legit assumption but basically, all the assumption mentioned above would somehow affect the estimates.

4.4 Available data for economic codfish calculations- assumptions

The proportional biomass of codfishes in the Trondheimsfjord proper was estimated by referencing to data for the total catch in Sør-Trøndelag assuming that to be representable for the actual proportion of codfish in the fjord. The same assumption was made for the composition of different codfish species. Here, data of landing were from all of Trøndelag, not just Sør-Trøndelag. Clearly, this assumption is only approximately correct. Its validity is affected by differences in fish fauna and fishing gear used as well as fishing grounds and local traditions. The topography and depths of fishing grounds may have effects on habitats and thus the biology and distribution of the local codfish species (See Figure 1.1.-1.6. and Table 1.1.-1.5. in APPENDIX 1) (Figure 8.4. APPENDIX 8. may be supportive of this statement). Catch and landings data from Trondheimsfjorden, if available, would have been more representative.

However, based on the present available data, the present analytical approach was considered the best practical solution. The mentioned assumptions and simplifications will probably have affected the estimates to some degree. The robustness of the present findings and conclusions, should be perceived in lieu of that fact.

4.4.1 Differences between the fjord basins in ecological and economic impacts

As shown in Table 6.1. APPENDIX 6., there are large differences in the density, carbon demand, production, and size distribution of Periphylla between the fjord basins. These differences will affect how severe the ecological and economic consequences are.

For example, basins with primarily smaller individuals will probably not be as damaging for the fishermens' livelyhood with respect to harm to fish and net gear, health issues and increased working hours. Smaller individuals are not caught by the gill-net gear used and, due to their small sizes, also the stinging effects will be smaller.

The biomass production and carbon demand, on the other hand, will be larger in basins with mainly smaller individuals. This is because smaller individuals demand proportionally more energy for maintenance than larger ones. Thus, it is possible that the economic loss would be quite large after all in terms of loss in available carbon and alterations of the ecosystem by changes in the species composition.

Differences in total Periphylla biomass and density, will affect the ecology and the economic loss in all four basins. Basins with high densities would probably be affected more than basins with lower densities (depending on preferred depth and Periphylla size distribution). Basins with more Periphylla in the water layers which the fishermen aim for are likely to suffer the largest economic impacts.

The ecological impacts of the Periphylla proliferation in the Trondheimsfjord has probably also been harmful for the production of other fish species than the codfishes. The economic effects of this are probably less severe since the contemporary landings of those are much lower than that of the codfishes.

4.5 Prospects

The figures presented for the energy budgets of Periphylla and codfishes, are based on what is supposed to be a reasonable set of assumptions. The best improvement on the methodology in future studies would probably be to achieve more firm knowledge of the diet of Periphylla. The focus should be on Periphyllas' diet at different life stages as well as through the year. Such information would also help to position Periphylla correctly in the local food web in the Trondheimsfjord.

Detailed knowledge of the advection forces, and Periphyllas' behavioral characteristics, would increase the precision and validity of the estimates. It appears that characteristics of Periphylla physical presence may be very dependent on local conditions related to topography, hydrography and hydrology. Thus, this information need to be based on local studies.

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APPENDIX -contents

APPENDIX 1 – Volume and maps of Trondheimsfjorden

APPENDIX 2 – Periphylla - biomass estimates

APPENDIX 3 – Periphylla - biomass in different depth intervals

APPENDIX 4 – Periphylla – plots of size by depth

APPENDIX 5 – Periphylla – plots of abundance by depth

APPENDIX 6 – Periphylla - properties of the populations

APPENDIX 7 – Periphylla - size distributions

APPENDIX 8 – Codfish - species composition

APPENDIX 9 – Codfish - possible production

APPENDIX 10 – Codfish - prices

APPENDIX 11 – Codfish - economic loss per species and for all codfish (average)

APPENDIX 1. Volume and maps of Trondheimsfjorden

Verrabotn

Table 1.1. Area and volume of depth intervals in Verrabotn in Trondheimsfjorden, Norway.

Depth (m)	Area (km^2)	Volume (km^3)
0	0	0
1	5	0.005
20	5	0.08
40	3	0.01
60	1	0.00
80	0	
Total:		0.095

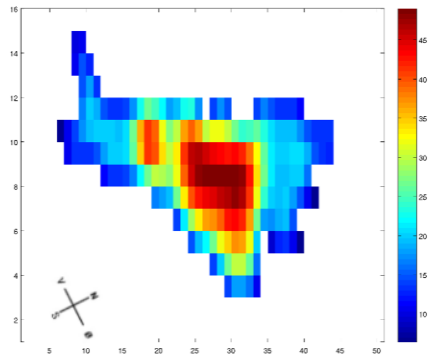

Figure 1.1. Map of Verrabotn constructed in SINMOD with 160 m horizontal resolution (1 unit equals 160m). Colour scale is depth in m.

Verrasundet

Table 1.2. Area and volume of depth intervals in Verrasundet in Trondheimsfjorden, Norway. .

Depth (m)	Area (km^2)	Volume (km^3)
0	0	0.00
1	23	0.02
20	16	0.38
40	9	0.15
60	4	0.08
80	3	0.05
100	1	0.01
120	0	
Total:		0.693

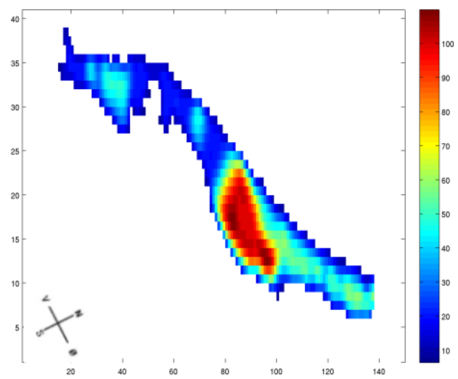

Figure 1.2. Map of Verrasundet constructed in SINMOD with 160 m horizontal resolution (1 unit equals 160m.). Colour scale is depth in m.

