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Population trend of Periphylla periphylla in inner Trondheimsfjord

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Preface

This thesis is a part of a two year Master of Science program in Marine Costal Development, at the institute of biology at the Norwegian University of Science and Technology (NTNU), Trondheim. My results are built on data collected during a cruise with NTNU's R/V "Gunnerus" week 13 in 2011.

I would like to thank my supervisor, professor Jarle Mork (NTNU), for suggesting this MSc project, and for supervising throughout my master period.

I would also like to thank my co-supervisor, professor Ulf Båmstedt (Umeå Marina Forskningscentrum, Umeå Universität), for use of his own design, the LVPP. He has also spent some of his time to guide me and answer many questions, of which I am grateful.

The staff onboard R/V "Gunnerus" has been of great help collecting data for the thesis. I would like to thank all onboard, especially captain Arve Knudsen, for being patient and helpful during the cruise. Thanks to Dr. Torkild Bakken for analyzing the samples of *polychaeta*.

At last I would like to thank my family and friends for support, especially my boyfriend and my mother.

Trondheim, May 2012

Hilde Solheim

Picture on cover: *Periphylla periphylla* caught with bottom trawl. Photo by Hilde Solheim.

Abstract

Periphylla periphylla (Scyphozoa, Coronatae) is a deep sea jellyfish first described by Péron & Lesueur in 1809. It is distributed in all of the world's oceans except for the Arctic. *P. periphylla* avoids light and is well adapted to a life in the dark. It performs diel vertical migrations (DVM) in the water column.

Relatively recently, since the first observation in Lurefjorden near Bergen in the 1970s, it has established dense populations in several Norwegian fjords including the Trondheimsfjord, the focus of this study. The main goal of this thesis was to estimate the current biomass of the *P. periphylla* population in the inner Trondheimsfjord (Beitstadfjorden), which has three smaller basins with different depths. Most of the data was collected by a Lightweight Video Profiling Platform (LVPP) which provided information on the vertical distribution of jellyfish, their numbers, and the size (CD: coronal diameter) of each individual.

The population in Verrabotn, the shallowest and innermost basin of Beitstadfjorden, had a higher percentage of large individuals (CD >121 mm) than the other basins. Most of the jellyfish individuals in the other two basins tended to be small, with CD ≤ 40 mm. However, the total biomass estimated at each location was mainly made up by large *P. periphylla*. Comparing the present biomass estimate with a previous one in 2007, it appeared that the population had decreased.

However, the presence of large numbers of small individuals of different sizes suggests that a successful local recruitment is still taking place.

Sammendrag

Periphylla periphylla er en dyphavsmanet først beskrevet av Péron & Lesueur i 1809. Den er utbredt i alle verdenshav unntatt Arktis. Maneten er lyssky og godt tilpasset et liv i mørket, og gjennomfører vertikale døgnvandringer i vannsøyla. Noen steder går den helt til overflaten om natten. Maneten har i de siste 40 år etablert tette populasjoner i flere norske fjorder inklusive Trondheimsfjorden, hvor tette forekomster ble oppdaget i 1999.

Hensikten med denne oppgaven var å estimere biomassen til den lokale *P. periphylla* populasjonen i indre Trondheimsfjord (Beitstadfjorden), og sammenligne denne med tidligere estimat for å se om det hadde skjedd forandringer i størrelse. Innsamling av data ble gjennomført ved hjelp av en Lightweight Video Profiling Platform (LVPP). Dette instrumentet samlet inn informasjon om den vertikale fordelingen til maneten, antall og størrelsen på hvert individ.

Beitstadfjorden har en sidearm med to grunnere bassenger (Verrasundet og Verrabotn). Den stående populasjonen i Verrabotn besto av en større andel store maneter (coronal diameter (CD) >121 mm) enn i Verrasundet og Beitstadfjorden. De fleste individene ved de sistnevnte lokalitetene var ganske små, med CD ≤ 40 mm. Imidlertid; store maneter utgjorde mesteparten av den totale biomassen ved hver stasjon.

Resultatene i denne studien tyder på at totalbestanden av *P. periphylla* i indre Trondheimsfjord er noe lavere enn estimatet fra 2007. Det forekom store mengder små individer av varierende størrelse, noe som tyder på at vellykket rekruttering fremdeles finner sted.

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1. Introduction

1.1. Ecology of *Periphylla periphylla*

Gelatinous plankton is causing a variety of problems worldwide. Large abundances of jellyfish are known to clog and damage fishing gear, often spoiling the catches. Aquaculture and hydroelectric power plants operations are frequently hindered by jellyfish clogging problems as well, and mass occurrences of jellyfish are affecting the beach life of people many places in the world (Purcell *et al*., 2007).

In recent years the concerns have grown about the increasing *Periphylla periphylla* abundance in several Norwegian fjords, including Trondheimsfjorden, the study area of this thesis. As early as in 1970, however, this jellyfish was reported in large numbers in Lurefjorden near Bergen. Later, dense populations have been reported successively in fjords northwards on the coast, e.g. in Sognefjorden and Halsafjorden (Fosså, 1992), where several studies have been conducted, reporting on the species' impact on the local environment.

P. periphylla is a cnidarian, belonging to the class *Scyphozoa*, order *Coronatae* and the family *Periphyllidae* (Russell, 1970). It has a dome-shaped umbrella, consisting of a thick jelly-like substance called *mesoglea*, with twelve tentacles (three tentacles in four groups) and four *rhopalia* (sensory structures) situated around the umbrella. The shape of the umbrella changes as the individual grows, being more flat at early stages and gaining more height as it reaches its mature stage.

P. periphylla is present in all of the world's oceans, except from the Arctic (Russell, 1970). It has been registered at depths of 2700 m, but is more likely to dwell at 400-1100 m and even shallower at higher latitudes.

This cnidarian has a holopelagic lifecycle (Fosså, 1992), lacking the benthic stages (*planula* and *polyp*) of other jellies (Jarms *et al.,* 1999). It is the only known coronate scyphozoan with a direct development, and has a total of fourteen defined morphological stages (Jarms *et al.,* 2002). Figure 1.1.1 illustrates different development stages of *P. periphylla*. The eggs of *P. periphylla* are some of the largest found within the phylum *Cnidaria*, and this jellyfish is assumed to reach sexual maturity with a coronal diameter (CD) of at least 5 cm (Tiemann and Jarms, 2009). Under stable conditions, it is suggested that this cnidarian spawn continuously regardless of season (Jarms *et al.,* 1999; Youngbluth and Båmstedt, 2001). Except for its early stages, this jelly has few if any important natural predators in Norwegian waters. Apparently, its low death rate, planktonic spreading, high fecundity and long life expectancy enable the establishing and maintenance of large local stocks in Norwegian fjords.

P. periphylla has a bright red hue, derived from the pigment protoporphyrin, a pigment which is present in several bathypelagic species (Herring, 1972; Bonnett *et al.*, 1979). Most of the coloration from the pigment in the jellyfish lies within the wall of the stomach and in the *manubrium*. Figure 1.1.2 illustrate the different internal structures of a Scyphozoan with similar construction; *Aurelia aurita*. Porphyrin is photoreactive, and in contact with light it will transform into compounds highly toxic to the organism, creating damage to the tissue (Arai 1997).

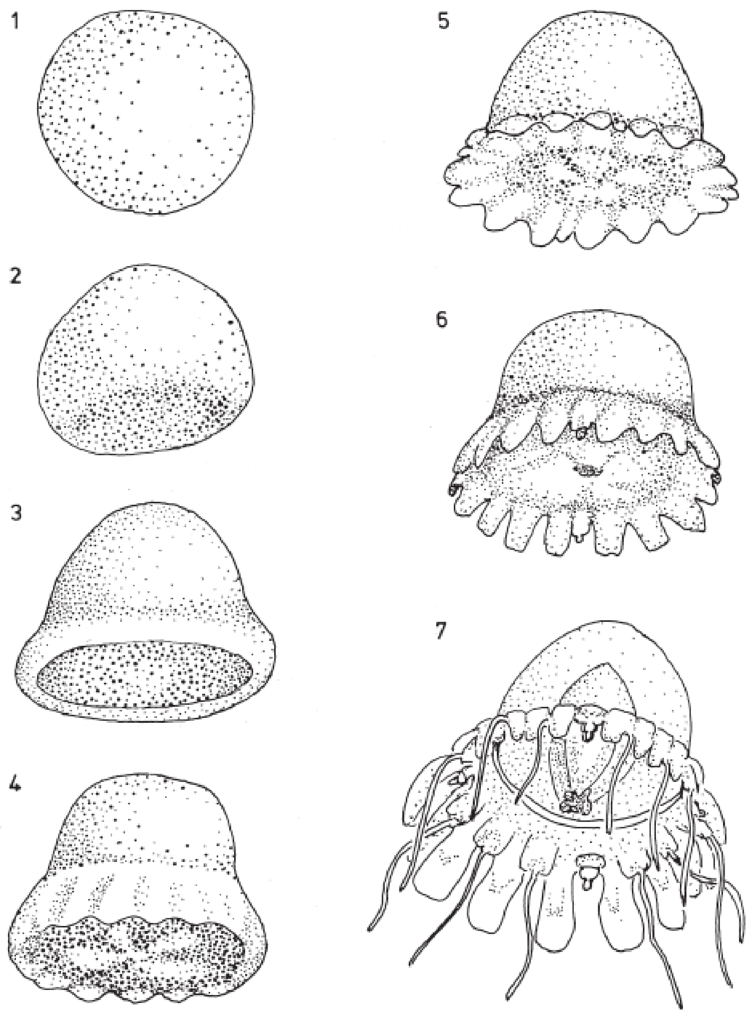


Figure 1.1.1: Seven morphological development stages of *P. periphylla* (Jarms *et al.*, 1999).

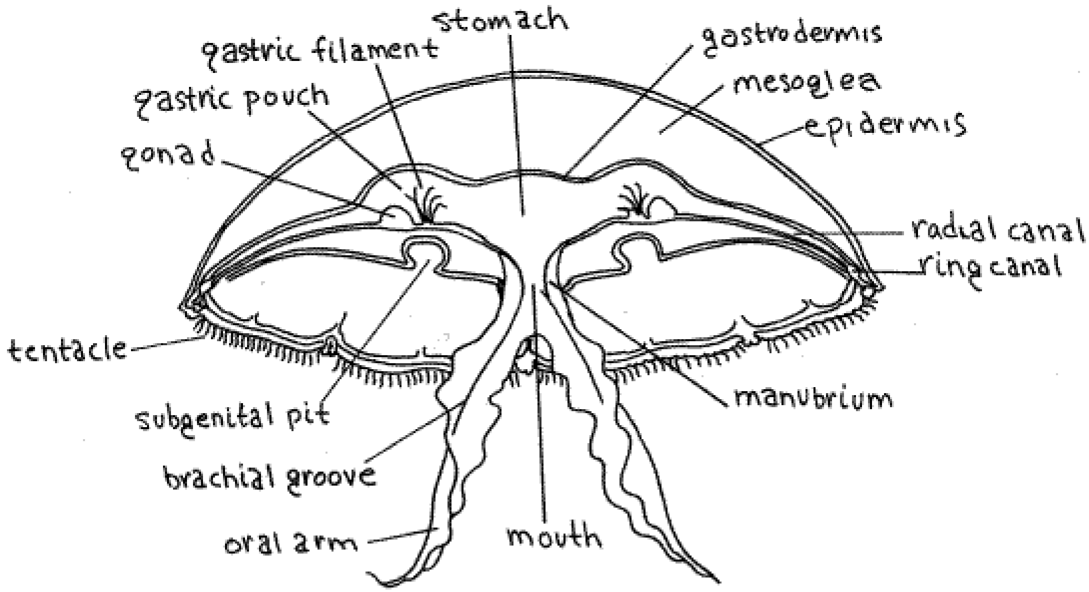


Figure 1.1.2: Internal structures of a Scyphozoan; *Aurelia aurita* (Fox, 2001).

