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Recruitment dynamics of *Periphylla periphylla* in the Trondheimsfjord

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Preface

This Master's Thesis was written at Trondheim Biological Station (TBS), Department of Biology, Norwegian University of Science and Technology (NTNU) from autumn 2011 to spring 2013.

The thesis is a part of a project on *Periphylla periphylla* in the Trondheimsfjord led by Professor Jarle Mork at TBS, NTNU.

I would like to thank my supervisor, Professor Jarle Mork, for suggesting this thesis, for his wonderful spirit and great support and supervising during this project.

Thanks to my co-supervisor Professor Ulf Båmstedt from Umeå Marina Forskningscentrum, Umeå Universitet, for help and support during writing and identification of the *Periphylla periphylla* developmental stages.

I would like to thank Dr. scient. Associate Professor Torkild Bakken, head of Section Museum of Natural History and Archaeology, and Karstein Hårsaker at the Museum of Natural History and Archaeology for providing me with the historical plankton samples at the museum.

I would also like to thank the captain and crew onboard R/V "Gunnerus" for their help and their good spirit on our week- long cruises.

I thank my patient boyfriend, my wonderful family, my friends and coworkers at TBS for great support and helpful discussions throughout this work.

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Åshild Løvås Borgersen

Cover picture: Drawing of *Periphylla periphylla* by Åshild Løvås Borgersen.

Abstract

Periphylla periphylla (Péron and Lesueur 1809) is a deep sea coronate scyphomedusa distributed in all oceans of the world, where it is normally found in low abundances. Over the last decades, however, it has established itself in some Norwegian fjords where it has reached very high biomasses and taken over the role as top-predator in the ecosystems. It is naturally adapted to the deep and dark environment of world oceans, but has nevertheless proliferated in comparably shallow waters of many Norwegian fjords.

This MSc project aimed at shedding light on the physical factors, environmental characteristics and biological traits which has enabled this jellyfish to establish itself so successfully in the Trondheimsfjord, where it has multiplied rapidly to a large population and to some degree out-competed its ecosystem rivals. The recruitment appears to be a crucial success factor.
Thus to achieve the listed goals, studies were focused on the recruitment cycle of the Trondheimsfjord *Periphylla periphylla* stock, in fresh as well as preserved historical plankton samples from the fjord. The distribution in time and space of the eggs and young specimens of the jellyfish among the plankton in the water column on five fixed plankton sampling locations in the fjord was investigated.

The results indicate that *Periphylla periphylla* spawns continuously in the Trondheimsfjord, with a possible peak in autumn and winter months. The main spawning areas seem to be the middle and inner basins of the fjord (the Ytterøya and Beitstadfjord basins). The pelagic eggs are probably transported outwards from the inner parts of the fjord, as eggs were most abundant on the most coastward sampling station. From its first appearance to a recent peak in population size in the Trondheimsfjord it seems to have taken approximately 10-12 years.

Sammendrag

Periphylla periphylla (Péron and Lesueur 1809) er en dypvannsmanet som finnes i alle verdenshav hvor den normalt blir funnet i lave konsentrasjoner fordelt i vannsøylen. Maneten tar skade av sollys, og har gjennom et langt evolusjonært tidsrom tilpasset seg et liv i mørket på dypt vann. Maneten har i de siste 40 år etablert seg i tette populasjoner i flere norske fjorder, inklusive Trondheimsfjorden, hvor den har vært observert siden 1999 og fra og med 2003 dominert bunntrålfangster i fjorden. Det ser ut til at spredningen skjer i en nordgående retning langs norskekysten, hvilket tyder på at den norske kyststrømmen er en viktig del av dens spredningsmekanikk. Til nå (2013) er Saltenfjorden nord for Bodø den nordligste fjorden maneten har invadert.

Målet for denne oppgaven var å kaste lys over de fysiske og biologiske mekanismene som muliggjør for denne maneten å etablere seg i fjorder, øke raskt til store populasjoner og utkonkurrere rivaler i økosystemet for så å fortsette spredningen nordover til nye fjorder langs norskekysten. For å nå dette målet ble reproduksjonsmønsteret til maneten i Trondheimsfjorden undersøkt. Fordelingen i tid og rom av egg og yngre individer av maneten (dvs i planktonprøver fra vannsøylen) på fem regulære stasjoner i fjorden ble undersøkt gjennom en full årssyklus. Videre ble frekvensen av egg og juvenile stadier av Periphylla undersøkt i historiske planktonprøver fra tre av dem, som har vært standard hydrograferingsstasjoner ved Trondhjem Biologiske Stasjon siden 1963.

Resultatene tyder på at maneten gyter kontinuerlig i Trondheimsfjorden, med et tyngdepunkt høst og vinter. Hovedgyteområdet synes å være de midtre og indre bassengene i fjorden (ved Ytterøya og i Beitstadfjorden). De pelagiske eggene blir sannsynligvis transportert med strømmen utover i fjorden, da flest egg ble funnet i de ytre deler. De øvrige unge utviklingsstadiene, som er rapportert å ha en dyp fordeling i vannsøylen, synes i større grad å bli holdt tilbake i den indre del av fjorden. Fra dens første betydelige opptreden i bunntrålfangster og planktonprøver i Trondheimsfjorden og til nå hvor den ser ut til å ha nådd fjordens bærekapasitet har det gått 10-12 år.

Contents

1. Introduction

Mass occurrence of jellyfish is an increasing problem worldwide. Causes for these blooms may vary from natural ecological fluctuations to effects of anthropogenic activity in the marine environment. Eutrophication (Arai 2001), over-fishing, chemical pollution and introduction of exotic species are the main anthropogenic factors that cause such blooms (Hay 2006; Purcell et al. 2007). The most important direct negative consequences of jellyfish blooms are ecological losses, reduced tourism due to stinging danger, reduced catches due to malfunction of net gear in the fisheries, catastrophic fish mortality due to stinging and oxygen deprivation in aquaculture and finally, blocking of water inlets of power plants (Hay 2006; Hay et al. 1990; Purcell et al. 2007). Climate changes which alter temperatures, distributions and nutrient fluxes can cause rapid regime shifts in marine ecosystems in favor of jellyfish (Lynam et al. 2004; Hay 2006).

Norway has had its share of jellyfish blooms. The aquaculture industry on the Norwegian coast has experienced heavy losses due to jellyfish clogging the fish cages and stinging the gills of the fish, causing suffocation and mortality (Båmstedt et al. 1998). The traditional fisheries have experienced high densities of jellyfish clogging their nets and thus reducing their catches. The jellyfish have become a nuisance as they sting fishermen when handling the catch, the working hours are longer and the fishing season is often amputated. Also, fish species are found to avoid dense jellyfish swarms, leading to forced fishing relocations for fishermen in the Trondheimsfjord (Jarle Mork, Trondhjem Biologiske Stasjon, Institutt for biologi, NTNU, pers. comm.).

One particular jellyfish is of special concern as it is currently increasing in abundance in fjords along the Norwegian coast. The deep sea coronate *Periphylla periphylla* (Peròn and Lesueur 1809) hereafter called just Periphylla, first appeared in large numbers in the Lurefjord near Bergen in the 1970's (Fosså 1992). Since then the jellyfish has spread northwards along the Norwegian coast, where the Sognefjord, Storfjord, Halsafjord, Trondheimsfjord and the Vefsnfjord so far been focused on in scientific reports and projects. Fjords north of the Vefsnfjord have also been invaded; the jellyfish has currently reached the Saltenfjord in Bodø (J.

Mork, pers. comm.). It is likely that the Norwegian Coastal Current (NCC) plays a central role in the spreading mechanism of Periphylla in these waters including the Trondheimsfjord.
Due to increases in precipitation in Northern Europe over the last part of the 20th century (IPCC 2001), the river run-off to estuaries is increased. The NCC collects brackish water from various fjords in its way northwards along the coast, and thereby brings dissolved organic matter into the fjords, darkening their water mass. This enables deep-sea species like Periphylla to survive even in relatively shallow fjords along the Norwegian coast (Sørnes et al. 2007). It is the typical threshold fjords that are prone to invasions, while open coastal waters seem to be less vulnerable. Scientific reports from the infested localities report that the fjords' ecosystems are altered; the traditional hegemonies as top-predators are challenged. In Norway these hegemonies are often occupied by species in the cod family and thus marine harvesting including the traditional fisheries is affected. Ecological effects in the form of reduced benthic fish biodiversity on infested locations have also been observed in the inner parts of the Trondheimsfjord (J. Mork, pers. comm.).

Periphylla competes with a range of other species feeding on zooplankton resources. Søtje et al. (2007) found in their study of three Norwegian fjords that the zooplankton biomass was negatively correlated with the abundance of Periphylla. Periphylla performs diurnal vertical migrations (DVM) in the water column, possibly following the zooplankton as they perform DVM to feed (Sørnes et al. 2007). The jellyfish migrate to the surface at dusk and go deep down at dawn. The vertical diurnal migration of Periphylla can be substantial; up to 400 meters (Marsh et al. 2001). Field studies in the Lurefjord since 1998 have shown that there is a higher biomass of Periphylla in the deeper parts of the fjord (Tiemann et al. 2009). Periphylla is sensitive to daylight due to the pigment protoporhyrin, which is photo-degraded into toxic compounds by natural light. Exposure to daylight over time has a lethal effect on the medusa (Jarms et al. 2002).