Beitstadfjorden

Table 1.3. Area and volume of depth intervals in Beitstadfjorden in Trondheimsfjorden, Norway. .

Depth (m)	Area (km^2)	Volume (km^3)
0	0	0.00
1	192	0.19
50	131	7.53
100	89	5.30
150	50	3.32
200	14	1.36
250	0	
Total:		17.83

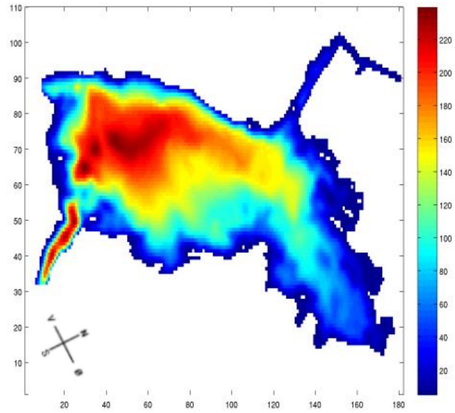

Figure 1.3. Map of Beitstadfjorden constructed in SINMOD with 160 m horizontal resolution (1 unit equals 160m.). Colour scale is depth in m.

Midtfjorden

Table 1.4. Area and volume of depth intervals in Midtfjorden in Trondheimsfjorden, Norway. .

Depth (m)	Area (km^2)	Volume (km^3)
0	0	0.00
1	404	0.40
50	285	16.29
100	218	12.33
150	173	9.34
200	140	7.81
250	106	5.93
300	73	4.31
350	56	3.12
400	36	2.28
420	6	0.26
Total:		62.07

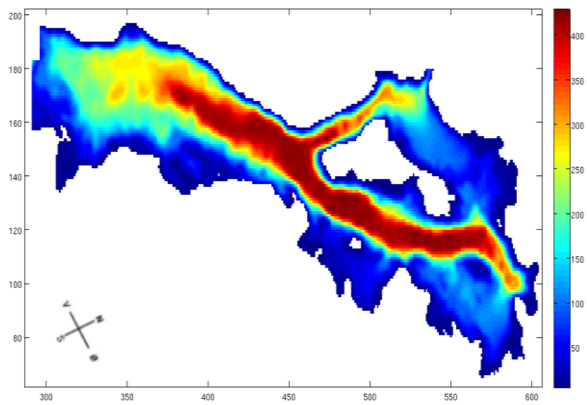

Figure 1.4. Map of Midtfjorden constructed in SINMOD with 160 m horizontal resolution (1 unit equals 160m.). Colour scale is depth in m.

Ytterfjorden

Table 1.5. Area and volume of depth intervals in Ytterfjorden in Trondheimsfjorden, Norway. .

Depth (m)	Area (km^2)	Volume (km^3)
0	0	0.00
1	729	0.73
50	588	32.08
100	487	26.17
150	419	22.25
200	361	19.31
250	304	16.28
300	254	13.75
350	212	11.46
400	176	9.65
Total:		155.00

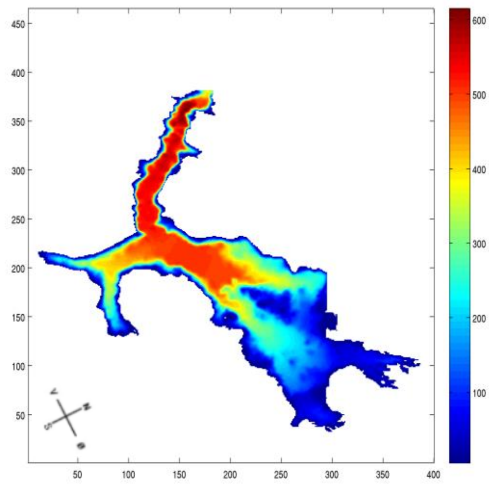

Figure 1.5. Map of Ytterfjorden constructed in SINMOD with 160 m horizontal resolution (1 unit equals 160m). Colour scale is depth in m.