Several studies show that *P. periphylla* participate in diel vertical migration (DVM) (Youngbluth and Båmstedt, 2001; Kaartvedt *et al.,* 2007). DVM imply two migrations in the water column in the cause of a day, one up to the surface at dusk and one down to the deep at dawn.

Vertical migration is often executed by aquatic organisms in larger groups, for different reasons and with different patterns (Pearre, 2003). Several organisms perform vertical migration to pursue their prey, which travel up to the surface and down again after feeding, while others might follow this pattern to prevent getting eaten. *P. periphylla* is known to prey on copepods (especially *Calanus* spp), chaetnoghnats, ostracodes and the krill *Meganyctiphanges norvegica* (Sørnes *et al.,* 2007), and several of them tend to perform DVM, a possible explanation why the jellyfish does the same.

P. periphylla have been observed fleeing when exposed to light (Youngbluth and Båmstedt, 2001). It is a tactile predator (Klevjer *et al.*, 2009), and is not dependent on light when hunting. Lack of light has even been suggested being an advantage for the jellyfish compared to other competitive species in certain locations (Eiane *et al.,* 2003). The jellyfish are known to compete with species from the family *Gadidae*, which are known to predate on *P. periphylla* (Arai, 1988), and cannibalism might also occur (Ulf Båmstedt, personal comment). Gelatinous plankton may impact fish stocks in several ways; by consuming zooplankton and hence limiting the food availability, or directly predate fish eggs and juveniles (Purcell *et al.*, 2007).

Feeding and light exposure seem to be the main cause for gross DVM in *P. periphylla*, but the hunger level, maturation, and size of each individual might explain why individuals tend to follow an asynchronous pattern in their vertical migration (Pearre, 2003).

1.2. Location

Trondheimsfjorden lies between 63°30’ and 64° N, and 9 °30’ and 11°30’ E (Wendelbo, 1970). It measures 126 km in length, from Agdenes to Hjellebotnen near Malm, and lies in both Sør- and Nord-Trøndelag County. It is the third longest and seventh deepest fjord system in Norway, and is naturally divided into three main basins, divided by three sills (Jacobson, 1983; Sakshaug and Sneli, 2000). From the outermost to the innermost part of the fjord, the basins are called Ytterfjorden, Midtfjorden and Innerfjorden. Ytterfjorden lies between the Agdenes sill and the Tautra sill, and is the deepest basin in Trondheimsfjorden with 617 m at its deepest. Midtfjorden lies between Tautra and the Skarnsundet sill and is 425 m at its deepest, while Innerfjorden, also called Beitstadsfjorden, is located inwards of Skarnsundet and reaches a depth of 270 m. Figure 1.2.1 shows a map of Trondheimsfjorden, and table 1.2.1 shows data on volume, area and average depth at different locations in Trondheimsfjorden.

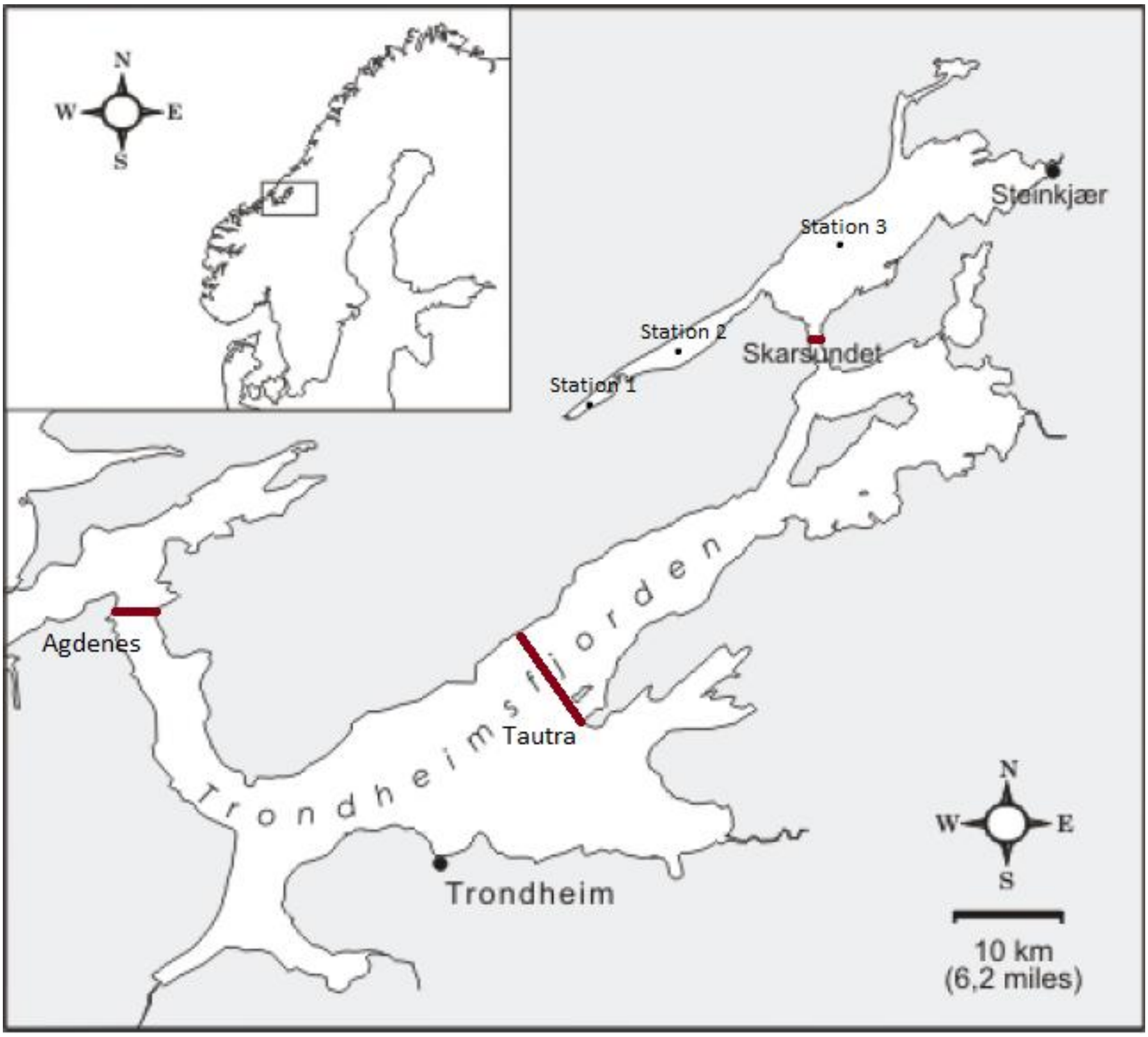


Figure 1.2.1: Map of Trondheimsfjorden. Station 1, 2 and 3 indicate Verrabotn, Verrasundet and the main basin of Beitstadfjorden, respectively. Sills at Agdenes, Tautra and Skarnsundet are indicated by red bars (Sneli, 2003).

Table 1.2.1: Volume (km³), area (km²) and average depth (m) of Trondheimsfjorden (Jacobson, 1983).

	Volume (km³)	Area (km²)	Average depth (m)
Ytterfjorden	158	746	212
Midtfjorden	57	441	130
Beistadfjorden	20	233	86
Total Trondheimsfjorden	235	1420	165

The Agdenes sill is relatively deep, 330 m, enabling water to be exchanged at a high rate. The Tautra sill is shallower, reaching 100 m at its deepest, and the Skarsundet sill is 140 m. The depth of the sills plays an important part of the exchange rate and the mixing rate of water in the fjord (Aksnes *et al.,* 1989). Shallow sills, in particular, have a much higher impact on the water exchange than deeper ones. The advective layer is often limited to the sill depth (Sørnes *et al*., 2007).

Several forces affect the mixing of water in Trondheimsfjorden; tidal waves, wind generated waves and water from the local rivers are some of the contributors (Sakshaug and Sneli, 2000). Mixing of sea water relies on differences in the density gradients, mainly created by difference in salinity and temperature. In fjords the salinity is the main force in density gradients, while in the open seas, temperature has the biggest influence. The difference in density creates a pycnocline; a layer which divides bodies of water with different densities. On average, the bottom water in Trondheimsfjorden gets exchanged twice a year (Jacobson and Sneli, 1984), while the surface layer has a higher exchange rate mostly due to estuarine circulation. Estuarine circulation magnitude depends largely on seasonal changes that affect the input of fresh water.

1.3. Objectives

The main objective of this thesis was to provide an updated biomass estimate of the local *P. periphylla* population in Beitstadfjorden, and compare it to earlier estimates. Beitstadfjorden, the main basin, has a side-arm with two shallower basins; Verrabotn and Verrasundet. The sampling sites in these three basins were named Station 1, 2 and 3, (Verrabotn, Verrasundet and Beitstadfjorden, respectively) (Fig. 1.2.1). It has been assumed that the first population of the jellyfish in Trondheimsfjorden settled in Beitstadfjorden, and later dispersed into Verrasundet and Verrabotn. The population biomass of this jellyfish was estimated in October 2007 to be at least 20.000 tons altogether on these three locations (Hetland, 2008).

Together with the biomass estimate, the individual size distribution would give valuable information concerning a continuous recruitment, and thus in turn to assess whether or not the jellyfish population is sustainable in this local environment. The main cruise took place from 28th of March to 1st of April in 2011. Due the lack of sufficient data from this trip, additional data from a previous cruise in April 2010 were added.

2. Methods

2.1. Sampling

2.1.1. Vessel

The research vessel R/V "Gunnerus" was used for sampling throughout the study. The vessel is owned by the Norwegian University of Science and Technology (NTNU), and measures 31.25 m (Loa) and 9.90 m (B), and has a dead weight of 107 tons (NTNU, 2012).

The Olex® map system, installed in R/V “Gunnerus”, was used to map and visualize the seafloor. Also, the total water volume on sampling Stations 1, 2, and 3 in Beitstadfjorden was calculated with this software.

2.1.2. ROV

To get an overview of the seafloor topography and condition in Verrabotn, NTNU’s remotely operated vehicle (ROV) "Minerva" was used. The ROV hovered, close to the seabed, a several hundred meters long transect. The video images were transmitted to a control room onboard in real time, allowing the pilot to steer the ROV and focus on interesting features. Figure 2.1.1 shows some of the sampling equipment, including the ROV.

2.1.3. Grab

A Van Veen grab was used for sampling benthos in Verrabotn. Several samples were collected at 50-60m depth at different locations, and filtered through a sieve. The remaining benthos animals, mainly *polychaeta*, were collected onboard and later classified by Dr. Torkild Bakken (Museum of Natural History and Archaeology, NTNU).