Studies in the Lurefjord showed that Periphylla has a direct development with 14 developmental stages before it reaches maturity (Jarms et al. 2002). It has a holopelagic life cycle, and is the only coronate scyphozoa without planula or ephyra stages (Jarms et al. 1999, 2002; Tiemann and Jarms 2010). The eggs of Periphylla are huge compared to those of other jellyfish, with a diameter of 1.28-1.68 mm (Jarms et al. 1999). Periphylla has the largest eggs of all cnidarians; compared to other coronates like *Nausithoe aurea* with a diameter of 0.175 mm, Periphylla eggs are almost ten times larger in diameter. A common medusa in European waters, *Aurelia aurita*, has an egg diameter of 0.15-0.23 mm (Berrill 1949). Periphylla eggs contain large amounts of yolk, which is crucial for a direct development which demands lots of energy (Avian and Rottini Sandrini 1991; Berrill 1949).

After the first observations of high densities in trawl catches in the inner parts of the Trondheimsfjord in year 1999, Periphylla has established itself as a top-predator in the Trondheimsfjord ecosystem and increased dramatically in abundance. From 2003 and onwards, the jellyfish has dominated the trawl catches. Simultaneously, the abundance of the formerly most common bottom fish species has been reduced in trawl catches, especially at the shallow localities Verrabotn (~ 60 m) and Verrasundet (~ 100 m) in the inner fjord (J. Mork, pers. comm.). Two previous studies in the Trondheimsfjord (Hetland 2008; Solheim 2012) has estimated the total biomass of the inner fjord to be >20 000 tons. Hetland (2008) suggested that the "mother population" (where most of the reproduction takes place) is located in the inner parts of the fjord (the Beitstadfjord). In the Trondheimsfjord, a jellyfish with few enemies and high reproduction rate may rapidly reach the environments' carrying capacity. Despite the mass death observed in 2010-2011, a high abundance of young individuals during the spring 2012 indicated that the recruitment capacity was not seriously affected (Solheim 2012). The hydrodynamic and biological mechanisms which enable such a high reproduction capacity within certain Norwegian fjords need to be understood for an assessment of the future situation for resource management as well as biodiversity issues along the coast of Norway.

This MSc project aimed at shedding light on the physical factors, environmental characteristics and biological traits which has enabled this jellyfish to establish itself so successfully in the Trondheimsfjord, where it has multiplied rapidly to a large population and to some degree out-competed its ecosystem rivals. The recruitment dynamic appears to be a crucial success factor. Thus to achieve the listed goals, studies were focused on the recruitment cycle of the Trondheimsfjord Periphylla stock, in fresh as well as preserved historical plankton samples from the fjord. The distribution in time and space of the eggs and young specimens of the jellyfish among the plankton on five fixed sampling locations in the fjord was investigated.

2. Materials and Methods

2.1 Study Area

2.1.1 The Trondheimsfjord

The Trondheimsfjord is located in the central part of Norway and it is the third longest and seventh deepest fjord in Norway. From Agdenes (63° 40 N, 09° 45 E) to Steinkjer (64° 00 N, 11° 30 E) it is ~ 135 km and has a total volume of ~ 235 km³ (Wendelbo 1970). The fjord is divided into three main basins by sills. From the outermost to the innermost parts of the fjord the basins are Ytterfjorden, Midtfjorden and Beitstadfjorden with sills at Agdenes, Tautra and Skarnsundet (Fig. 1).

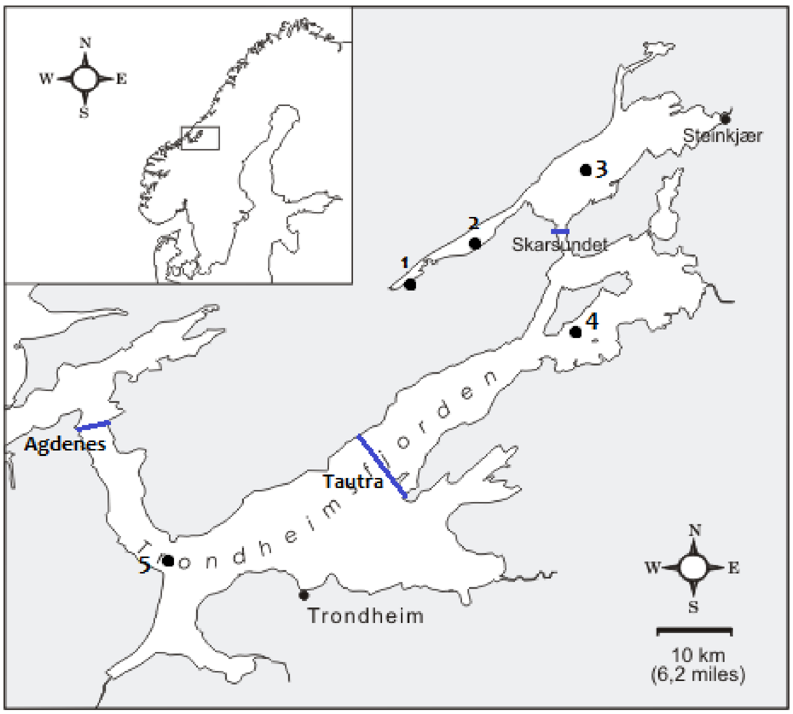

Figure 1. The Trondheimsfjord: The purple lines indicate the sills. TBS stations used in this study are 1: Verrabotn, 2: Verrasundet, 3: Beitstadfjorden, 4: Ytterøya and 5: Røberg. Adopted from Sneli (2003).

Table 1. Topographical data of the Trondheimsfjord. Adopted from Jacobson (1983).

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

The water in the Trondheimsfjord is affected by several forces throughout the year. Density differences due to salinity and temperature gradients influence the extent of water mixing. The main forces responsible for water mixing are waves (both tidal and wind generated), depth of the sills and fresh water discharge from several large rivers in the fjord (Jacobson 1983). The tidal water is responsible for most of the mixing (Fig. 2). The tidal energy in the fjord can be up to a thousand times stronger than wind and river energy combined. One tidal cycle reaches as far into the fjord as the Beitstadfjord, where 47 % of the tidal volume passes the Tautra sill into the middle basin, and 16 % reaches the Beitstadfjord. The outgoing tidal water may mix substantially with water masses in each basin and change the composition of the water there. (Jacobson 1983).

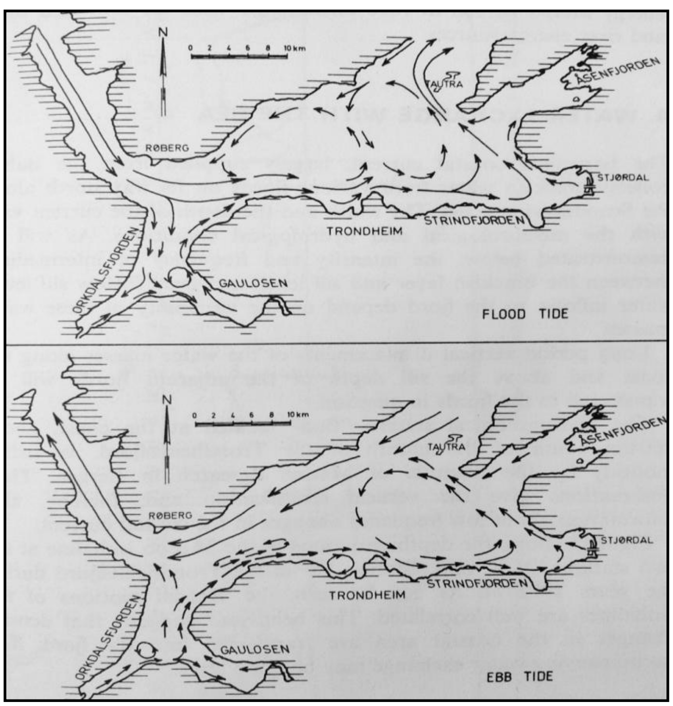

Figure 2. Flood and ebb tide for the seaward basin. Adopted from Jacobson (1983).

The depth of sills affects the water exchange and mixing of the water below the sills (Sørnes et al. 2007). In the Trondheimsfjord, the Tautra sill is the shallowest; 100 meters. The Skarnsundet sill is 140 meters and the Agdenes sill is 330 meters (Wendelbo 1970).

The bottom water in Trondheimsfjorden is normally exchanged twice a year by inflows of water. In late winter and spring, the "old" bottom water is replaced high salinity water of Atlantic origin (Fig. 3 left). This inflow may go on for several months until May-June. Because of its innermost position, the Beitstadfjord basin is filled up later than the others. A second inflow, this time in the autumn and of NCC origin, may also penetrate to the innermost parts of the fjord. The inflowing water near the surface in August-September have been found to carry zooplankton species also resident in the fjord. (Wendelbo 1970; Jacobson 1983).