Trondheimsfjorden

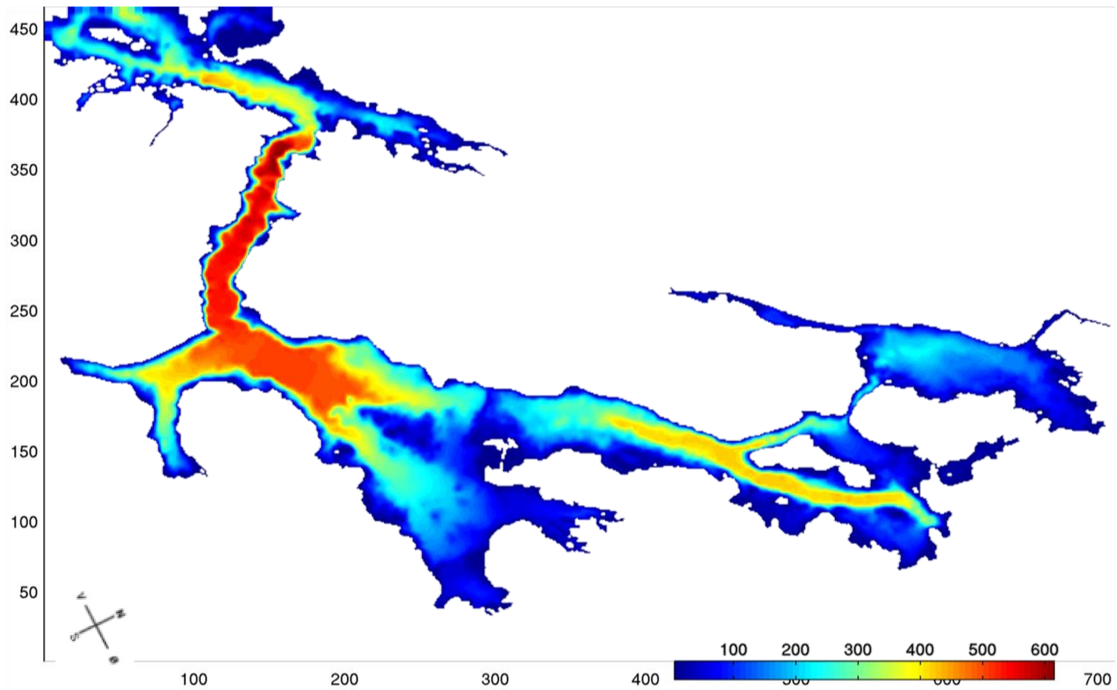

Figure 1.6. Map of Trondheimsfjorden constructed in SINMOD with 160 m horizontal resolution (1 unit equals 160m). Colour scale is depth in m

APPENDIX 2. Periphylla - biomass estimates

Table 2.1. Periphylla periphylla. Estimated biomass (10^3kg) for all basins in Trondheimsfjorden, Norway. 2007, 2010, 2011 and 2014. Modified and adopted from Hetland (2008) and Borgersen (2013).

	Estimated biomass (10^3kg)			
Location:	2007 (October)	2010 (April)	2011 (March)	2014 (June)
Verrabotn	95	57	-	278
Verrasundet	941	164	-	239
Beitstadfjorden	11291	2230	3548	63998
Midtfjorden	-	-	-	36951
Ytterfjorden	-	-	-	41498

APPENDIX 3. Periphylla - biomass in different depth intervals

Table 3.1. Periphylla periphylla biomass (10^3 kg) estimates in depth intervals (m and km^3) in all basins in Trondheimsfjorden , Norway. Year 2014.

	Beitstadfjorden		**Midtfjorden**		**Ytterfjorden**	
Depth(m)	**Volume(km^3)**	**Biomass(10^3kg)**	**Volume(km^3)**	**Biomass(10^3kg)**	**Volume(km^3)**	**Biomass(10^3kg)**
0	0.00	0.00	0.00	0.00	0.00	0.00
1	0.19	0.00	0.40	0.00	0.73	0.00
50	7.53	0.00	16.29	0.00	32.08	0.00
100	5.30	29742.82	12.33	0.00	26.17	0.00
150	3.32	27316.69	9.34	0.00	22.25	0.00
200	1.36	6938.99	7.81	424.67	19.31	788.49
250	0.13	0.00	5.93	4028.09	16.28	18680.28
300	-	-	4.31	10132.80	13.75	14566.43
350	-	-	3.12	18959.23	11.46	7463.40
400	-	-	2.28	3406.32	9.65	0.00
Total	17.83	63998.50	62.07	36951.11	155.00	41498.59
Fjord total			**Volume: 235.69 (km^3)**			**Biomass: 142965.80×10^3kg**

	Verrabotn		**Verrasundet**	
Depth(m)	**Volume(km^3)**	**Biomass(10^3kg)**	**Volume(km^3)**	**Biomass(10^3kg)**
0	0.00	0.00	0.00	0.00
1	0.005	0.14	0.02	0.00
20	0.08	264	0.38	0.00
40	0.01	14.43	0.15	0.00
60	0.00	0.00	0.08	120.53
80	0.00	0.00	0.05	118.51
100	-	-	0.01	0.00
120	-	-	0.00	0.00
Total	0.095	278.6	0.69	239.04

APPENDIX 4. Periphylla - plots of size by depth

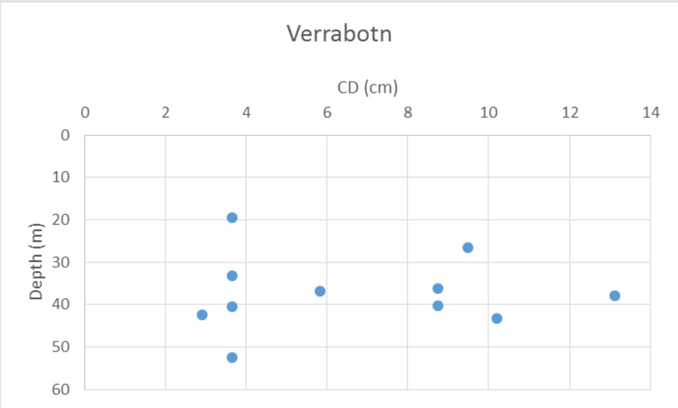

Figure 4.1. Periphylla periphylla - Coronal diameter (CD) in cm versus depth in m for Verrabotn in Trondheimsfjorden, Norway. Year 2014. n=11. Each dot represents one Periphylla.

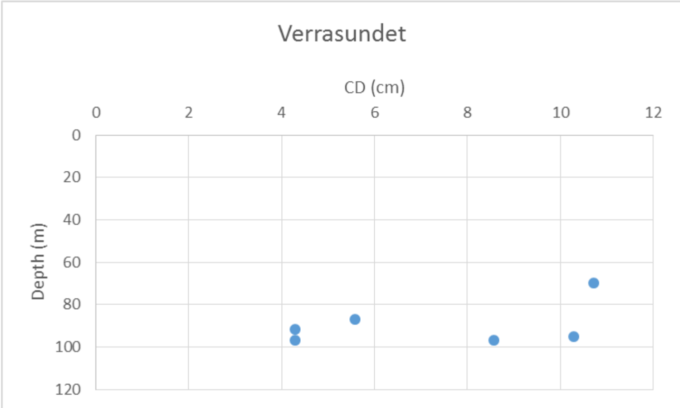

Figure 4.2. Periphylla periphylla - Coronal diameter (CD) in cm versus depth in m for Verrasundet in Trondheimsfjorden, Norway. Year 2014. n=6. Each dot represents one Periphylla.