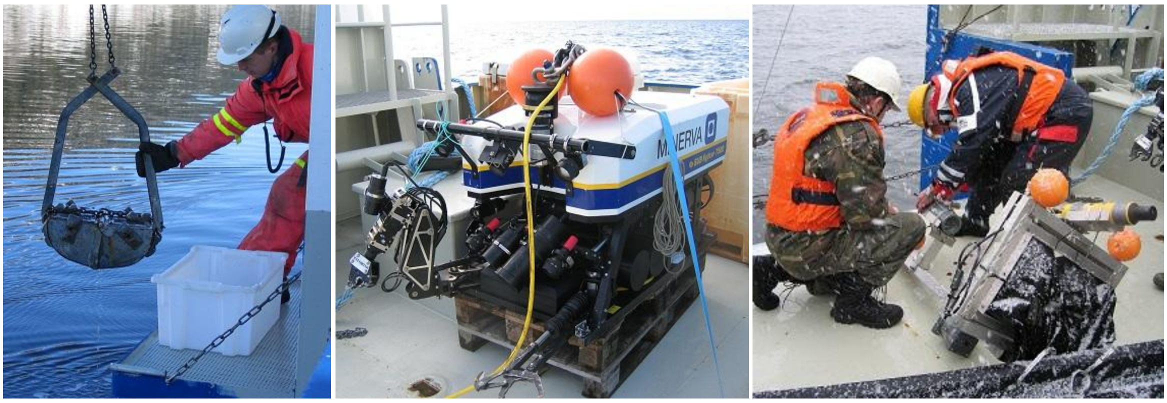


Figure 2.1.1: Different sampling gear used to collect data. The picture on the left shows the Van Veen grab with a sample of the seabed, the picture in the middle shows the ROV "Minerva", and the picture to the right shows the LVPP used in the dives from April 2011. Photos: Hilde Solheim.

2.1.4. Trawl

It has been hypothesized that the dense *P. periphylla* population may have negative impacts on the local fish stocks in Trondheimsfjorden, particularly in Beitstadfjorden (Jarle Mork, personal comment). Local fishermen in this area have reported frequent encounters with this gelatinous plankton, even net gear catches consisting exclusively of the jellyfish. During the cruise in March 2011 two hauls with a shrimp trawl (inner lining of fine mesh net, stretched mesh 36 mm) were performed to get a visual impression of the density of *P. periphylla* there. The jellyfish from the haul were not collected, but evidence for amphipod parasitic attacks on weakened specimens was recorded and documented. The first haul was conducted March 29th in Beitstadfjorden, and the second in Verrabotn (the shallowest location), on 31st of March.

2.1.5. LVPP

A Lightweight Video Profiling Platform (LVPP), designed by Ulf Båmstedt, was used to record the vertical distribution of *P. periphylla* in the water. The LVPP is constructed with a frame, allowing a measurement of filtered volume, a video camera and a SAIV CTD (conductivity, temperature and depth) instrument attached. The LVPP is towed similar to a trawl, creating a depth profile of records throughout the dive.

There are several versions of the LVPP, and three different types were used during the different cruises. One of the dives done in April 2010 and the dives from March 2011 utilized a collecting device with the LVPP (two different types), concentrating individuals into a narrow opening towards the camera. The LVPP used in the other dives was not equipped with this collecting device.

The measurement of the LVPP (frame) used in March 2011 was 132 cm x 252 cm, and the frame used in April 2010, measured 105 cm x 150 cm.

The profiles of the dives were recorded with a video camera, and were analyzed frame by frame using various computer software. The best functioning analyzing method was the use of the video player of Sony's PlayStation 3. The video was frozen each time a medusae appeared, creating an image which allowed manual measuring the coronal diameter (CD) of the medusae. The CD was measured across the coronal groove, and adjusted to actual size utilizing the size relation between CD and frame measurement. Due to poor resolution of the video image, and the variable spatial coordination of the medusae, the accuracy of the measurements was not optimal. The medusae were divided into size classes raging from ≤ 20 mm to >121 mm in CD, with 20 mm intervals. Figure 2.1.2 shows an individual *P. periphylla* as a drawing and as a photo.

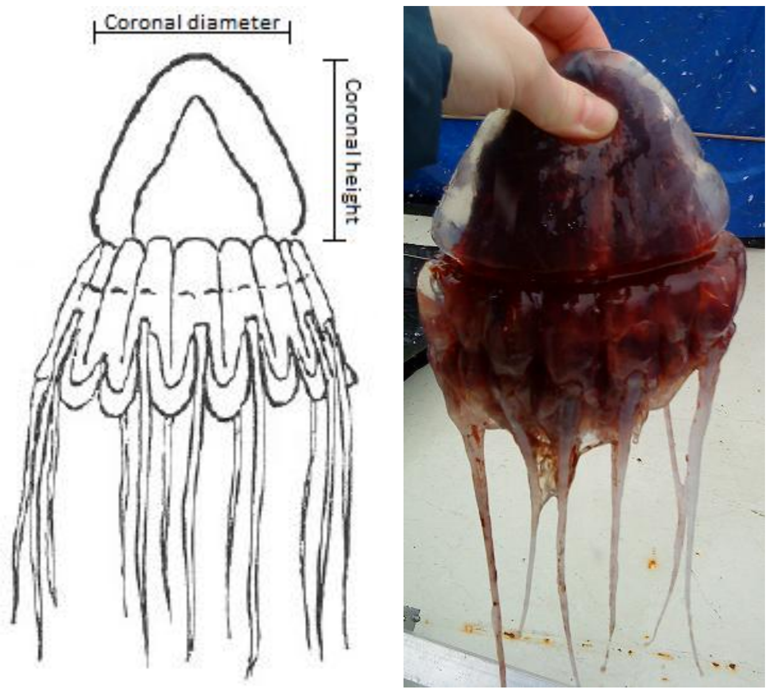


Figure 2.1.2: Individual *P. periphylla*. The drawing to the left is from Russell (1970). Photo to the right by Hilde Solheim.

The ROV transcend, the LVPP depth profiles, the grab sampling and the hauls are all parts of a project monitoring the local *P. periphylla* population in Verrabotn (Station 1). The data collected by these different methods were sampled approximately at the same location, creating a holistic image of the jellyfish population.

2.2. Calculations

To calculate total volume filtered by the LVPP, several equations were used. The distance traveled by the LVPP was calculated by the equation:

$$k_z = t_z \text{ x } \varsigma \qquad (1)$$

k_z is the distance (m) traveled by the LVPP for interval z, t_z is the time (s) spent in interval z, and ς is the average speed (m/s) of the vessel. During the dives, the average speed was set to be from 1 to 1.5 knots, depending on the dive. Each depth interval was set to be 10 m.

The volume filtered by the LVPP was calculated with the formula:

$$V_z = k_z \text{ x } A_{LVPP} \qquad (2)$$

where V_z is the volume (m^3) filtered for interval z and A_{LVPP} was the area of the LVPP (m^2).

Knowing the CD of the jellyfish it is possible to calculate the wet weight (WW). Both CD and coronal height (CH) correlate with the actual WW. However, there seems to be a better linear correlation between the CD and the weight than between the CH and weight (Youngbluth and Båmstedt, 2001). The equation for the linear regression is:

$$lnWW = -0.6702 + (2.7311 \text{ x } lnCD) \qquad (3)$$

This method has previously been used successfully to estimate the population biomass of *P. periphylla* in Trondheimsfjorden (Hetland, 2008), and was thus chosen in this study for comparison purposes.

An example of the method used to calculate the total biomass is given in the appendix (Table A to C show the data from dive [*a2*]).

3. Results

3.1. Hydrography

Due to technical failure with the SAIV CTD instrument no data was collected with this equipment.

The water volume at the three stations in Beitstadfjorden, was calculated by Olex® to be 0.14 km^3 in Verrabotn, 1.18 km^3 in Verrasundet and 19.95 km^3 in the main basin in Beitstadfjorden, with a total water volume of 21.27 km^3.

However, the Olex® did not calculate volumes of different layers of water; hence data from Hetland (2008) were used. Hetland estimated the total volume to be 142.1 $x10^6$ m^3 at Verrabotn; 66.5 $x10^6$ m^3 below 20 m and 20.1 $x10^6$ m^3 below 40 m. At Verrasundet the total estimate of water volume was 1170 $x10^6$ m^3, with 286.2 $x10^6$ m^3 below 60 m, 118.6 $x10^6$ m^3 below 80 m and 21 $x10^6$ m^3 below 100 m. At Beitstadfjorden the total volume was estimated to be 14 694 $x10^6$ m^3; 4 930 $x10^6$ m^3 below 100 m and 140 $x10^6$ m^3 below 200 m.

3.2. ROV

The recordings from the ROV "Minerva" showed many decaying *P. periphylla* lying on the seafloor (Fig. 3.2.1). They were all relatively large specimens. The dying process seemed to start with a whitening of the tentacle tips, thereafter of the entire tentacle which ultimately fell off. Dying and dead specimens were attacked by an amphipod, which species identity could not be determined since they did not follow with the jelly onto the deck in the bottom trawl.

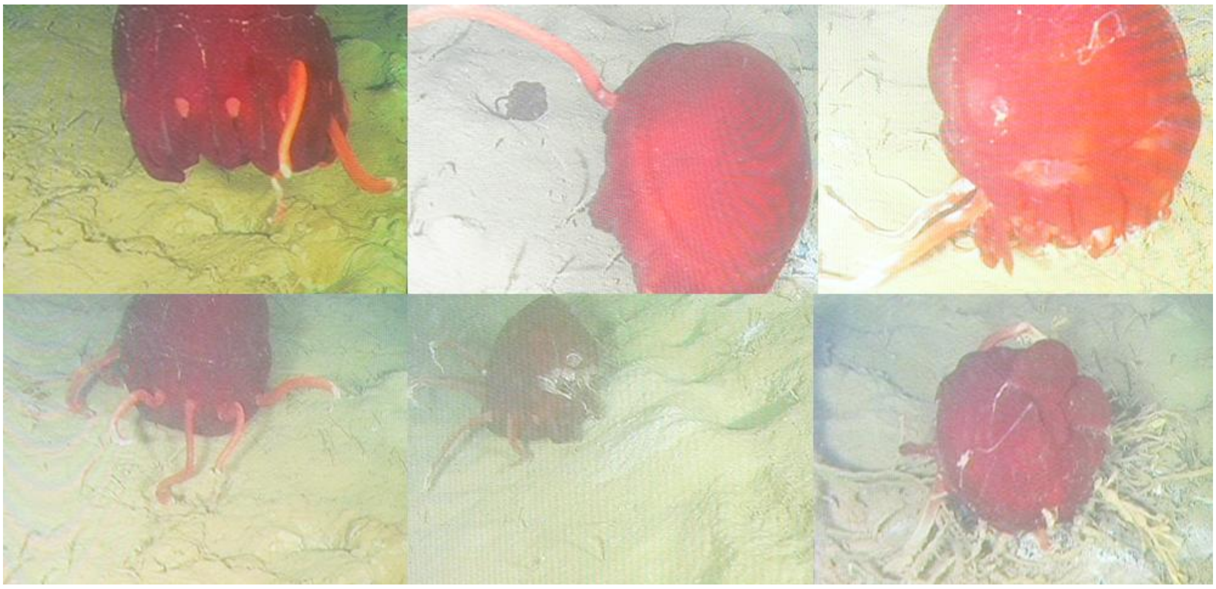


Figure 3.2.1: Pictures taken of the monitor displaying the images from the ROV, showing several decaying *P. periphylla* lying on the seabed. Photos: Jarle Mork.