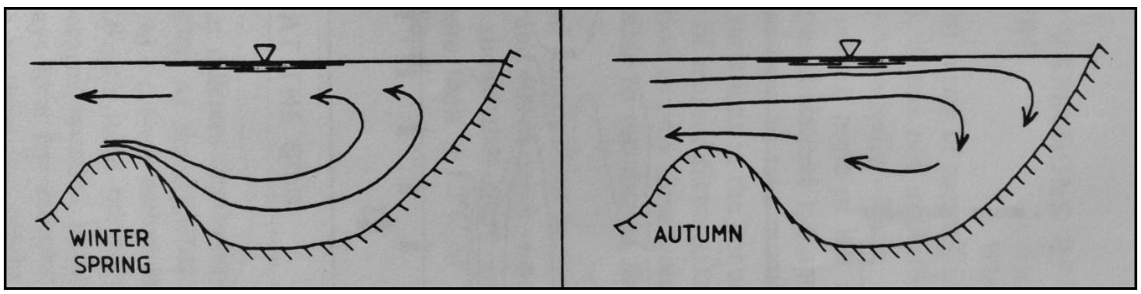

Figure 3. A schematic description of the annual deep water exchange. Adopted from Jacobson (1983).

The river-driven estaurine circulation is the mechanism which renewes most of the surface layer of the fjord (Fig. 4). The brackish surface water moving seawards is mixed with the more saline water from below, creating an estaurine circulation with a compensating ingoing current below the surface layer. Varying amounts of fresh water supply from the large rivers in the fjord creates seasonal variation in the circulation (Wendelbo 1970).

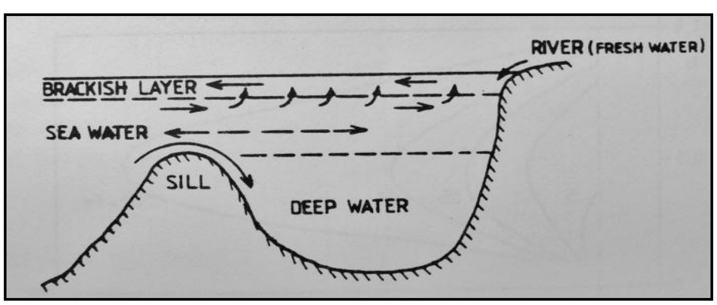

Figure 4. The estuarine circulation. Adopted from Jacobson (1983).

2.2 Present project plankton hauls and trawls methods

2.2.1 Vessel

The vessel used for sampling was R/V “Gunnerus”, owned by the Norwegian University of Science and Technology (NTNU) in Trondheim, Norway.
"Gunnerus" is equipped with a Kongsberg SDP-11 dynamic positioning system, a HighPap 500 underwater navigation system, two echo sounders (Furuno FCV-120 and Furono T-2026) and the OLEX system for navigation and chartplotting.

2.2.1.2 Plankton hauls

The abundance of eggs and young specimens of Periphylla in the water column was studied during four week-long cruises; in March 2012, November 2012, February of 2013 and April 2013. Samples were collected with a Nansen zooplankton-net (100 cm diameter, 500 µm meshes and a total area of 0.7854 m^2). Each sample was divided in three parts while onboard. One part was used as a fresh sample for plankton species identification; a second part was fixed in 4 % formaldehyde for long-term storage and a third part was fixed in ethanol for potential later identification by DNA barcode ID. Hauls were taken twice at each station on each cruise from approximately 10 meters above the bottom and to the surface. The abundances of eggs and young specimens of Periphylla were calculated from filtered water volume (V) (Table 3) using the formula $V= r^2 \pi m$, where r= 0.5 m and m= meters of depth hauled. On Stations 3, 4 and 5 the plankton samples were accompanied by full hydrographical profiles of the water column. The hydrographical profiles were recorded with a Sea-bird© CTD instrument from Sea-bird electronics, Inc.

Table 3. Filtered volume water for two hauls at the stations with their respective depths.

Station	Depth (m)	Filtered volume water (m^3)
5	500	392.70
4	400	314.16
3	230	180.64
2	100	78.54
1	60	47.12

2.2.1.3 Bottom Trawls

Standardized bottom trawl hauls near Station 3 (depth 230 m, standard time 10 minutes at bright daylight) were done on each cruise. Records were collected of the biomass in the cod-end (L: liters) and the size distribution (coronal diameter: centimeters) of Periphylla specimens. The trawl was a shrimp trawl with 35 mm stretched-mesh net and with an inner lining of mesh size 11 mm in the cod-end. Medusae with coronal diameter less than 1.11 cm were thus not retained by the trawl (Appendix Table 14).

Table 4. Time and location of the trawls.

St.	Date	Start		Stop		Depth (m)
3	27.03.12	-		-		-
3	13.11.12	13:20	63°56.690N 11°05.084E	13:30	63°56.999N 11°05.215E	227-228
3	05.02.13	-	63°56.828N 11°04.998E	-	63°57.098N 11°05.093E	228
3	05.02.13	15:40	64°00.176N 11°24.589E	16:30	64°00.336N 11°21.347E	65-83
3	09.04.13	15:25	63°56.817N 11°05.078E	15:35	63°57.107N 11°05.181E	226-229

2.3 Sampling stations

The concentration of eggs and young specimens of Periphylla was surveyed at different distances from the assumed "mother population" located in Beitstadfjorden (Hetland 2008) and towards the coast. Five of TBS's regular hydrography stations were surveyed from January of 2012 to April of 2013 (Fig. 1 and Table 5). The sill between Verrabotn and Verrasundet is at 14 meters depth and that between Verrasundet and the Beitstadfjord at 70 meters.

Table 5. Positions of the stations and their respective depths.

Station	Position	Depth (m)
5	63°27.714 N 9°59.966 E	524
4	63°43.500 N 10°57.000 E	425
3	63°56.080 N 11°04.780 E	237
2	63°51.370 N 10°45.113 E	104
1	63°49. 183 N 10°38.445 E	62

2.4 Identification of the developmental stages of Periphylla

The identification of the developmental stages is based on the research from the Lurefjord, Bergen, by Jarms et al. (1999, 2002). Lucas and Reed (2010) distinguished mature eggs from immature eggs by their eosin red staining cytoplasm. The eggs found in the Trondheimsfjord were slightly yellow, distinguishable from other eggs present in the samples. Periphylla has 14 developmental stages before it reaches maturity. Photos were available for the identification of the first seven stages (Fig. 5). The remaining stages were identified using the morphological descriptions by Jarms et al. (1999, 2002). See table 14 in Appendix for detailed descriptions of the stages.

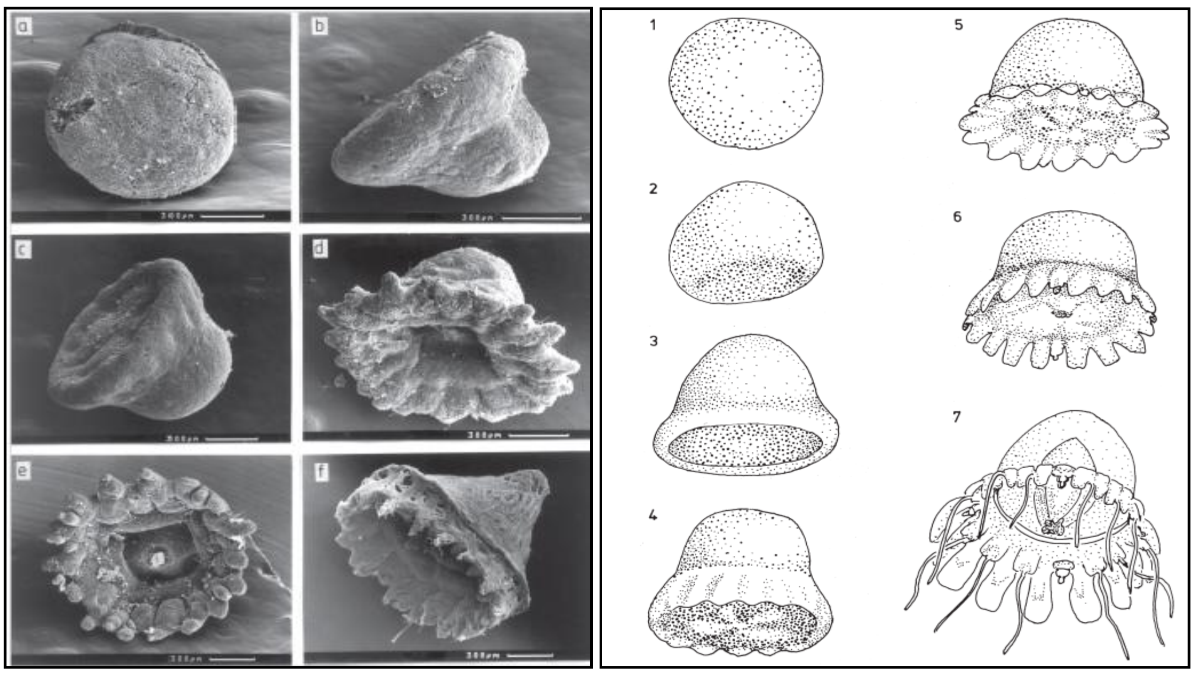

Figure 5. Left: SEM photographs of stages 2-7 of Periphylla. Right: drawing of stages 1-7. Adopted from Jarms et al. (1999).