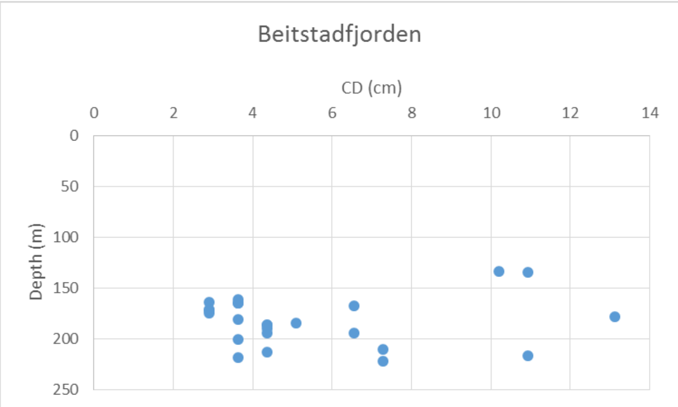

Figure 4.3. Periphylla periphylla - Coronal diameter (CD) in cm versus depth in m for Beitstadfjorden in Trondheimsfjorden, Norway. Year 2014. n=24. Each dot represents one Periphylla.

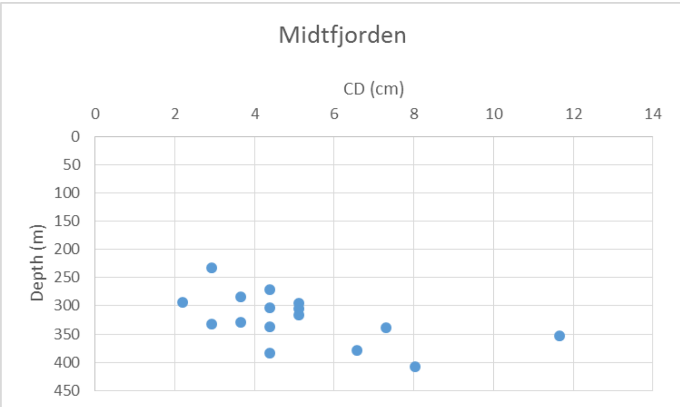

Figure 4.4 Periphylla periphylla - Coronal diameter (CD) in cm versus depth in m for Midtfjorden in Trondheimsfjorden, Norway. Year 2014. n=16. Each dot represents one Periphylla.

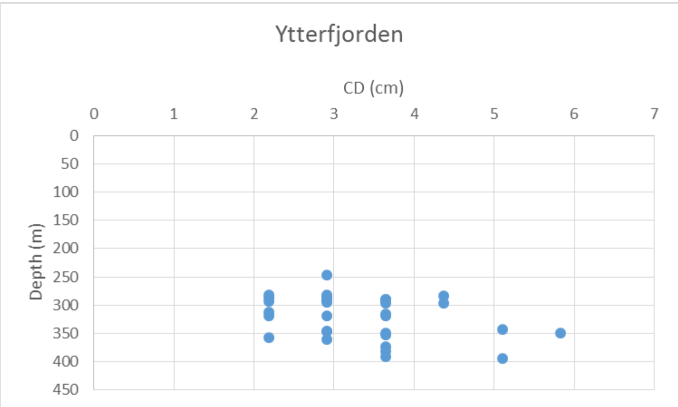

Figure 4.5. Periphylla periphylla - Coronal diameter (CD) in cm versus depth in m for Ytterfjorden in Trondheimsfjorden, Norway. Year 2014. n=37. Each dot represents one Periphylla. (Samples restarted only on the way down, and not to the full depth of the basin)

APPENDIX 5. Periphylla - plots of abundance by depth

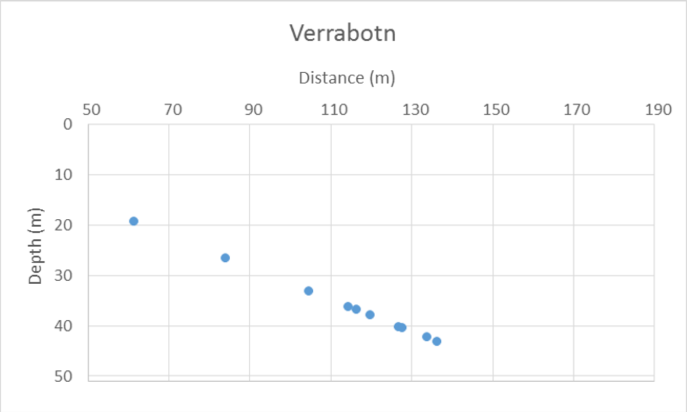

Figure 5.1. Periphylla periphylla - abundance in Verrabotn in Trondheimsfjorden, Norway. Each dot represents one Periphylla. Depth and distance are measured in m. Year 2014. n=11. (Samples restarted only on the way down)

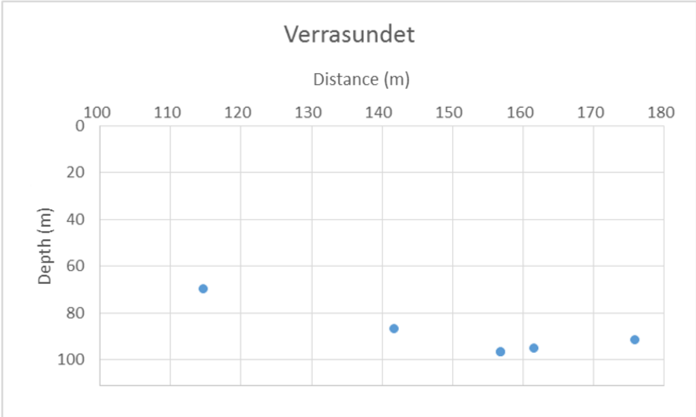

Figure 5.2. Periphylla periphylla - abundance in Verrasundet in Trondheimsfjorden, Norway. Each dot represents one Periphylla. Depth and distance are measured in m. Year 2014.n=6. (Samples restarted only on the way down)