3.3. Grab

Three samples of the benthos were collected with the Van Veen grab in and near the deepest part of the seabed on Station 1. The findings are summarized in Table 3.3.1.

Sample 1 and sample 2 were collected at 60 m, at N 63°49.409', E 10°38.992'. Sample 3 was collected at 61 m, at N 63°49.355', E 10°38.922'. Species were identified by Dr. Torkild Bakken (Museum of Natural History and Archaeology, NTNU).

Table 3.3.1: *Polychaeta* species identified in the grab samples.

	Number of individuals *Polychaeta*		
Species	Sample 1	Sample 2	Sample 3
Terebellides stroemi	1		
Phylo norvegica	3	7	1
Scalibregma inflatum	1		6
Nephtys hombergi	1		
Pectinaria auricoma	1	1	1
Paramphinome jeffreysi			2
Goniada maculata			3
Oweniidae indet.		1	
Capitellidae indet.			4
Polynoidae indet.			1

3.4. Trawl

Two hauls with a bottom trawl were executed, the first on March 29th 2011 in Beitstadfjorden and the other on March 31st 2011 in Verrabotn. In the first mentioned haul *P. periphylla* composed most of the catch, but in the second a considerable number of cod (*Gadus morhua*) was caught together with *P. periphylla* (Fig. 3.4.1 and 3.4.2).

Figure 3.4.1: Size distribution of *P. periphylla* collected by trawl. Photo: Hilde Solheim.

Figure 3.4.2: Picture to the left shows the catch from Verrabotn, picture to the right shows the clean up after haul. Photos: Hilde Solheim.

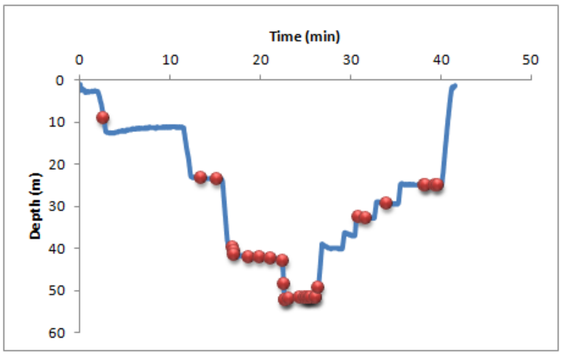
3.5. LVPP

Table 3.5.1 shows the data from the dives executed on the different locations in Beitstadfjorden. The data sampled by LVPP in Verrabotn, Verrasundet and Beitstadfjorden, Station 1, 2 and 3, respectively. Dive [*a1*] and [*a2*] were carried out in Verrabotn, dive [*b1*] in Verrasundet, and dive [*c1*] in Beitstadfjorden, all in April 2010. Dive [*c2*] was carried out in Beitstadfjorden, dive [*b2*] and [*a3*] in Verrasundet and Verrabotn respectively, all sampling done in March 2011.

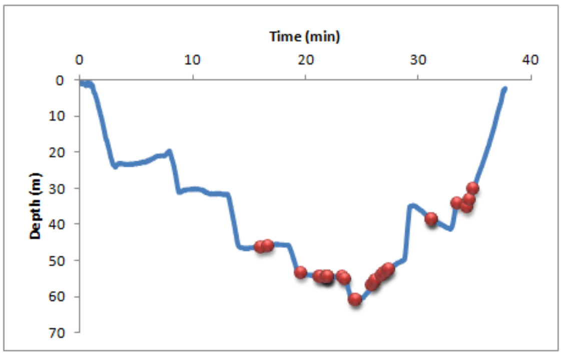
Table 3.5.1: Data from all seven dives with the LVPP. Coordinates for some of the dives were not available.

Dive	Date	Time start	Time stop	Start coordinates		Max depth (m)
[*a1*]	20.04.2010	09:55:00	10:36:00	63°48.829’ N	10°37.542’ Ø	52
[*a2*]	20.04.2010	14:42:00	15:20:00	63°55.640’ N	11°04.162’ Ø	61
[*b1*]	20.04.2010	16:14:00	17:13:00	-	-	108
[c1]	22.04.2010	17:23:00	18:38:00	63°57.901’ N	11°05.931’ Ø	215
[*c2*]	28.03.2011	16:52:50	17:30:20	63°56.060’ N	11°04.490’ Ø	211
[*b2*]	29.03.2011	11:10:20	11:40:25	-	-	95
[*a3*]	29.03.2011	16:33:00	16:55:00	-	-	48

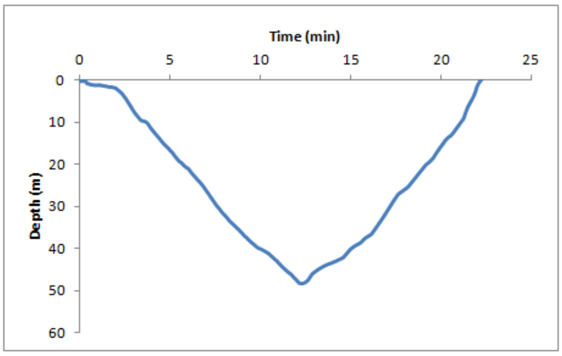
Figure 3.5.1 shows the distance travelled by the LVPP, and individual *P. periphylla* observed along the distance. The traveled distance of the dives were calculated by time data collected by the CTD connected to the LVPP. In general the graphs shows that the jellyfish tend to keep at the deepest part of the dive, with an occasional jellyfish in shallower parts. Figure 3.5.2 shows an individual *P. periphylla* detected along one of the dives.



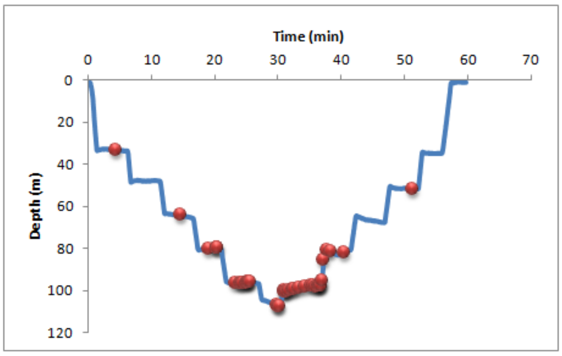
a) Station 1, [*a1*], n=30



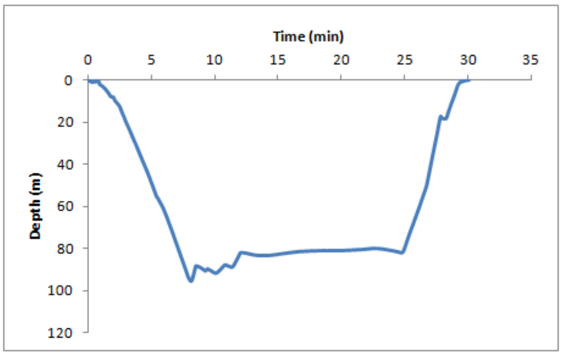
b) Station 1, [*a2*], n=28



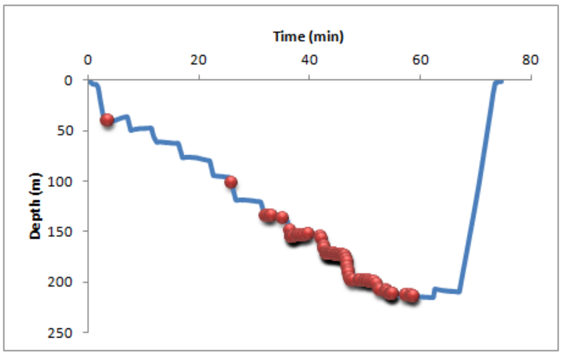
c) Station 1, [*a3*], n=0



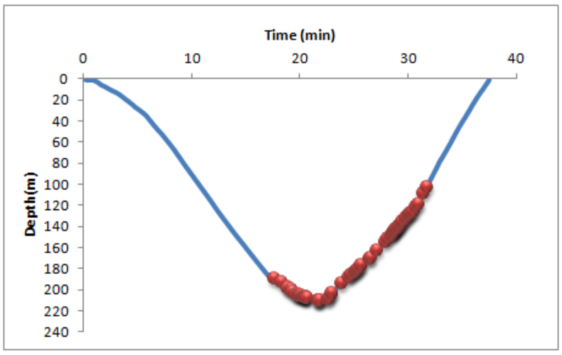
d) Station 2, [*b1*], n=41



e) Station 2, [*b2*], n=0



f) Station 3, [*c1*], n=107



g) Station 3, [*c2*], n=74

Figure 3.5.1: Pictures a) to g) show the depth profile of each dive executed. The blue line indicates the path of the LVPP, and the red dots indicate individual *P. periphylla* along the haul. In dive [*a3*] and [*b2*] no jellyfish were observed.

Figure 3.5.2: *P. periphylla in situ*. The photo is captured from the video recordings of the LVPP.

Table 3.5.2 shows collected data from the dives where *P. periphylla* were detected. Volume filtered at each dive was calculated by formula (1) and (2). The biomass was calculated by formula (3), where the CD of each individual *P. periphylla* was measured. The total biomass at each location (station) was estimated by dividing the biomass of the dive by the total volume filtered during the dive, and then multiplying with the total water volume in each fjord basin. An example is given in the Appendix (Table A-C).

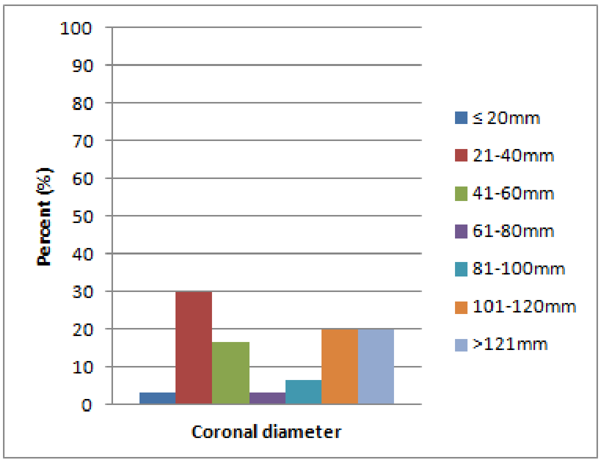
Table 3.5.2: Collected data from the different dives. The date include estimated biomass (g), number of *P. periphylla* and water volume (m³) filtered by the LVPP.