2.5 Historical plankton hauls

Preserved plankton samples (from the TBS time series) were used to track the start of the Periphylla invasion of the Trondheimsfjord. Monthly samples from Stations 3, 4 and 5 were available for the period 1963-2005.

All available samples from years 1994, 1995, 1998 and 2000-2011 were investigated using visual identification through a stereo Microscope (Appendix Table 13). Samples from years

1994-2004 were taken at Stations 3, 4 and 5 at depths 230-100, 400-100 and 500-100 meters respectively. In addition, all stations had a sample of 100-0 meters. From year 2005 and onwards, sampling was only done at Station 5. 96 % ethanol-preserved samples from years 1994-2002 were kindly provided by the NTNU Museum of Natural History and Archaeology. Samples from years 2003-2011 were stored at TBS, preserved on 4 % marine formaldehyde.

The zooplankton-net used in the TBS time series was a Juday-net with a diameter of 70 cm, a mesh size of 280 µm and a total area of 0.3840 m^2. One haul was taken for each monthly sample. Filtered volume of water (V) was estimated by $V = r^2 \pi m$, where r = 0.35 m (Table 6).

Table 6. Plankton haul information.

Station	**Bottom- 100 m**	**m^3**	**Surface- 100 m**	**m^3**
5	500-100	153. 94	100-0	38. 48
4	400-100	115. 45	100-0	38. 48
3	230-100	50.03	100-0	38. 48

2.5.1 Egg abundance at Station 5

Station 5 was visited 8 times in total (Appendix Table 12). Egg abundance at Station 5 was compared for the years 2002-2012. Since the TBS time series samples were collected with one haul at each station with the Juday- net, the total number of eggs collected at station 5 in 2012 with the Nansen-net were divided by two and multiplied with the total area of the Juday- net (0. 3840 m^2) to convert them into Juday-net samples.

2.6 Statistics

The statistical analyses were performed with the XLSTAT© by Addinsoft Company and Statgraphics Centurion XVI© from Informer Technologies Inc. The regression analyses were performed with Statgraphics for the egg and early stage individuals abundances in project materials as well as the historical samples.

3. Results

3.1 The project's plankton hauls results

3.1.1 Abundance of eggs and early stage individuals

Overall, the plankton survey data confirmed a lively Periphylla reproduction in the Trondheimsfjord. However, the abundance of eggs and early stage individuals showed a spatial as well as a temporal variation. The spatio-temporal abundance of early stage individuals indicates a main reproduction period lasting from autumn until late winter, with a main spawning area in the inner parts of the fjord. Eggs, however, were most abundant in the outer parts of the fjord, indicating a net outwards transport of eggs by the estuarine current system of the fjord.

3.1.1.1 Inter- and intra annual variation

On the full-week cruises, which allowed for spatial comparisons, eggs were found only in March (Stations 4 and 5) and November (Station 5), i.e. in the most coast-near parts of the sampling area. Early stage individuals were generally more abundant than eggs in the samples, with highest abundance at Station 3 in February and April of 2013 and at Station 4 in March and November of 2012. In the innermost parts of the fjord (Stations 1 and 2), no eggs but a few small adults were caught in the plankton nets (Fig. 6 and 7).

The early developmental stages found during the full-week cruises in the entire fjord spanned stages1-14 in March, 7-14 in February, 1-14 in November and 7-14 in April (Table 7 and Appendix Table 15). No hauls were taken at station 1 and 2 in February due to ice coverage.

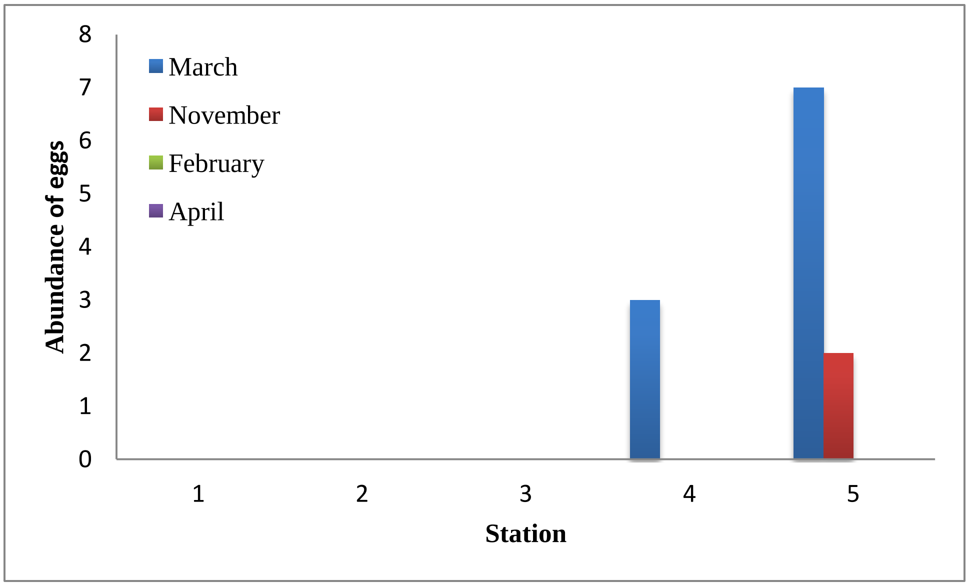

Figure 6. Abundance of eggs in March 2012, November 2012, February 2013 and April 2013.

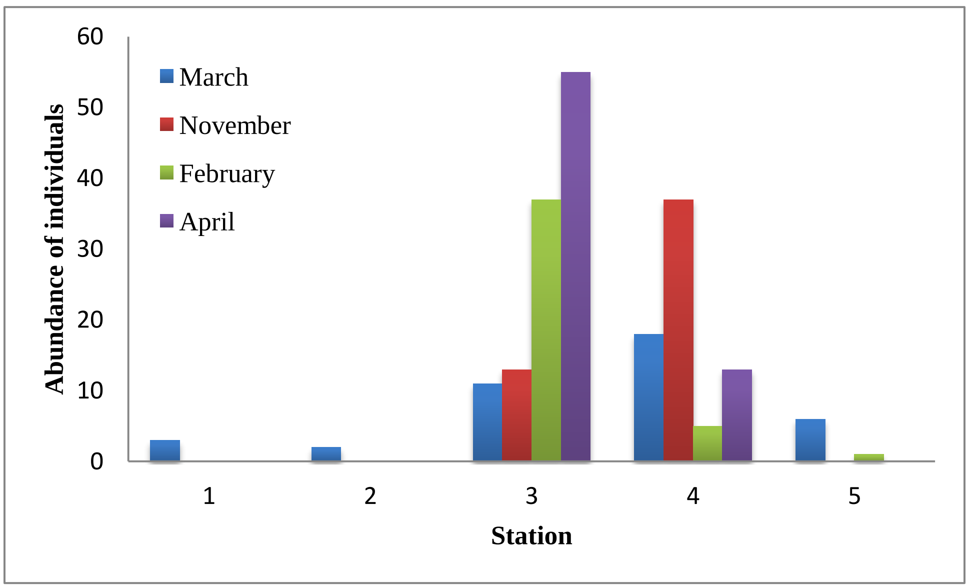

Figure 7. Abundance of early stage individuals in March 2012, November 2012, February 2013 and April 2013.

Table 7. Developmental stages of Periphylla in total cruise materials.

Station	Date	Eggs	Individuals	Developmental stages
5	20.1.12	2	0	1
5	26.3.12	7	6	1,5,6,7,8
4	26.3.12	3	18	1,5,7,8,9,10,12
3	27.3.12	0	11	8,9,11,12,13
2	28.3.12	0	2	14
1	28.3.12	0	3	14
5	20.8.12	5	3	1,8
5	16.10.12	6	3	1,8
5	12.11.12	2	0	1
4	12.11.12	0	37	4,5,7,8,9,10,11,12,13
3	13.11.12	0	13	7,8,9,11,12,14
2	14.11.12	0	0	
1	14.11.12	0	0	
5	15.1.13	0	0	
5	4.2.13	0	1	8
4	4.2.13	0	5	7,8,14 A, C, D
3	5.2.13	0	37	7,8,9,11,12,13,14
5	8.4.13	0	0	
4	9.4.13	0	13	7,8,9,11
3	9.4.13	0	55	7,8,9,10,11,12,13,14
2	10.4.13	0	0	
1	10.4.13	0	0	

When including the 1-day cruises on Station 5, eggs were found in January, March (highest abundance), August, October and November. Early stage individuals were found in February, March (highest abundance), August and October (next highest abundance) (Fig. 8).