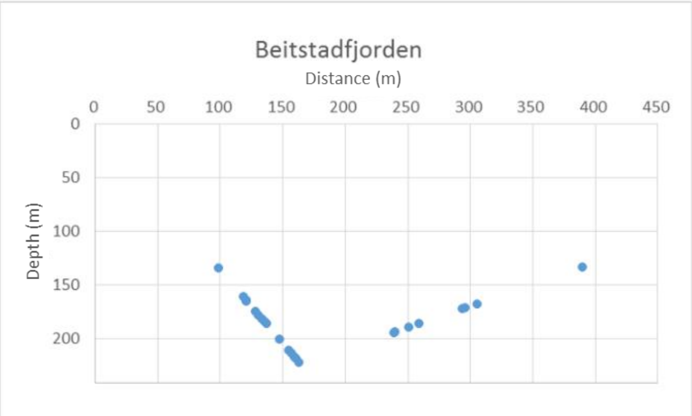

Figure 5.3. Periphylla periphylla - abundance in Beitstadfjorden in Trondheimsfjorden, Norway. Each dot represents one Periphylla. Depth and distance are measured in m. Year 2014. n=24.

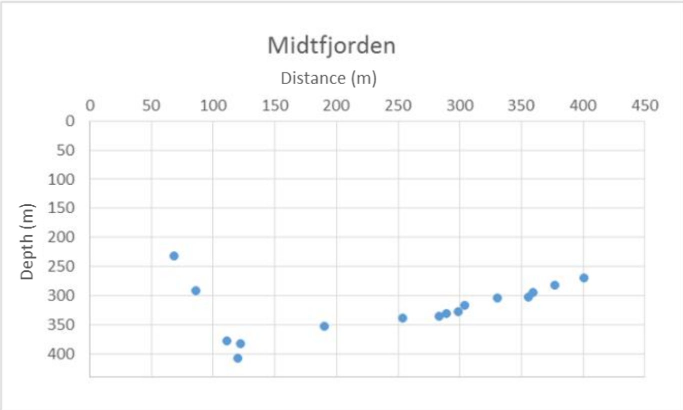

Figure 5.4. Periphylla periphylla - abundance in Midtfjorden in Trondheimsfjorden, Norway. Each dot represents one Periphylla. Depth and distance are measured in m. Year 2014.n=16

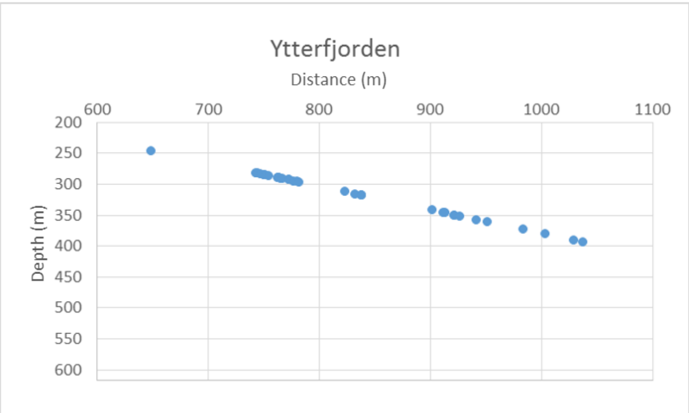

Figure 5.5. Periphylla periphylla - abundance in Ytterfjorden in Trondheimsfjorden, Norway. Each dot represents one Periphylla. Depth and distance are measured in m. Year 2014.n=37. (Samples restarted only on the way down, and not to the full depth of the

APPENDIX 6. Periphylla - properties of the populations

Table 6.1. Periphylla periphylla. Average production ($gCm^{-2}year^{-1}$), carbon demand($mgCm^{-3}$), carbon turnover rate (day^{-1}) and density(gm^{-3}) in the different basins in Trondheimsfjorden, Norway. year 2014.

Location	Production	Carbon demand	Carbon turnover	Density (gm^{-3})
Verrabotn	0.722	0.10	0.017	2.79
Verrasundet	0.154	0.01	0.013	0.35
Beitstadfjorden	5.098	0.15	0.020	3.59
Midtfjorden	2.063	0.04	0.020	0.60
Ytterfjorden	2.910	0.04	0.018	0.27

APPENDIX 7. Periphylla - size distributions

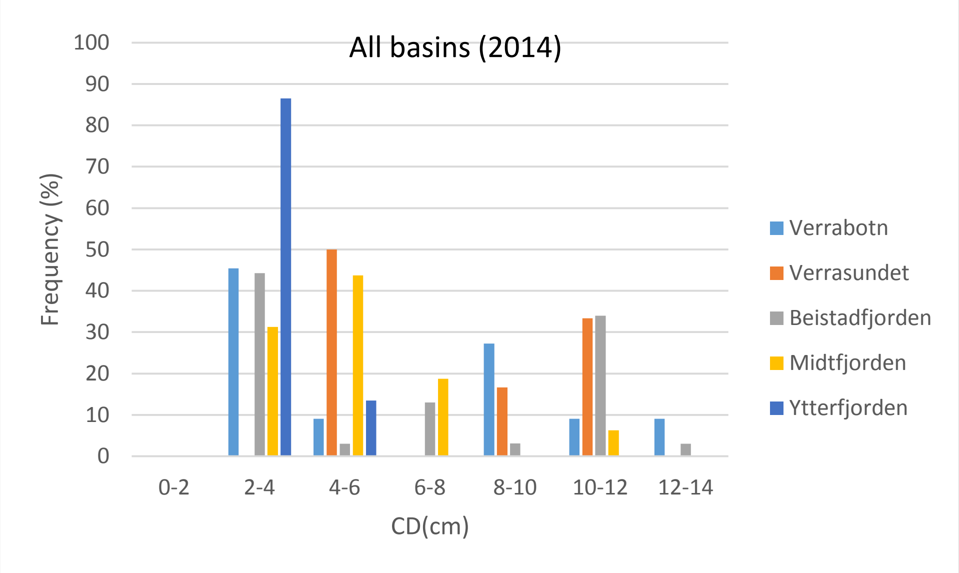

Figure 7.1. Periphylla Periphylla. Size distribution in all basins, given as frequency of the total number of individuals in each dive. Verrabotn n=11, Verrasundet n=6, Beitstadfjorden n=24 , Midtfjorden n=16 Ytterfjorden n=37. Trondheimsfjorden, Norway. Year 2014.