Dive	Duration (min)	Number *P.periphylla*	Volume filtered (m³)	Biomass (g)	Average WW (g)	Average CD (mm)
[*a1*]	42	30	2528	7740	258	76
[*a2*]	38	28	1504	7293	260	57
[*b1*]	60	41	3639	5054	123	49
[*c1*]	75	107	4566	4846	45	31
[*c2*]	38	74	3854	6711	91	36

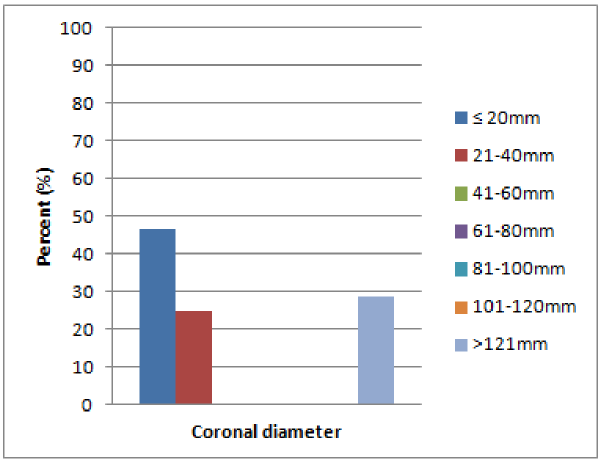
The biomass at dive [*a1*] was calculated to be 342 198 kg, and the biomass at [*a2*] was calculated to 316 666 kg, giving an average of 329 432 kg at Station 1, Verrabotn. At dive [*b1*], Station 2 in Verrasundet, the biomass was calculated to be 2 196 352 kg. The biomass at dive [*c1*] was calculated to be 8 788 223 kg, and dive [*c2*] to be 9 752 549 kg, both at Station 3 in Beitstadfjorden.

Figure 3.5.3 shows the distribution of the size classes in percent of *P. periphylla* at the different dives. In dive [*a1*], taken in Verrabotn, all size groups were observed, but with relatively few small individuals compared with the other dives. At dive [*a2*], taken at the same Station, only small individuals (CD ≤ 40 mm) and large individuals (CD > 121 mm) were observed. Dive [*b1*], taken in Verrasundet, shows a larger proportion of smaller individuals (CD ≤ 40mm) and relatively few individuals with CD from 41 mm to 100 mm. In dive [*c1*] most of the observed *P. periphylla* had CD ≤ 40 mm, mainly from 21 to 40 mm. In dive [*c2*] half of the individuals were up to 20 mm in CD; one third was from 21 to 40 mm, with few of the larger individuals.

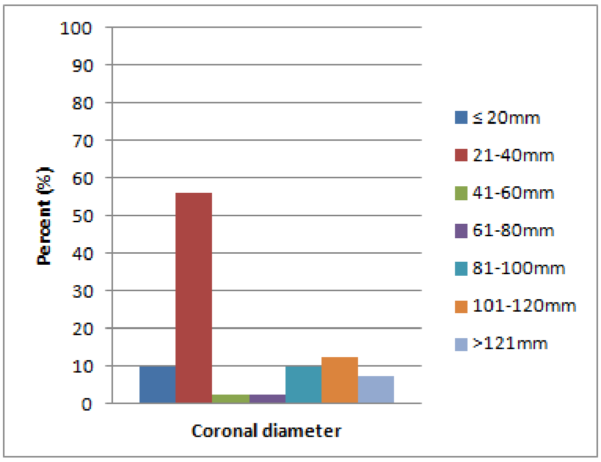
The graphs in figure 3.5.4 show the size distribution of the total percentage of the biomass. All the graphs, from a) to e) in figure 3.5.4, indicate that the majority of the WW of the jellyfish is in the size class where the CD is 121 mm or larger. Dive [*a1*] shows that most of the biomass was made up by *P. periphylla* with CD larger than 121 mm. In dive [*a2*] 99 percent of the biomass is composed of individuals with CD larger than 121 mm. About half of the biomass in dive [*b1*] consisted of individuals with CD larger than 121 mm, with a portion of individuals with CD raging from 81-120 mm. The biomass in dive [*c1*] mainly consisted of *P. periphylla* with CD larger than 101mm, but about 10 percent of the biomass is made up of jellyfish with CD from 21 to 40 mm. In dive [*c2*] 80 percent of the biomass is made up by individuals with CD larger than 121 mm.



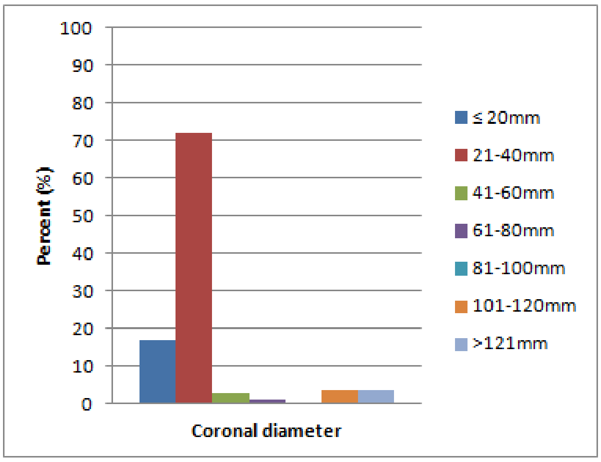
a) Station 1, [*a1*], n=30



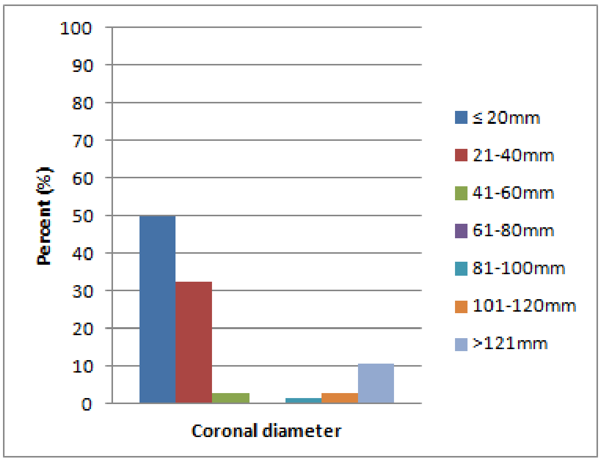
b) Station 1, [*a2*], n=28



c) Station 2, [*b1*], n=41

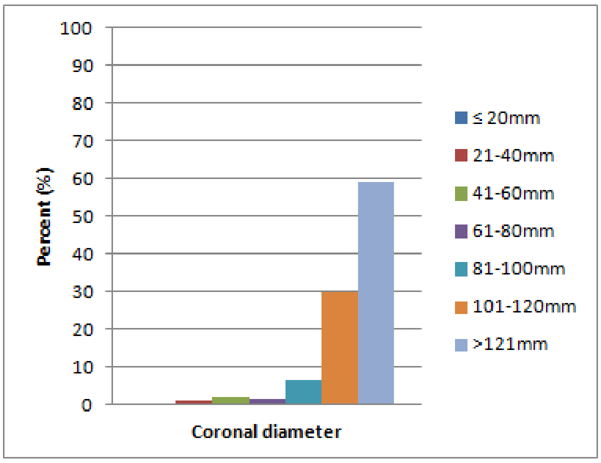


d) Station 3, [*c1*], n=107

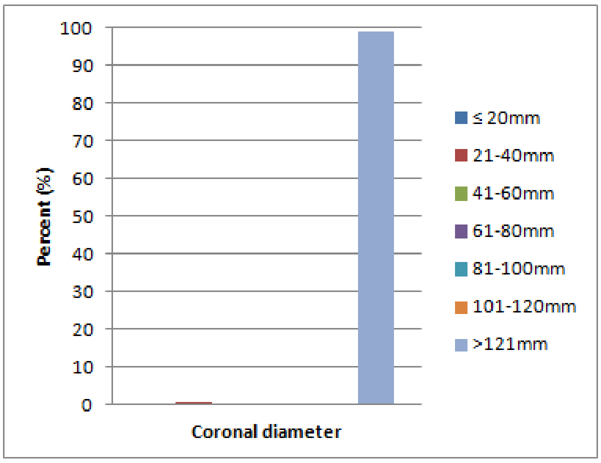


e) Station 3, [*c2*], n=74

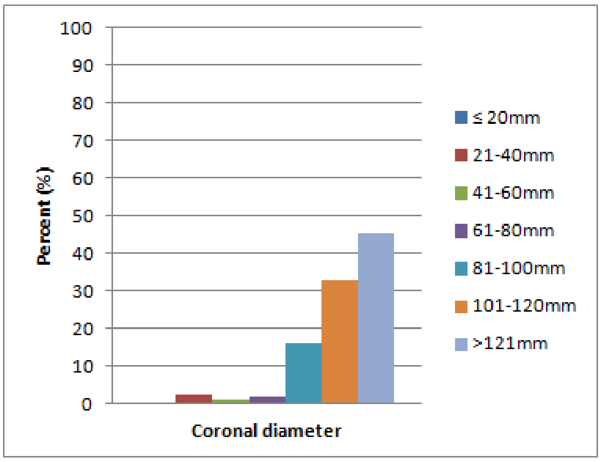
Figure 3.5.3: Graphs a) to e) show the percentage of the different size classes at each dive.



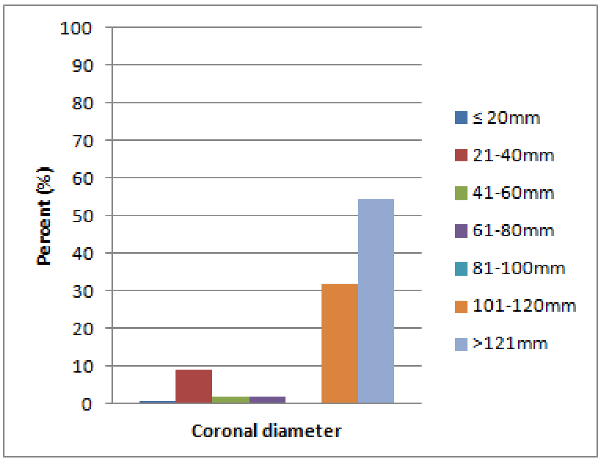
a) Station 1, [*a1*], n=30



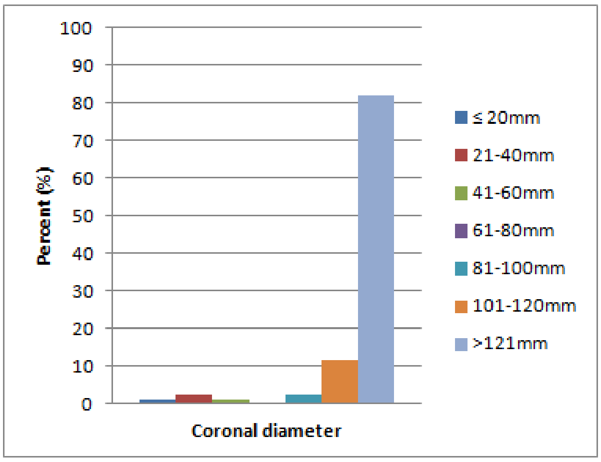
b) Station 1, [*a2*], n=28



c) Station 2, [*b1*], n=41



d) Station 3, [*c1*], n=107

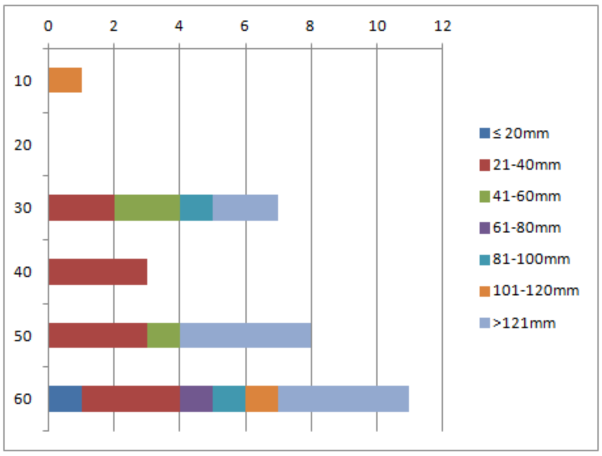


e) Station 3, [*c2*], n=74

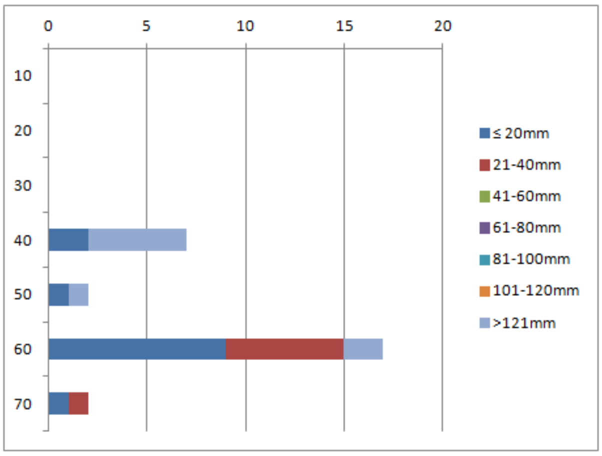
Figure 3.5.4: Graphs a) to e) show the dives executed by LVPP, and the percentage of the biomass at each size class for every dive.