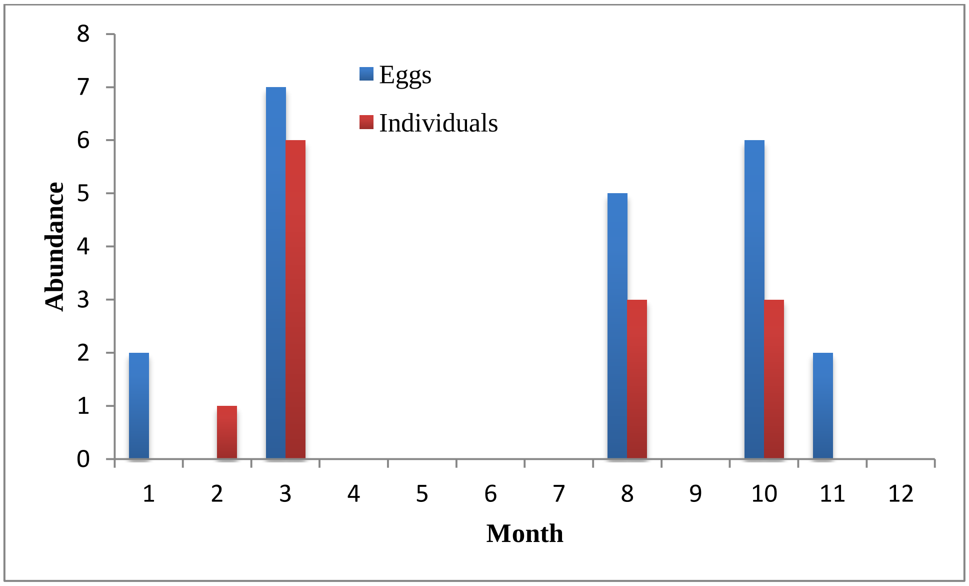

Figure 8. Monthly sampling at Station 5 in 2012-2013 and the respective numbers of individuals and eggs in the hauls. Note that the February data are from 2013 only, while the January data are from both years (cf. Table 7).

3.1.1.2 Spatial variation

The physical model for estuarine circulation and thereby coastward transport of pelagic organisms is more realistic when omitting Stations 1 and 2 from the analyses. When combining data from all full-week cruises, egg abundances increased from the inner to the outer parts of the fjord, while the trend was opposite for the early stage individuals abundances (Table 8).

Table 8. Distribution of eggs and early stage individuals on Stations 3, 4 and 5 in total materials from all cruises.

Station	**Eggs**	**Early stage individuals**
3	0	116
4	3	73
5	9	7

The nominal geographic trend in egg- and early stage individuals on Stations 3, 4 and 5 appeared directional and with opposite trends for the two stages although formally, none of them were statistically significant (Table 8 and 9 and Fig. 9).

Table 9. Data from the full-week cruises. Linear regressions of egg and early stage individuals abundance on Station number (Stations 3-5) in joint data set. The significances of the regression ($P_{regr.}$) and variation coefficients (R^2) are shown.

Linear regression	$P_{regr.}$	R^2
Spatial egg distribution	0.12	0.964
Spatial early stage distribution	0.07	0.985

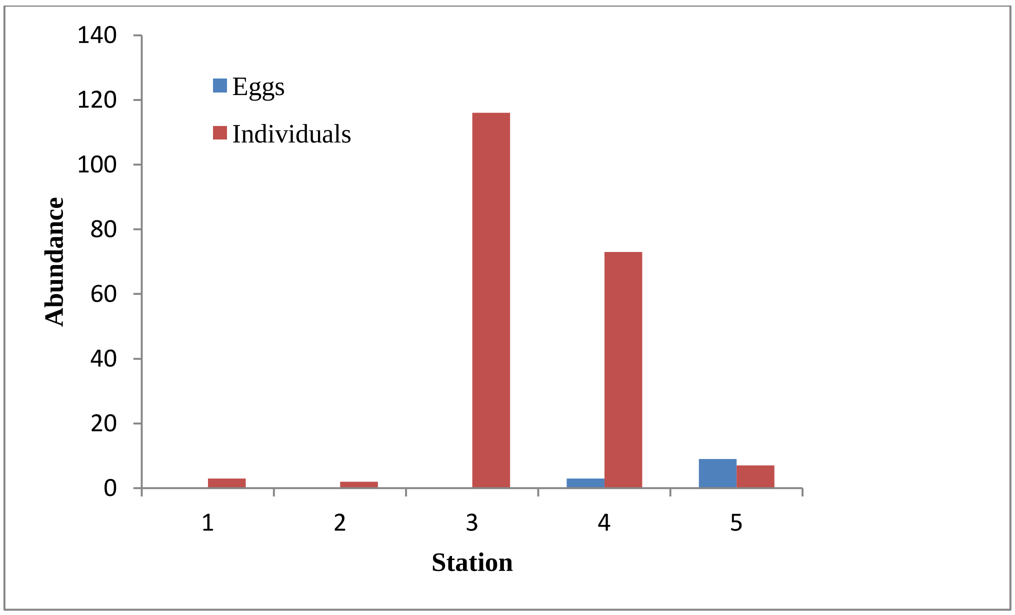

Figure 9. Total abundance of eggs and early stage individuals found at each station for cruises in March 2012, November 2012, February 2013 and April 2013.

3.2 Bottom trawl meadusae biomass estimates

The Periphylla biomass in the standardized bottom trawl hauls (cf. Table 4 in Materials and Methods) on Station 3 was invariable from March of 2012 and up to April of 2013, when the biomass was halved. The dominating size of Periphylla in these trawls was similar on all cruises (Table 10).

Table 10. Trawl results on Station 3 during the project. Standard trawl hauls were used (cf. Material and Methods Table 4). L=liter, CD=coronal diameter.

Date	Biomass (L)	Average size (CD)
27.03.12	600	>5 cm
13.11.12	600	>5 cm
05.02.13	600	>5 cm
08.04.13	300	>5 cm

3.3 Historical plankton haul results

3.3.1 Abundance of eggs and early stage individuals in historical samples

The historical plankton hauls revealed a single early stage individual of Periphylla on Station 4 in year 2002. The first eggs were observed on Stations 3 and 5 in year 2004. Eggs were most abundant in the autumn and winter months, and at depths below 100 meters. The present (Table 7) and historical (Table 11, Fig. 10) abundance of eggs at Station 5, together with a reported mass death of Periphylla in year 2011 (Solheim 2012) and the initial steep rise and subsequent steady state of bottom trawl catches of Periphylla from approximately year 2001 (J. Mork, pers. comm.), provide independent sources of information that the population has now reached its environmental carrying capacity. In line with this, a regression equation was chosen which allowed for an asymptotic regression curve. A regression of egg abundance on year in the period 2002-2012 revealed a curve which flattens out towards the end of the period (Fig. 11). The regression was statistically significant ($p < 0.05$) and explained 89% of the total variance in the abundance data (cf. Fig. 11; caption).

3.3.1.1 Inter- and intra-annual variation in the historic samples

Eggs and early stage individuals were only found at depths below 100 meters. Eggs were found in preserved samples from the years 2004, 2006 and 2008, and only in the September-December period (Fig. 10). The historical samples included only Station 5 in year 2005 and thereafter (Appendix Table 13). No early stage individuals were found at this station.

The material for analysis of mean egg abundance by year was extracted from Appendix Table 13. Egg abundances from January, March and August-December were compared as eggs were only found during these months, and samples were lacking for other months for some of the years (Appendix Table 13). For this analysis the number of eggs for year 2012 was adjusted to the Judy-net sampling gear used historically (cf. Materials and Methods section 2.5.1).

Table 11. Abundance of eggs in historical samples. Mean diameter (Mm). Depth in meters.