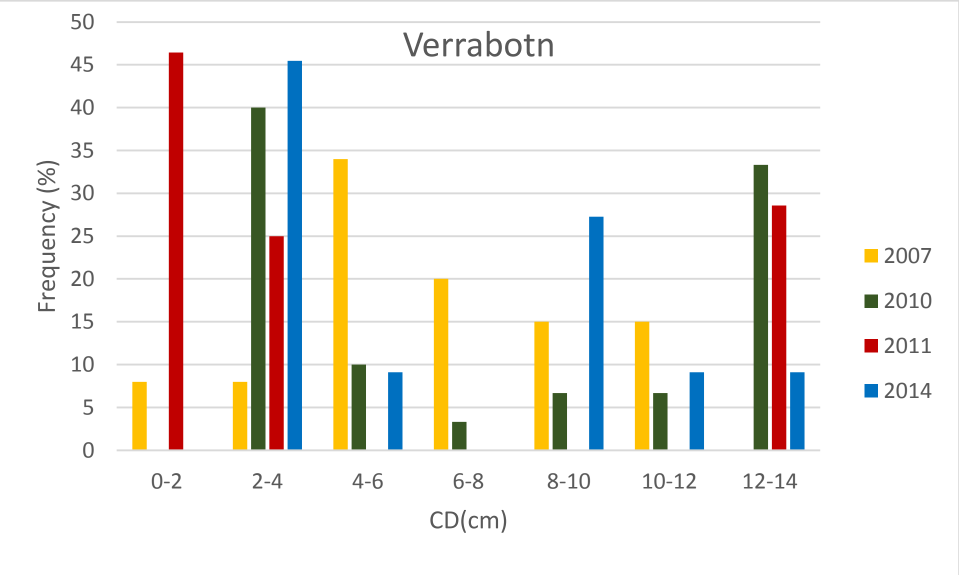

Figure 7.2. Periphylla periphylla. Size distribution in Verrabotn, given as frequency of the total number of individuals in each dive. Data collected from year 2007 till 2014 (2007: n=14, 2010: n=30, 2011: n=28, 2014: n=11). Trondheimsfjorden, Norway. Data for 2007, 2010, 2011 from Hetland (2008) and Solheim (2012) respectively.

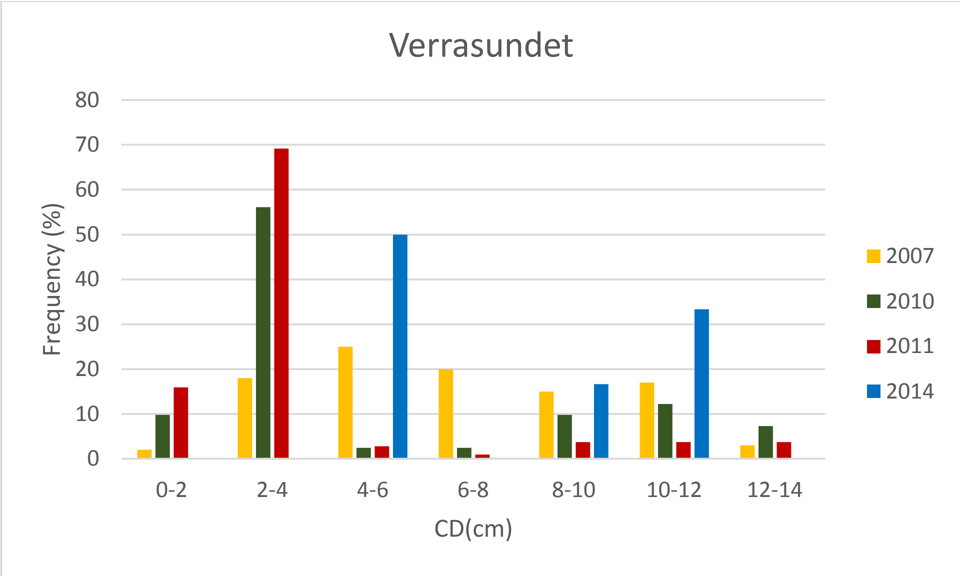

Figure 7.3. Periphylla periphylla. Size distribution given as frequency of the total number of individuals in each dive in Verrasundet. Data collected from year 2007 till 2014 (2007: n=101, 2010: n=41, 2011: n=107, 2014: n=6). Trondheimsfjorden, Norway. Data for 2007, 2010, 2011 from Hetland (2008) and Solheim (2012) respectively.