Figure 3.5.5 shows the size distribution of *P. periphylla* at the different depth intervals. Dive [*a1*] shows that most of the *P. periphylla* is found from 30 m and further down to the bottom. The size classes detected are evenly distributed between the different depth intervals, with most *P. periphylla* in the deepest interval. In dive [*a2*] the jellyfish were observed from 40 m and downwards, and the detected size classes were fairly evenly distributed. The densest population was found at 60 m. Dive [*b1*] shows that the majority of the *P. periphylla* tended to dwell at 80 m and below. The smallest individuals (CD ≤ 40 mm) were found in the deepest parts, at 90 m and below, while the occasional *P. periphylla* above 90 m tended to be larger (CD > 40 mm). The densest layer of *P.periphylla* was found at 100 m. Dive [*c1*] shows that the main part of the jellyfish tended to stay in the deep, at 140 m and below. The size classes seem to be evenly distributed, and the densest layer was detected at 180 m. Dive [*c2*] shows *P. periphylla* from 100 m and deeper. The size classes seem to be evenly distributed, and the densest layer was found at 200 m.

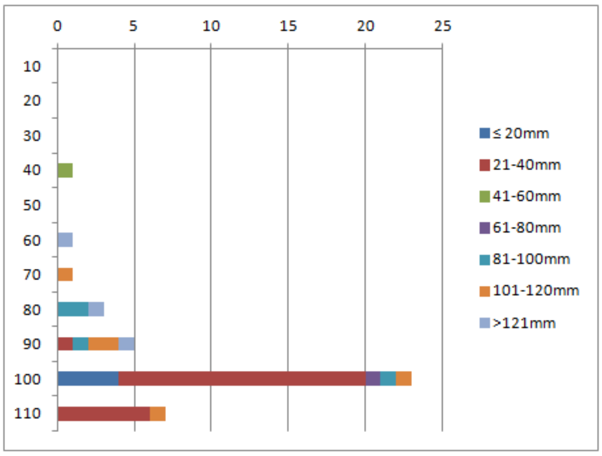
Figure 3.5.6 shows the biomass per volume at the different depths throughout the dives. Pictures a) to e) illustrate the density of the jellyfish based on the biomass of the detected *P. periphylla* and filtered water volume at each 10 m depth interval. Dive [*a1*] shows that the densest biomass is found at 60 m, while the densest *P. periphylla* biomass is found at 40 m in dive [*a2*]. In [*b1*] the biomass was densest at 80 m; this dive had the densest biomass of all the dives with ~1.9 kg 100 m^{-3}. Dive [*c1*] shows that the densest part of the jellyfish biomass was at 110 m, and the densest biomass in dive [*c2*] was at 220 m.



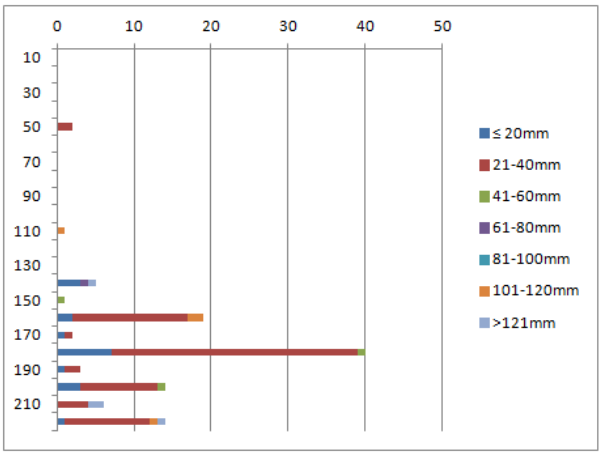
a) Station 1, [*a1*], n=30



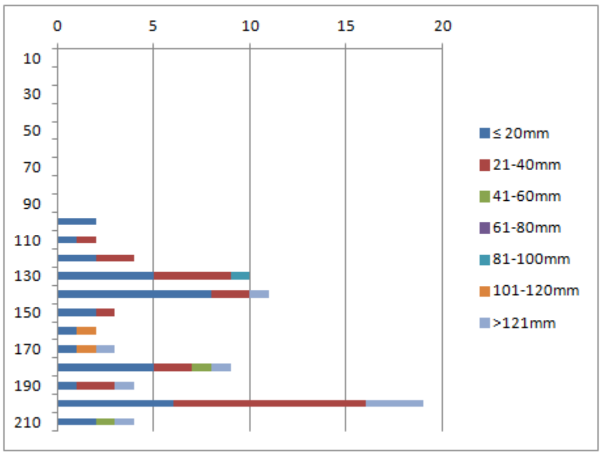
b) Station 1, [*a2*], n=28



c) Station 2, [*b1*], n=41

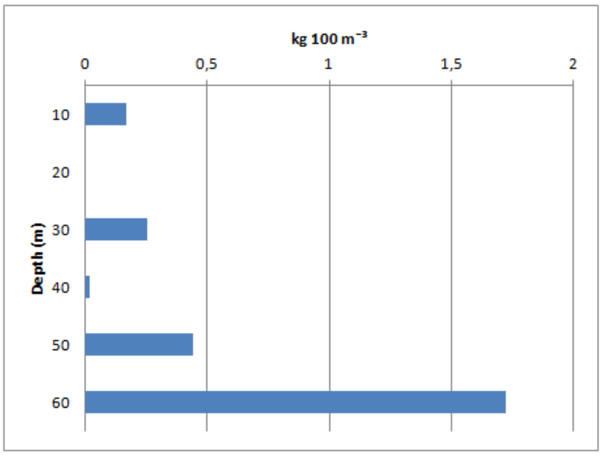


d) Station 3, [*c1*], n=107

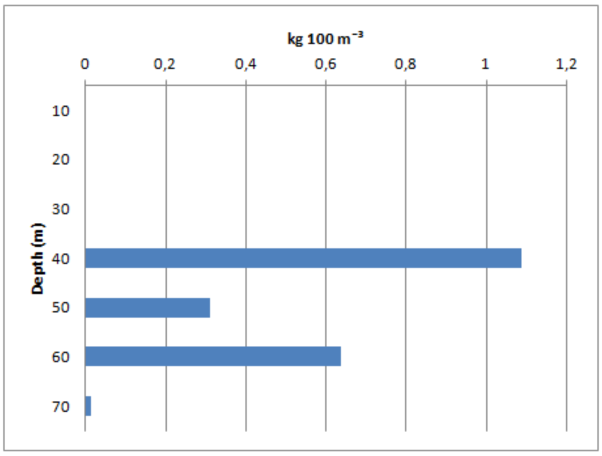


e) Station 3, [*c2*], n=74

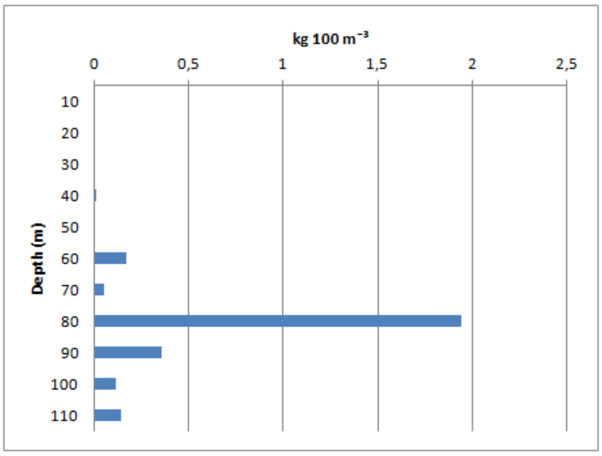
Figure 3.5.5: Number and size (CD) of *P. periphylla* at each 10 m depth interval at each dive.



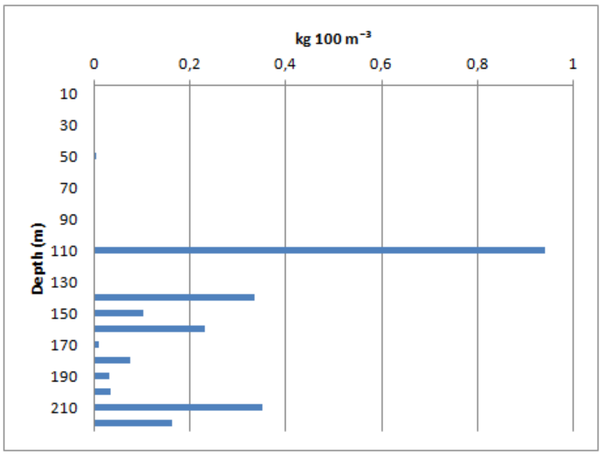
a) Station 1, [*a1*], n=30



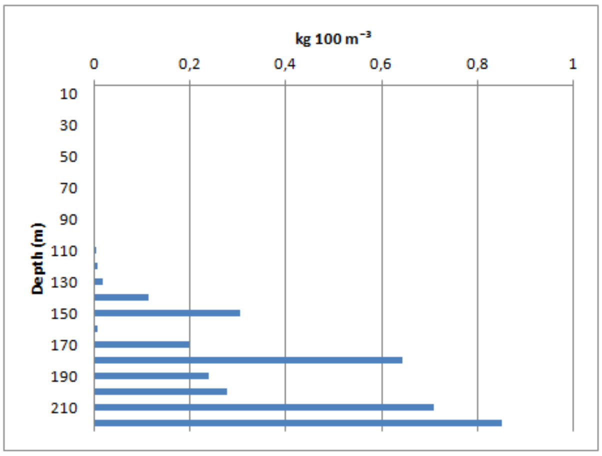
b) Station 1, [*a2*], n=28



c) Station 2, [*b1*], n=41



d) Station 3, [*c1*], n=107



e) Station 3, [*c2*], n=74

Figure 3.5.6: Biomass per water volume (kg 100 m^{-3}) of *P. periphylla* at each 10 m depth interval at each dive.