St.	Date	Eggs	Egg size	Depth
3	10.11.2004	1	1.2	100-230
5	10.11.2004	2	1.55	100-500
5	18.09.2006	1	1.4	100-500
5	18.09.2006	1	1.6	100-500
5	16.10.2006	1	1.45	100-500
5	22.09.2008	1	1.6	100-500
5	22.09.2008	1	1.35	100-500
5	13.10.2008	1	1.6	100-500
5	10.11.2008	1	1.6	100-500
5	08.12.2008	1	1.55	100-500

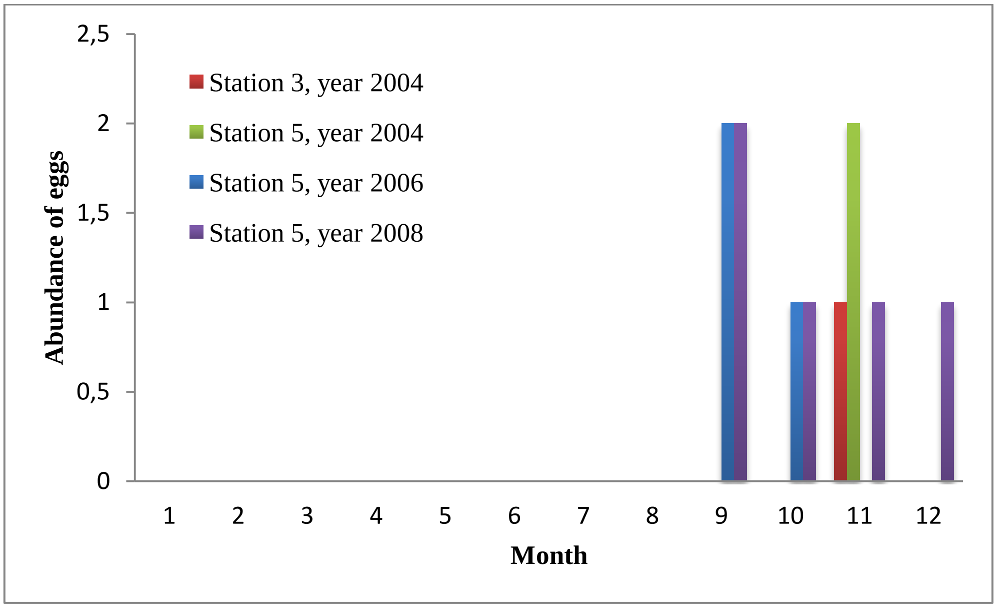

Figure10. Seasonal distribution of pelagic eggs in historical samples from Stations 3 and 5.

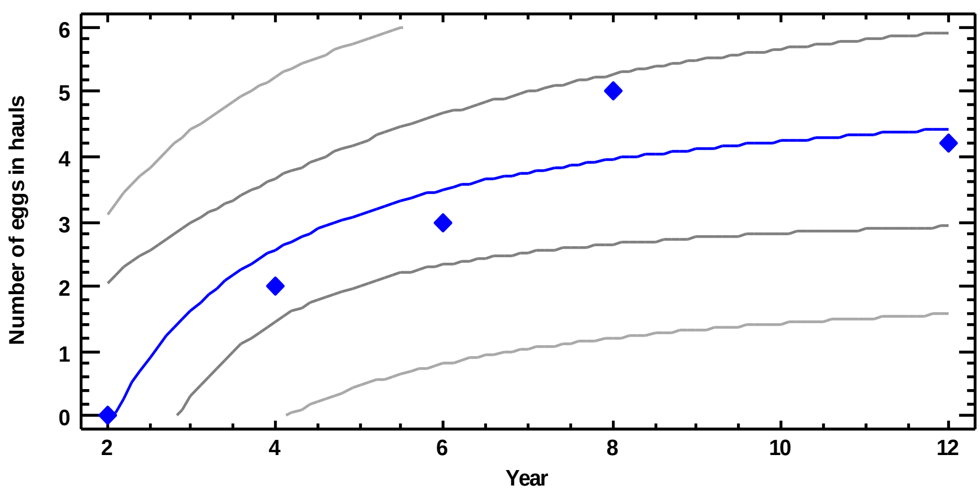

Figure 11. Egg abundance at Station 5. Regression of the mean number of eggs on years in the period 2002-2012. Regression line with 1 and 2 SD confidence limits. Data from Table 7 and 11. A reciprocal-X model regression (Statgraphics) was fitted for the number of eggs in the years 2002-2012 ($P_{regr.}$=0.0167, R^2= 0.887).

3.3.1.2 Spatial variation in the historical samples

The spatial coverage of the plankton samples included only Station 5 from years 2005 to 2012. Thus the material for analysis is very restricted and actually permits few if any conclusions on within-fjord distribution of eggs and early stage individuals in that period.

4. Discussion

The reproduction in Periphylla is thought to be continuous throughout the year, although peaks in the annual reproduction are also believed to occur (Jarms et al. 1999; Lucas and Reed 2010; Mauchline and Harvey 1983; Bozman 2010), and also for other coronates (Russel 1959; Lucas 1996). In this project, the present and historic plankton survey results from the Trondheimsfjord indicate a spawning peak in the autumn and winter months. Spatially, the inner parts of the fjord (Beitstadfjorden and the Ytterøya basin; Stations 3 and 4, respectively) appear to be the most important spawning areas. Thus; annual inflows, tidal currents, advective depths and the general estuarine circulation pattern in those basins are potential determinants for the observed distribution of egg- and early developmental stage individuals in the present plankton samples.

In the present plankton net results, Periphylla eggs were most abundant at Røberg (Station 5), while early development stage individuals were most abundant in Beitstadfjorden and Ytterøya. This pattern points strongly to a main reproduction activity in the inner parts of the fjord, where also the Periphylla population density is highest according to the bottom trawl catches. Possible explanations for the different representation of the 0-group stages at different distances from the spawning areas are discussed below, among others the effects of the physical estuarine forces mentioned above.

According to historic records of Periphylla eggs in plankton samples and the abundance of adults in bottom trawl catches reported in this study, the growth of the population from the initial founder group and up to the carrying capacity of the inner Trondheimsfjord seems to have taken a decade or well so.

4.1.1 Within-year egg and young-stage abundance variation in this study

The abundance of early stage individuals was high in February and highest in April. In these months, no eggs were found in the plankton samples. The developmental time from stage 1 to stage 9 is assumed to be 2-3 months (Jarms et al. 1999), thus indicating high spawning activity in the autumn and winter months. Plankton sampling during summer months would be needed to confirm this pattern for the Trondheimsfjord, but other studies have reported similar observations; Mauchline and Harvey (1983) found in their study from the Rockall Trough in the

North East Atlantic that Periphylla was approaching sexual maturity in July, had reached maturity in November, and the gonads appeared to be spent in February. Bozman (2010) found in her study in the Vefsnfjord that developmental stages of Periphylla without pigmentation (the youngest developmental stages) decreased in abundance from February until May, when the individuals had developed pigmentation and grown in size. Also, in the present historical plankton samples from the Trondheimsfjord, the eggs were most abundant in the autumn and winter months, and studies in the Lurefjord indicated a higher recruitment in autumn; eggs were most abundant in August, September and October (Jarms et al. 1999). In the present study, eggs were found at Røberg in August, October, November, January and March. Generally thus, the results in the present study are in line with previously published works.

Solheim (2012) reported (based on bottom trawl catches and video recordings) a mass death in the Periphylla population in the innermost part of the Trondheimsfjord (Verraboth; Station 1) in March of 2011. The small and shallow Verrabotn location is, however, probably not an important recruitment area for Periphylla, and the mass death observed there may not apply to the entire fjord. However, there is some independent support for the trawl catch observations in that local fishermen reported large amount of dead Periphylla on the beaches of the Beitstadfjord and Ytterøya basins in spring of year 2011 (J. Mork, pers. comm). The total reproduction capacity of the population does not seem to have been appreciably affected by the reported mass death, because the present "spring" materials show a high abundance of eggs in Røberg plankton samples in March of 2012.

4.1.2 Within-fjord egg and young-stage variation in this study

As judged from the abundance of eggs and early developmental stage individuals, recruitment appears to be lower in the outer than in the inner parts of the fjord, where Beitstadfjorden and Ytterøya probably represent the main spawning sites. Hetland (2008) suggested that the “mother population” was located in Beitstadfjorden due to the observed size distribution and large biomass of Periphylla in bottom trawl catches there. That view may have to be adjusted, because it did not take into consideration that Periphylla might simply not seek bottom depths at the >400 meters deep Ytterøya basin, and thus would not be catchable by the bottom trawl used. Including a substantial Ytterøya spawning segment would also fit better to the planktonic stage observations in this project.

Only mature individuals were found in Verrabotn and Verrasundet (present Station 1 and 2 respectively). Hetland (2008) assumed that the population in Beitstadfjorden exported mature individuals to Verrabotn and Verrasundet, which is also consistent with findings of this project. The reported mass death in the Verrabotn location during the winter of years 2010-2011 could be as trivial as starvation for its very dense population observed there the year before.

Eggs were abundant in the outer part of the fjord and absent from the inner part of the fjord. This total absence of eggs in Beitstadfjorden is peculiar since trawl catches have shown a dense population of large, sexually mature Periphylla there, both in this project and those of Hetland (2008) and Solheim (2012). In the Lurefjord, Periphylla stages 1-4 remain at about 230 meters depth due to their neutral buoyancy (Jarms et al. 2002). The water density corresponding to that depth is in the potential advection layers in the Beitstadfjord.

The above mentioned evidence for high Periphylla reproduction in Beitstadfjorden and Ytterøya and the knowledge of the main current systems in the fjord (Fig. 2) makes it reasonable that these parts of the fjord are the main providers of pelagic eggs for the outer fjord. If Periphylla spawning takes place in the upper water layers (Jarms et al. 2002), there might be a short period in which eggs near surface layers can be rapidly transported outwards by the estuarine and tidal currents.