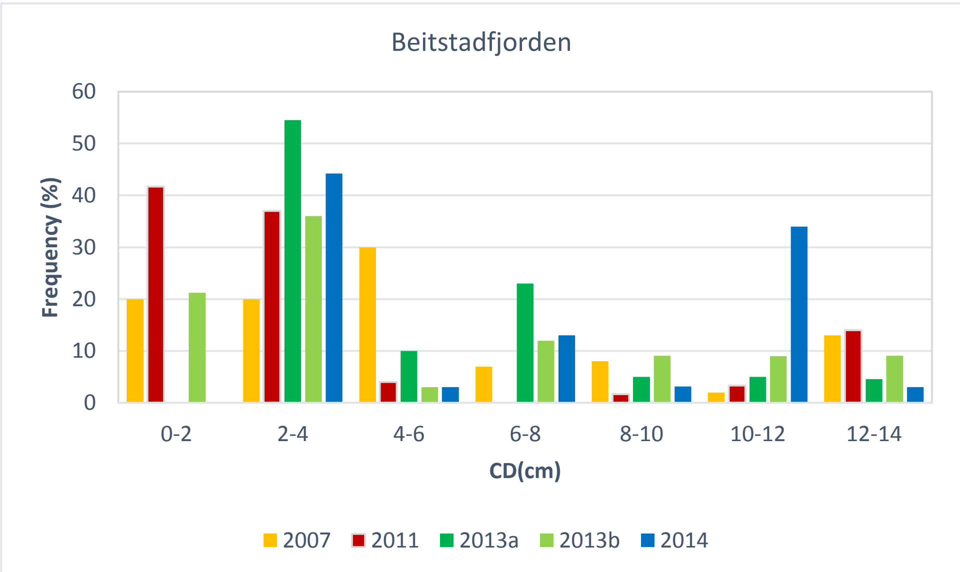

Figure 7.4. Periphylla periphylla size distribution given as frequency of the total number of individuals in each dive in Beitstadfjorden. Data collected from year 2007 till 2014 (2007: n=64, 2011: n=61, 2013a: n=21, 2013b: n=33, 2014: n= 24). Trondheimsfjorden, Norway. Data for 2007, 2010, 2011 from Hetland (2008) and Solheim (2012) respectively.

APPENDIX 8. Codfish - species composition and catches

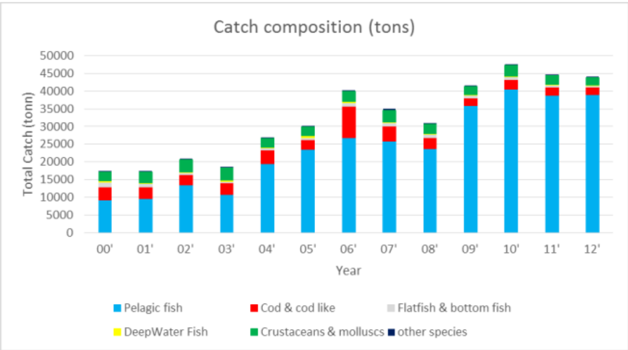

Figure 8.1. Catch composition (of total catch) of different marine fish, crustaceans and molluscs, in fisheries in Sør-Trøndelag, Norway, year 2000-2012.

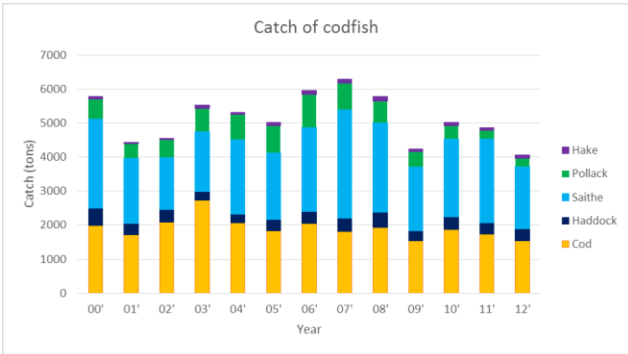

Figure 8.2. Codfish and selected codfish species (cod, haddock, saithe, pollack and hake), caught in Trøndelag, Norway. Year 2000-2012.

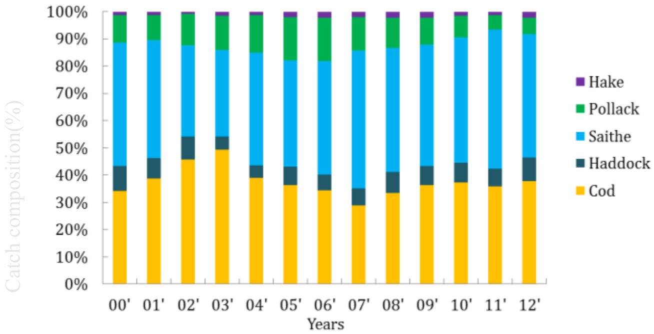

Figure 8.3. Shows the codfish species composition in Trøndelag, Norway, year 2000-2012.

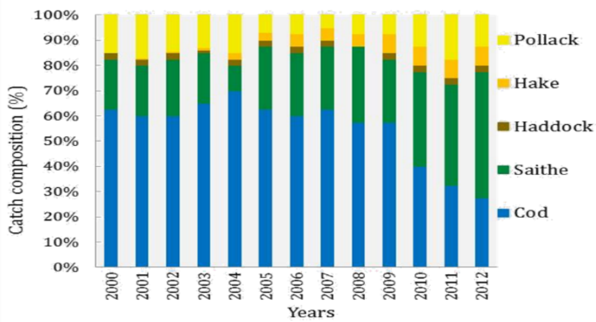

Figure 8.4. Catch composition of codfish species in the Trondheimsfjord, Norway. year 2000-2012. Adopted from Tiller R.et al (2014).