4. Discussion

4.1. Trawl

The trawl catches showed relatively dense aggregations of *P. periphylla* in both Beitstadfjorden and Verrabotn. The CPUE (Catch Per Unit of Effort) in the present study indicates a reduction of the jellyfish stock at both locations compared to hauls from previous years (Jarle Mork, personal comment), which is supported by the recording from the ROV.

4.2. ROV and grab

The recording from the ROV in March 2011 showed several decaying *P. periphylla* on the seabed. This is the first time this phenomenon has been observed in Trondheimsfjorden, and it is uncertain why it occurred. Other jellies often have shorter lifespan than the *P. periphylla* (Russell, 1970), and dead specimens might accumulate on the seabed due to mass death at the end of the season. An example of this is the jellyfish *Crambionella orsini*, which has been observed to aggregate on the seafloor after death, creating a thick layer of jellyfish detritus (Billett *et al.*, 2007). *P. periphylla* is not known to have seasonal variations in reproduction and death, and thus would not be expected to aggregate on the seabed in large quantities (Jarms *et al.*, 1999; Youngbluth and Båmstedt, 2001). The recording from the ROV supports the data from the trawl catches in March 2011.

The decaying *P. periphylla* observed on the seafloor were large individuals, going through different stages of decay. The cause of a higher mortality is unknown. Possible explanations would include high population densities in combination with insufficient prey resources during winter.

The sampled *polychaeta* collected by Van Veen grab did not show any particularities with respect to species composition. However, it appeared to be few individuals of each species in the infauna. Large amounts of decaying tissue from the jellyfish would expectedly result in anoxic conditions. According to Dr. Torkild Bakken (Museum of Natural History and Archaeology, NTNU), none of the *polychaeta* species found are typical for sea beds with oxygen depletion. It seems like the benthic fauna is relatively healthy; hence there are not any conclusive signs that decaying *P. periphylla* accumulating on the seabed in Verrabotn has a negative impact on the benthos fauna.

4.3. LVPP

Considering that all of the dives were executed during daytime, it was expected that the *P. periphylla* would dwell relatively close to the bottom. In fact, most of the jellyfish individuals were recorded at the deepest part of the dive, being consistent with the theory of DVM. All hauls were conducted in March and April, a time of the year were the light intensity is increasing. It may also be considered that in particular Verrabotn is a shallow location, where the jellyfish may choose to stay close to the seabed also during daytime.

Dive [*a2*] detected more *P. periphylla* on the way up. This might be due to the fact that the LVPP used in this particular dive was equipped with a collecting device, concentrating the jellyfish towards the camera. Apparently, some of the big *P. periphylla* aggregated at the opening, hampering the through-put. Dive [*c2*], from March 2011 showed the same tendency. The LVPP used in this haul had another type of collecting device and a larger opening at the end. Despite larger opening, the device might have affected the recorded depth distribution of *P. periphylla*.

In the samples from dive [*b2*] and [*a3*] there were no observed *P. periphylla*. A probable reason for this is technical difficulties with the gear. During one of the dives the collecting device connected to the LVPP got twisted, probably preventing water and jellyfish to flow through. It is also known that *P. periphylla* reacts strongly to light, which may have triggered a flight reaction when sensing the light of the LVPP.

Size distribution

Data from dive [*a1*] and [*a2*] indicate that the population at this location consists of individuals of all size classes, with a higher percentage of large individual than the populations in Verrasundet and Beitstadfjorden. The data sampled from [*a3*], however, lack any observation of *P. periphylla.*

The data from dive [*b1*] indicate that the population in Verrasundet mainly consist of small individuals and some large. The sample from dive [*b2*] did not contain any *P. periphylla*.

The samples from [*c1*] and [*c2*] were quite similar considering the size distribution. The most interesting difference however is the higher percentage of the smallest individuals (CD ≤ 20 mm) in the dive from 2011. This indicates an ongoing recruitment.

In a population where many small and few large individuals are observed, it can be assumed that the mortality rate is very high at the early stages and that it drops with age (Fosså, 1992).

The recruitment might be lower in certain years, thus creating gaps in the size distribution of a population.

In general, few *P. periphylla* with CD from 41 to 100 mm were found in all of the dives. A possible explanation for this phenomenon is related to advection. Small individuals tend to dwell at greater depth than larger and older individuals, who participate in DVM to a much larger extent (Ulf Båmstedt, personal comment). Being less motile than the larger individuals, they are at higher risk of being transported by the currents, as well as being subjects to predation. The small sized individuals travelling up and down the water column might not be capable of withstanding the force of the currents as effectively as the larger *P. periphylla* due to less swimming capacity, making them more exposed to advection. Less time spent in the uppermost layers in the water column means lesser chance of being affected by the currents. This hypothesis, however, assumes that the population has adapted genetically to the environment in the particular area (Pearre, 2003), which is a doubtful suggestion in newly established populations.

It might also be that the sampling missed the exact occupied zone preferred by *P. periphylla* of certain size classes. This theory could explain the large difference in size distribution in dive [*a1*] and [*a2*]. Both dives were performed in Verrabotn on the same day, but at different times of the day; at 09:55 and 14:40. Under the assumption that the light intensities were approximately equal at these two times of the day, light intensity might not be a crucial factor explaining the difference in size distribution.

Distribution of biomass

Most of the biomass was made up by large individuals, (CD > 101 mm). Comparing the two dives in 2010 and 2011 in Beitstadfjorden, there seem to have been a change in the biomass composition. There were fewer of the smallest individuals with CD less than 40 mm in 2011 than in 2010, and a higher percentage of individuals with CD > 121 mm. Figure 3. 5. 4 indicates that there has been a shift from the smallest size class (CD ≤ 20 mm) into the next size class. It appears that the jellyfish with CD from 81 to 100 mm in 2010 have grown into a larger size class in 2011. Little is known about the growth rate, reproductive rate and lifespan of *P. periphylla* in Norwegian waters, and it is thus difficult to estimate how much an individual grows in a year.

Comparing with data from 2007

Table 4.1.1 shows the estimated biomass of *P. periphylla* in October 2007, April 2010 and March 2011. The data for 2007 is from Hetland (2008).

Table 4.1.1: Estimated biomass of *P. periphylla* from October 2007, April 2010 and March 2011.

	Estimated biomass (10^3 kg)		
Location	2007	2010	2011
Verrabotn	95	329	-
Verrasundet	941	2196	-
Beitstadfjorden	11291	8788	9753

The data in table 4.1.1, along with the trawl catches and the ROV recording, suggests a recent reduction of the *P. periphylla* population in all of the three locations (stations) investigated. The biomass estimates from 2010, however, suggests that the population was increasing at Verrabotn and Verrasundet, but reduced in Beitstadfjorden. The reason for the reduction in the population in 2011 cannot be determined with any security. One may speculate that the food availability for the previously large jellyfish population became scarce in this period of time. The many large, dead individuals of the jellyfish detected by ROV points to a high mortality for the oldest individuals. Large and unexplained oscillations in natural population sizes are often observed in many species (Berryman, 2002). A population of the size in which was estimated in 2007 might simply be too big for the local prey resources available for *P. periphylla*, and hence not sustainable over time.

4.4. Sources of Errors

There are several sources of errors that might have affected the present results. At the bottom lies that the quality of the video recordings from the LVPP was not very high, reducing the accuracy of the measuring of the medusae, as well as their spatial position.

Also, three different LVPPs were used during the dives. The LVPP used in 2011 had two frames, the smallest near the camera. The frame worked as a reference point in the recorded video when measuring the *P. periphylla*, making it easier to measure each individual. This LVPP had no light attached to the outermost frame, preventing a flight reaction before the medusae reached the camera. The LVPP used at dive [*a1*], [*b1*] and [*c1*], however, did not have a frame visible in the recording, making it harder to decide the size and how far away from the camera the object was. In dive [*a2*] a LVPP with a plastic pipe at the end was used. This LVPP worked very well until it got clogged by jellyfish too big for the opening.

4.5. Further work

None of the dives were executed during the night, making it difficult to assess to which degree the jellyfish were performing DVM, thus night sampling would have been desirable. It would also have been advantageous to sample data during different seasons, to see if climatic factors affect the vertical and horizontal distribution of *P. periphylla*.

Few samples were taken at each location, and there is a lack of samples in some periods. It would be optimal to sample at the same stations at the same time of the year, over several years, to get a more complete picture of population trends.

Further studies on *P. periphylla* in Trondheimsfjorden is being conducted at the time of writing, which will focus on the distribution of the *P. Periphylla* eggs in different parts of the fjord and at different times of the year. Potentially, such studies can shed light on the dynamics of the recruitment process of the population.

4.6. Conclusion

The biomass estimates conducted in March 2011 were lower than the estimates from October 2007, indicating a reduction of the local *P. periphylla* population in Beitstadfjorden in this period. However, the presence of many small individuals (CD ≤ 40 mm) in the 2010/2011 materials indicates that a considerable local recruitment is still taking place.

The samples of the benthos and its infauna in Verrabotn showed no specific signs of unhealthy or anoxic conditions in the seabed. On this location, where a drastic reduction of the population density was indicated by much smaller bottom trawl catches than in 2007, corroborated by video records of many dead and dying specimens on the seafloor, the grab samples gave little or no evidence that this apparent mass death has affected the benthos on this location.

Also in Verrasundet and in Beitstadfjorden proper, the current biomass estimates (2011) are smaller than those in 2007. The same is true for the bottom trawl catches of the jelly in Verrabotn in 2011, which were only approximately one twentieth of the size of comparable catches a few years before (Jarle Mork, personal communication). Thus, the present study suggests that the 2007 *P. periphylla* population in the inner Trondheimsfjord had grown too large for the available food resources, resulting in a population size regulation acting through a mass death which seems to have taken place in the late winter.

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Appendix

Table A: Data and calculations from dive [*a2*]. Table shows the CD of each individual *P. periphylla* detected, its depth and calculated biomass, and filtered water volume and biomass at each 10 m interval.