4.2 Historical plankton hauls

4.2.1 Historical abundance of eggs and early stage individuals

Periphylla (one adult individual) was first reported from the Trondheimsfjord in 1984 (Sneli 1984), but it was assumed that the jellyfish had not yet settled in the fjord. Adult individuals were found in trawl catches from year 1999 and onwards (J. Mork, pers. comm). The first evidence of local recruitment in the historical samples was an individual of developmental stage 8 found in May 2002 on Station 4 (Ytterøya). Assuming a local Trondheimsfjord recruitment this individual would have been born in the February-March. After this finding, only eggs were present in the historical samples.

4.2.1.1 Historical inter- and intra annual variation

It appears that the Periphylla population in the fjord has reached its carrying capacity (cf. section 3.3.1.1; Table 10 and Fig. 11). Historically, the abundance of pelagic eggs has increased with time from year 2004 until 2012 when it seems to flatten out (Fig. 11). The plankton abundance history fits well to the trawl catch data, where Periphylla has been the dominant species since year 2003. Intra-annually, the main picture is that spawning is taking place in autumn-winter (Table 10) but with an exception for the year 2012 when considerable numbers of egg were found in March (Table 7).

4.2.1.2 Historical spatial abundance variation

The relatively high abundance of eggs observed at Røberg in this project is most likely due to transport from the inner parts of the fjord, which points to those areas as the main reproduction areas. The possibility that eggs observed at Røberg origin from coastal water inflow is considered unlikely. Røberg is positioned right in the middle of the main outgoing current in the Trondheimsfjord (Fig. 2) and is thus unlikely to function as a retention area for any planktonic organisms of either coastal or internal fjord origin. Also, a net outgoing flow direction will be the effect of the annual bottom water renewal by water masses of Atlantic and coastal origin (Jacobson 1983). The egg abundance at Røberg, thus, would depend mainly on a supply from the inner parts of the fjord, either by the general estuarine circulation or by the annual inflows from the coast.

4.3 Causes for Periphylla invasions

The Norwegian fjords that Periphylla have invaded share some characteristics that would enable successful establishment of Periphylla populations. They are for the most “real” fjords with sills, river discharges and estuarine circulations. The lack of a river discharge in the Lurefjord makes it deviate somewhat from this pattern (Eiane et al. 1999). The infested fjords have suitable temperature regimes for Periphylla, since it as a cosmopolitan species is found to be able to survive under large temperature ranges (Fosså 1992; Larson 1986). Also, the infested fjords have substantial zooplankton production and sufficient depths for this jellyfish which has a preference for the darkness in the deep basins (Farmer and Freeland 1983; Wassmann et al. 1991; Gorsky et al. 2000; Jarms et al. 2002). It has also been found to survive at relatively low prey abundances (Youngbluth and Båmstedt 2001). The deep-dwelling also reduces transport out of the fjords by advective currents (Eiane et al. 1998). The relatively shallow sills at the entrance or within the fjords work to retain Periphylla within the fjord after having entered in the first place (Sørnes et al. 2007). After the egg- and early development stage period, the species have few natural enemies and parasites in Norwegian fjord waters (Youngbluth and Båmstedt 2001; Fosså 1992).

The Norwegian coastal current and the coast-near part of the "Gulf Stream" act as conveyor belts for northwards transport of planktonic and adult specimens of Periphylla along the Norwegian coast. In line with this, the general pattern of infestation seems to have been from south to north over the last 3-4 decades. Fosså (1992) suggested that large individuals are transported all the way up to Spitzbergen and the Barents Sea by the Atlantic current. Kramp (1968) observed that Periphylla only ascended to the advective surface waters in cold areas, and also suggested that it was carried northwards along the western coast of Norway by the currents.

On a larger time scale, Periphylla has existed in some Norwegian fjords for over a hundred years (Fosså 1992), although it was not until the late parts of the 20th century that it became a nuisance for gillnet fisheries. The historical records of detection suggest that the Lurefjord near Bergen was one of the first fjords to be invaded (in the 1970's), followed by the Sognefjord (Fosså 1992). In the Halsafjord, a mass occurrence was first reported in 1984 (Sneli 1984), and high densities were still observed almost two decades later (Sørnes et al. 2007). Recently (2008 and later) mass occurrences has been reported orally by fishermen from the Storfjord in Møre og Romsdal, the Vefsnfjord in Nordland (Bozman 2010) and the Saltenfjord in Bodø (J. Mork, pers. comm.).

The Periphylla population densities and size distributions in the infested fjords vary. Sørnes et al. (2007) found that the mean density of Periphylla was highest in the Sognefjord (100-300 individuals m^{-2}), and lowest for the Lurefjord (25-50 individuals m^{-2}) and the Halsafjord (10-20 individuals m^{-2}). Fosså (1992) found that the density in the Sognefjord increased with depth, and Sørnes et al. (2007) found the population there to be dominated by small individuals (<4 cm in coronal diameter). The populations in the Halsafjord and the Lurefjord show wider size distributions and a dominance of large individuals (Sørnes et al. 2007). In the Trondheimsfjord, the population consists of larger individuals (coronal diameter >12 cm) in the inner parts of the fjord (Verrabotn and Verrasundet) and a wider variation of sizes and a dominance of smaller individuals in the Beitstadfjord (coronal diameter ≤ 4 cm; Solheim (2012)).

In addition to the current systems along the Norwegian coast, the internal current systems in the fjords (i.e. the estuarine and tidal currents) can play important roles in the distribution mechanisms of Periphylla. In fjords, the physical exchange of water is mainly restricted to the layers above the sill depth (Jacobson 1983). Animals that live in the deep fjord basins therefore tend to remain undisturbed by advective forces for long periods (Sørnes et al. 2007) and may thus accumulate dense populations. This is certainly applicable to inner Trondheimsfjord. Aside from the annual inflows of Atlantic and NCC water, the deep parts of the inner fjord are relatively unaffected by advection forces. However, this may apply differently to different size classes of Periphylla. The smaller individuals (4-10 cm in coronal diameter) performing diurnal vertical migrations are probably more prone to advection as they are inferior swimmers compared to the larger individuals, and thus less able to withstand the forces of the currents (Solheim 2012). Lind (2008) found that smaller individuals (6-8 cm in coronal diameter) moved throughout the entire water column during night time in the Lurefjord, which might be the case in the Trondheimsfjord as well. Hetland (2008) found that Periphylla extend very little into the advective layers in the Beitstadfjord, but those studies were only conducted during day time. At high tides, the advective layer will expand downwards and thus affect the out- and inwards transport of Periphylla specimens, especially the small individuals.

Dupont and Aksnes (2010) found that local Periphylla retention is affected by a combination of the light attenuation of the water, basin depth and sill depth. They found that increased light attenuation leads to increased advective loss. Sørnes et al. (2007) suggested that large individuals in the Sognefjord were more prone to advection due to the relatively deep advective layer in the fjord, and that this could explain the dominance of smaller individuals, as no small individuals were observed in the advective layers.

The neutral buoyancy depth for Periphylla eggs and developmental 3 and 4 corresponds to approximately 230 meters in the Lurefjord (Jarms et al. 2002). According to their figure 1, this depth corresponds to a water density of approximately 26.0 Kg/m^3. In the Trondheimsfjord, this water density corresponds to a range of approximately 25-67 meters in the Beitstadfjord and 28-73 meters at Ytterøya, depending on the season (Appendix Table 16). This is well above the sill depths for those two basins (140 and 100 meters respectively), and thus in the zone prone to advection. It is assumed that ideally, the eggs would benefit from staying deep, but with a sufficient distance from the sea floor where they would be more prone to predation (Ulf Båmstedt, Umeå University, pers. comm.). If eggs in the Trondheimsfjord have neutral buoyancies similar to those of the Lurefjord, they would easily be transported outwards above sill depths by the currents. This might explain why eggs are most abundant at Røberg. Simultaneously, the apparent high recruitment in the middle and inner basins indicate that sufficient amounts of eggs are retained there to support and increase the standing crop.

4.4 Previous findings on the reproduction dynamics of coronate jellyfishes

After the early report of Maas (1897), Tiemann and Jarms (2010) were the first to study the gonadic structure and egg development in Periphylla. In their study in the Lurefjord they found a continuous presence of many young developmental stages which indicated continuous spawning during the year. Other studies also indicate that the reproduction is continuous; Jarms et al. (1999) found that female individuals in the Lurefjord carried thousands of eggs of different sizes in their ovaries at the same time. Eckelbarger and Larson (1992) suggested that the females produce only a few mature eggs per day. Morandini and de Silveira (2001) suggested that continuous egg release could also be a result of natural selection, to maximize the success of sexual reproduction. Larson (1986) speculated that coronates like *Atolla wyvillei* and *Atolla chuni* produce eggs very slowly and has a continuous release of a few eggs at the same time, and that this might also be the case for Periphylla. Larson (1986) also suggested that continuous reproduction is universal for all the oceanic scyphomedusa, and if there is any seasonality in the reproduction, it would relate to the seasonality of the prey; from his study in the southern ocean, he related the finding of eggs of broad range sizes in several coronates and the minimal seasonal changes in the biomass of the zooplankton, to a continuous reproduction in these coronates. The Trondheimsfjord reproduction cycle could be related to the nutritional status of the Periphylla at different times of the year, thus the high abundance of eggs in autumn months.