APPENDIX 9. Codfish - energy loss - possible production

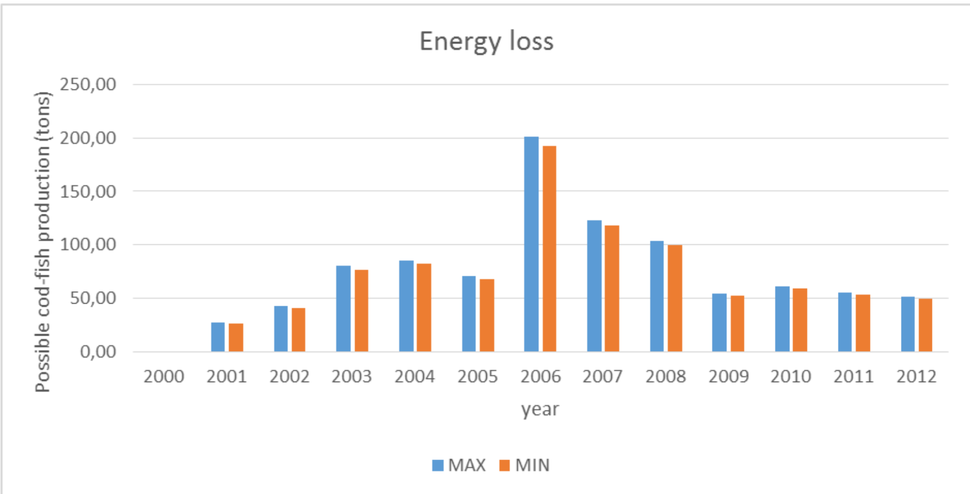

Figure 9.1. Shows the maximum and minimum possible codfish production (in tons) in the Trondheimsfjord, Norway. Year 2000-2012. Based on data from Trøndelag.

APPENDIX 10. Codfish - prices

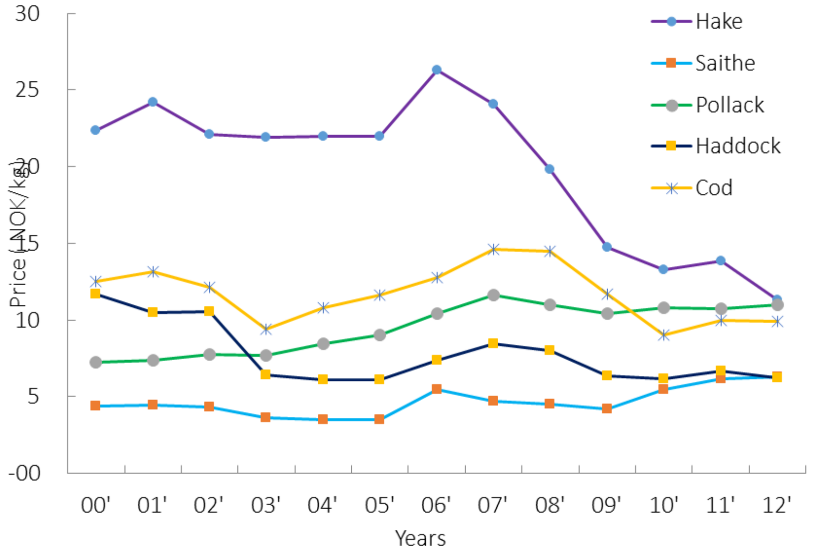

Figure 10.1. Shows price development in NOK/kg for different codfish from year 2000 -2012 in Sørtrøndelag, Norway. Data from Sør-trøndelag. Year 2000-2012.

APPENDIX 11. Codfish - economic loss per species and for all codfish (average)

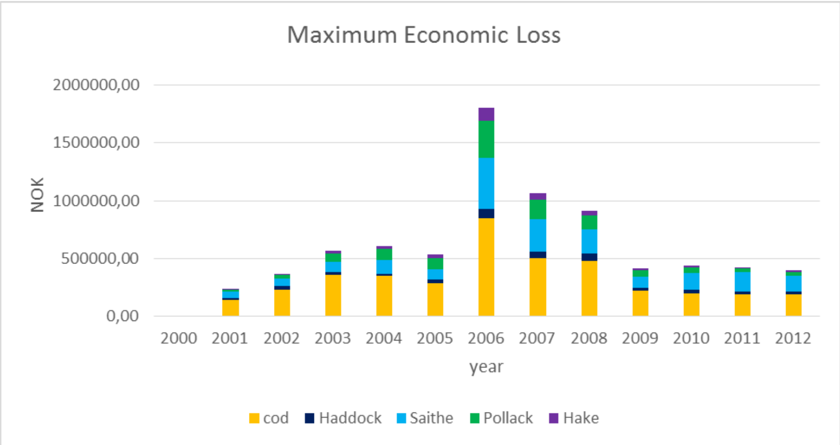

Figure 11.1. Shows the maximum amount of money lost due to bloom and maintenance of Periphylla periphylla in Trondheimsfjorden, Norway. Year 2000-2012. Based on Model B.

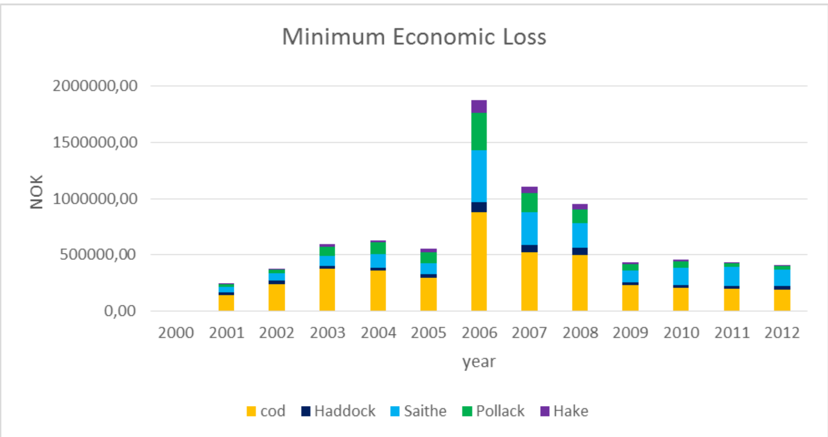

Figure11.2. Shows the maximum amount of money lost due to bloom and maintenance of Periphylla periphylla in Trondheimsfjorden, Norway. Year 2000-2012. Based on Model A.