Record	Depth (m)	Time observed (min)	Measured CD on screen (mm)	CD (mm)	CD (cm)	lnWW	WW (g)
1305	46,4	16,083334	6	10,4347826	1,043478261	-0,55396544	0,574666482
1322	46	16,666667	80	139,130435	13,91304348	6,52031322	678,7909619
1410	53,7	19,6	75	130,434783	13,04347826	6,34405206	569,0976654
1460	54,5	21,266667	15	26,0869565	2,608695652	1,94851618	7,018266013
1465	54,5	21,383334	11	19,1304348	1,913043478	1,10145206	3,00853141
1478	54,5	21,85	5	8,69565217	0,869565217	-1,05190384	0,349272157
1479	54,5	21,9	13	22,6086957	2,260869565	1,55769347	4,747857514
1483	54,7	22,033334	12	20,8695652	2,086956522	1,33908883	3,815565284
1483	54,7	22,033334	10	17,3913043	1,739130435	0,84115042	2,319033314
1484	54,7	22,05	20	34,7826087	3,47826087	2,73420469	15,39749277
1521	54,7	23,283334	105	182,608696	18,26086957	7,26299139	1426,517429
1528	55,3	23,533334	8	13,9130435	1,391304348	0,23172307	1,260770537
1553	61,1	24,366667	10	17,3913043	1,739130435	0,84115042	2,319033314
1556	61,1	24,466667	12	20,8695652	2,086956522	1,33908883	3,815565284
1600	57	25,933334	15	26,0869565	2,608695652	1,94851618	7,018266013
1605	56,4	26,083334	11	19,1304348	1,913043478	1,10145206	3,00853141
1610	55,7	26,266667	8	13,9130435	1,391304348	0,23172307	1,260770537
1625	54,1	26,75	11	19,1304348	1,913043478	1,10145206	3,00853141
1633	53,4	27,033334	14	24,3478261	2,434782609	1,76008975	5,812959081
1640	52,8	27,266667	9	15,6521739	1,565217391	0,55340032	1,739156664
1645	52,4	27,433334	8	13,9130435	1,391304348	0,23172307	1,260770537
1758	38,7	31,2	92	160	16	6,90201706	994,2782125
1759	38,7	31,216667	87	151,304348	15,13043478	6,74940194	853,5481363
1760	38,7	31,266667	8	13,9130435	1,391304348	0,23172307	1,260770537
1826	34,3	33,466667	80	139,130435	13,91304348	6,52031322	678,7909619
1852	35,3	34,333334	95	165,217391	16,52173913	6,98965346	1085,34529
1860	33,4	34,583334	90	156,521739	15,65217391	6,84199047	936,3510571
1869	30,1	34,883334	9	15,6521739	1,565217391	0,55340032	1,739156664

Frame on screen:23cm	
Frame real size: 40 cm	
Faktor real size (40 cm/23 cm):	1,73913043
Area frame(m^2) 133cm*75cm:	0,9975
Total time dive (t) (2260 s/3600 s):	0,62777778
Average speed: 1,25 knop	
Average speed(m/s):	0,64305556
Lenght surface (m):	1453,30556

Interval	Time in water (s)	Tid spent in interval (s)	Tot.time in depth (s)	Distance(m)	# *P. periphylla*	Depth (m)	Volum filtered (m^3)	WW (g) in interval
1	110	110	156	100,316667	0	10	100,065875	0
2	156	46	102	65,5916667	0	20	65,4276875	0
3	518	362	426	273,941667	0	30	273,2568125	0
4	818	300	652	419,272222	7	40	418,2240417	4551,313585
5	1136	318	342	219,925	2	50	219,3751875	679,3656284
6	1432	296	504	324,1	17	60	323,28975	2056,640869
7	1510	78	78	50,1583333	2	70	50,0329375	6,134598598
-6	1718	208						
-5	1742	24					1449,672292	7293,454682
-4	2094	352						
-3	2158	64						
-2	2214	56						
-1	2260	46						

Table B: Formulas used to calculate the data in Table A.

Record	Depth (m)	Time observed (min)	Measured CD on screen (mm)	CD (mm)	CD (cm)	lnWW	WW (g)	Frame on screen:23cm	
=A4	=B4	=C4	=D4	=D4*L5	=E4/10	=(-0,6702)+(2,7311*LN(F4))	=EKSP(G4)	Frame real size: 40 cm	
=A5	=B5	=C5	=D5	=D5*L5	=E5/10	=(-0,6702)+(2,7311*LN(F5))	=EKSP(G5)	Faktor real size (40 cm/23 cm):	=L5
=A6	=B6	=C6	=D6	=D6*L5	=E6/10	=(-0,6702)+(2,7311*LN(F6))	=EKSP(G6)	Area frame(m^2) 133cm*75cm:	=L6
=A7	=B7	=C7	=D7	=D7*L5	=E7/10	=(-0,6702)+(2,7311*LN(F7))	=EKSP(G7)	Total time dive (t) (2260 s/3600 s):	=L7
=A8	=B8	=C8	=D8	=D8*L5	=E8/10	=(-0,6702)+(2,7311*LN(F8))	=EKSP(G8)	Average speed: 1,25 knop	
=A9	=B9	=C9	=D9	=D9*L5	=E9/10	=(-0,6702)+(2,7311*LN(F9))	=EKSP(G9)	Average speed(m/s):	=L9
=A10	=B10	=C10	=D10	=D10*L5	=E10/10	=(-0,6702)+(2,7311*LN(F10))	=EKSP(G10)	Lenght surface (m):	=L10
=A11	=B11	=C11	=D11	=D11*L5	=E11/10	=(-0,6702)+(2,7311*LN(F11))	=EKSP(G11)		
=A12	=B12	=C12	=D12	=D12*L5	=E12/10	=(-0,6702)+(2,7311*LN(F12))	=EKSP(G12)		
=A13	=B13	=C13	=D13	=D13*L5	=E13/10	=(-0,6702)+(2,7311*LN(F13))	=EKSP(G13)		
=A14	=B14	=C14	=D14	=D14*L5	=E14/10	=(-0,6702)+(2,7311*LN(F14))	=EKSP(G14)		
=A15	=B15	=C15	=D15	=D15*L5	=E15/10	=(-0,6702)+(2,7311*LN(F15))	=EKSP(G15)		
=A16	=B16	=C16	=D16	=D16*L5	=E16/10	=(-0,6702)+(2,7311*LN(F16))	=EKSP(G16)		
=A17	=B17	=C17	=D17	=D17*L5	=E17/10	=(-0,6702)+(2,7311*LN(F17))	=EKSP(G17)		
=A18	=B18	=C18	=D18	=D18*L5	=E18/10	=(-0,6702)+(2,7311*LN(F18))	=EKSP(G18)		
=A19	=B19	=C19	=D19	=D19*L5	=E19/10	=(-0,6702)+(2,7311*LN(F19))	=EKSP(G19)		
=A20	=B20	=C20	=D20	=D20*L5	=E20/10	=(-0,6702)+(2,7311*LN(F20))	=EKSP(G20)		
=A21	=B21	=C21	=D21	=D21*L5	=E21/10	=(-0,6702)+(2,7311*LN(F21))	=EKSP(G21)		
=A22	=B22	=C22	=D22	=D22*L5	=E22/10	=(-0,6702)+(2,7311*LN(F22))	=EKSP(G22)		
=A23	=B23	=C23	=D23	=D23*L5	=E23/10	=(-0,6702)+(2,7311*LN(F23))	=EKSP(G23)		
=A24	=B24	=C24	=D24	=D24*L5	=E24/10	=(-0,6702)+(2,7311*LN(F24))	=EKSP(G24)		
=A25	=B25	=C25	=D25	=D25*L5	=E25/10	=(-0,6702)+(2,7311*LN(F25))	=EKSP(G25)		
=A26	=B26	=C26	=D26	=D26*L5	=E26/10	=(-0,6702)+(2,7311*LN(F26))	=EKSP(G26)		
=A27	=B27	=C27	=D27	=D27*L5	=E27/10	=(-0,6702)+(2,7311*LN(F27))	=EKSP(G27)		
=A28	=B28	=C28	=D28	=D28*L5	=E28/10	=(-0,6702)+(2,7311*LN(F28))	=EKSP(G28)		
=A29	=B29	=C29	=D29	=D29*L5	=E29/10	=(-0,6702)+(2,7311*LN(F29))	=EKSP(G29)		
=A30	=B30	=C30	=D30	=D30*L5	=E30/10	=(-0,6702)+(2,7311*LN(F30))	=EKSP(G30)		
=A31	=B31	=C31	=D31	=D31*L5	=E31/10	=(-0,6702)+(2,7311*LN(F31))	=EKSP(G31)		

Interval	Time in water (s)	Tid spent in interval (s)	Tot.time in depth (s)	Distance(m)	*# P. periphylla*	Depth (m)	Volum filtered (m^3)	WW (g) in interval
=A35	=B35	=B35	=C35+C47	=D35*L9	=F35	=G35	=E35*L6	=0
=A36	=B36	=B36-B35	=C36+C46	=D36*L9	=F36	=G36	=E36*L6	=0
=A37	=B37	=B37-B36	=C37+C45	=D37*L9	=F37	=G37	=E37*L6	=0
=A38	=B38	=B38-B37	=C38+C44	=D38*L9	=F38	=G38	=E38*L6	=SUMMER(H25:H31)
=A39	=B39	=B39-B38	=C39+C43	=D39*L9	=F39	=G39	=E39*L6	=SUMMER(H4:H5)
=A40	=B40	=B40-B39	=C40+C42	=D40*L9	=F40	=G40	=E40*L6	=SUMMER((H6:H15)+(H18:H24)
=A41	=B41	=B41-B40	=C41	=D41*L9	=F41	=G41	=E41*L6	=SUMMER(H16:H17)
=A42	=B42	=B42-B41						
=A43	=B43	=B43-B42					=SUMMER(H35:H41)	=SUMMER(I35:I41)
=A44	=B44	=B44-B43						
=A45	=B45	=B45-B44						
=A46	=B46	=B46-B45						
=A47	=B47	=B47-B46						

Table C: Data, calculations and formulas from dive [*a2*]. The table shows water volume filtered, biomass, biomass/filtered water volume (kg km^{-3}), all in each 10 m interval, and the total estimated biomass of the dive.

Depth (m)	Volume filtered (m³)	Volume filtered (km³)	WW (g) interval	WW(kg) interval	kg/km³ interval			km³	Avrg. kg/km³	WW(kg)	WW(1000 kg)
10	100,065875	1,00066E-07	0	0	0		Volume over 20 m	0,0756	0	0	0
20	65,4276875	6,54277E-08	0	0	0		Volume between 20 to 40 m	0,0464	5441238,585	252473,4703	252,4734703
30	273,2568125	2,73257E-07	0	0	0		Volume under 40 m	0,0201	3193678,131	64192,93044	64,19293044
40	418,2240417	4,18224E-07	4551,313585	4,551313585	10882477,17						
50	219,3751875	2,19375E-07	679,3656284	0,679365628	3096820,731					Tot.	316,6664008
60	323,28975	3,2329E-07	2056,640869	2,056640869	6361602,462						
70	50,0329375	5,00329E-08	6,134598598	0,006134599	122611,2018						

Depth (m)	Volume filtered (m³)	Volume filtered (km³)	WW (g) interval	WW(kg) interval	kg/km³ interval			km³	Avrg. kg/km³	WW(kg)	WW(1000 kg)
=A4	=B4	=B4/1000000000	=D4	=D4/1000	=E4/C4		Volume over 20 m	=I4	=GJENNOMSNITT(F4:F5)	=J4*I4	=K4/1000
=A5	=B5	=B5/1000000000	=D5	=D5/1000	=E5/C5		Volume between 20 to 40 m	=I5	=GJENNOMSNITT(F6:F7)	=J5*I5	=K5/1000
=A6	=B6	=B6/1000000000	=D6	=D6/1000	=E6/C6		Volume under 40 m	=I6	=GJENNOMSNITT(F8:F10)	=J6*I6	=K6/1000
=A7	=B7	=B7/1000000000	=D7	=D7/1000	=E7/C7						
=A8	=B8	=B8/1000000000	=D8	=D8/1000	=E8/C8					Tot.	=SUMMER(L4:L6)
=A9	=B9	=B9/1000000000	=D9	=D9/1000	=E9/C9						
=A10	=B10	=B10/1000000000	=D10	=D10/1000	=E10/C10						