Periphylla is distributed in all deep oceans, in very low abundances compared to those in the invaded Norwegian fjords (Delpedado et al. 1998). It is not known how they are able to find mates in open oceans. Jarms et al. (1999) suggested that fertilized eggs are released in the deep water where they remain for several months as free-floating. However, Tiemann et al. (2009) found that in the Lurefjord, sexually mature individuals aggregated into groups of both sexes in surface layers during night time. This is probably an effective mating strategy developed in the open ocean (Larson 1986), even if the same strategy performed in the fjords would make eggs more prone to advection. Studies of other jellyfishes support that the surface aggregation of sexually mature medusa is a widespread mechanism for reproduction (Lewis and Long 2005; Hay et al. 1990).

Youngbluth and Båmstedt (2001) found that the surface aggregations in the Lurefjord occurred from late autumn until spring. If the same behaviour applies also to the Trondheimsfjord, it could explain why eggs are mostly found during autumn and winter months. Periphylla has not been observed in surface layers in the Trondheimsfjord, but few night-time studies have been conducted, and not throughout the year. Also, it might be that aggregations occur at shallow depths although not in the very surface. This aspect deserves focus in future studies.

The most detailed studies of the reproduction cycle of Periphylla have been conducted in the Lurefjord. Local spawning has been found to take place in the fjord in all years since 1993, and there is evidence for a more intense reproduction during summer and autumn (Jarms et al. 1999). Figure 12 shows a comparison of egg and young individual abundance from the Lurefjord (years 1994-1997) and the Trondheimsfjord (years 2004-2008, including data from year 2012 in the present study). Most eggs were found in September for both fjords, with abundances in later autumn months as well. The difference seems to be that eggs are present also during winter months in the Trondheimsfjord.

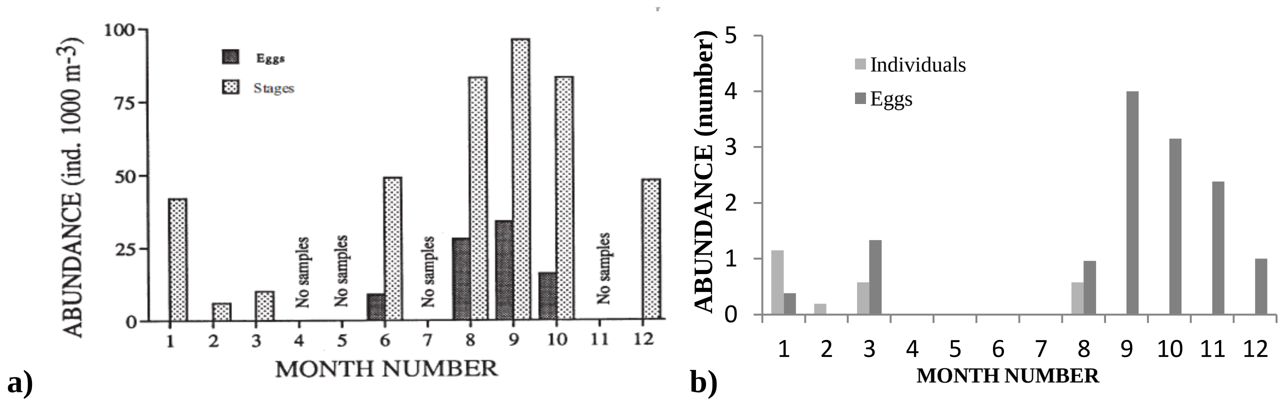

Figure 12. Comparison of Periphylla eggs and early stage individuals abundances from the Lurefjord (a) and the Trondheimsfjord (b). Fig. (a) shows the average abundance of eggs and early stage individuals of Periphylla in the Lurefjord from years 1994-1997, adopted from Jarms et al. 1999. Fig (b) shows the average abundance of eggs of Periphylla at Røberg Station in the Trondheimsfjord from years 2004-2008, including data from year 2012 (data from year 2012 is converted into the Juday-sampling method (see Materials and Methods section 3.2.5).

4.5 Bottom trawling results

A recent study by Solheim (2012) from years 2011 and 2012 on the population trend of Periphylla in the Trondheimsfjord revealed that the biomass in the three innermost basins was dominated by large individuals (coronal diameter >12 cm). She also found that the population appears to have been decreasing in biomass since the former study by Hetland (2008). Nevertheless, she found a large amount of smaller individuals (coronal diameter ≤ 4.0 cm) in Verrasundet and Beitstadfjorden, which strongly indicated a continued strong local recruitment. Additional trawling done in Verrabotn and Verrasundet during this study revealed that the population in the innermost part of the fjord in years 2012-2013 was dominated by individuals <5 cm in coronal diameter. The larger individuals (coronal diameter >5 cm) were pale and seemed weakened in April of 2013. There are indications that Periphylla have a higher mortality rate during winter and spring months, as suggested by Solheim (2012) and Hetland (2008) who found weakened large Periphylla with holes in their hoods at the innermost Stations Verrabotn and Verrasundet. It is possible that the weakened individuals found at these stations are weakened due to trapping in unfavorable environment conditions like shallow depths (60 and 100 meters, respectively, in Verrabotn and Verrasundet), and insufficient food resources during the winter.

4.6 Predators and parasites of Periphylla

Except perhaps for the eggs and early development stages of Periphylla, the Trondheimsfjord harbours few natural predators of Periphylla. Some fishermen have reported observations of whiting (*Merlangius merlangus*) with stomachs full of small Periphylla, but this has so far not been substantiated scientifically (J. Mork, pers. comm.). Some actinians are known to predate on small and medium sized Periphylla specimens. Indeed, the abundance of the sea anemone *Urticina eques* has increased in recent years in bottom trawl catches in Verrasundet, the next innermost location of the present study (J. Mork, pers. comm.).

The "jellyfish amphipod" *Hyperia medusarum* (Müller 1776) (Fig. 13), was found on Periphylla in bottom trawl catches in Verrabotn, Verrasundet and Beitstadfjorden in February and April of 2013. Probably the same amphipods species were video filmed while dwelling in the mesoglea of apparently weakened Periphylla specimens in March of 2011 (Solheim 2012) on the Verrabotn location.

Hyperia medusarum is confined to the northern parts of the North Sea. The amphipod is considered a marine parasitoid, and it remains on the medusa through adulthood. Eggs are laid on the medusa, and juveniles stay on the host and eats off the hosts prey. Both adults and juveniles also feed on the host, primarily the tentacles and gonads (Laval 1980). Juveniles were observed in the gonad of a Periphylla in Verrabotn in April of 2013. Accidental predation on the jellyfish can occur when predators pluck the amphipod attached to the medusa. Juvenile, female and male *H. medusarum* have been found to parasite on the scyphozoan *Phacellophora camtschatica;* in late summer, all individuals of the scyphozoan were attacked by hundreds of amphipods. Adult males were found to be clinging on the host throughout the season (Towanda and Thuesen 2006). It might be that Periphylla is weakened in the winter due to food scarcity. In the present study, the larger medusa (coronal diameter >5 cm) found in trawl catches on the three innermost stations were more frequently attacked by the amphipod than the smaller ones (coronal diameter <5 cm). The mass death of Periphylla observed in Verrabotn in November of 2011 was reportedly paralleled by masses of large, dead medusae being washed ashore on other locations in the inner fjord. The mass death in Verrabotn was documented on video from ROV (Solheim 2012).

The biomass in the Beitstadfjord in April of 2013 was only half of those measured in previous years (cf. Table 10), indicating that Periphylla specimens in fact may be weakened during the winter in the Trondheimsfjord. *H. medusarum* have previously been found to be symbiotic with a small proportion of the individuals in the Lurefjord in the late 1990's (Marsh et al. 2001), where damage was found on tentacles and mesoglea of the medusae.

Bottom trawl catches in the Beitstadfjord in February of 2013 indicated that approximately one third of the Periphylla were attacked by the amphipod. All sizes down to 4 cm in coronal diameter of Periphylla were attacked, and the number of amphipods on each individual ranged from 1-5 individuals. In addition, grooves from previous attacks in the mesoglea of the jellyfish were observed.

Figure 13. Periphylla individual (coronal diameter = 5 cm) with *Hyperia medusarum* crawling out of the mesoglea. Photos: Åshild Løvås Borgersen.

The gadoid fish whiting (*Merlangius merlangus*) has been associated with scyphozoans both as a competitor for planktonic prey and as a predator (Hay et al. 1990). Local fishermen in the Trondheimsfjord (J. Mork, pers. comm.) have observed small Periphylla in the stomachs of whiting. However, in the Trondheimsfjord the whiting abundance on the locations most heavily infested by Periphylla has decreased in the last decade in concert with the increase in Periphylla abundance (J. Mork, pers. comm.). Any causal relationship of these phenomena has not yet been established. Aksnes (2007) suggests that that increased light attenuation (as measured by e.g. shallower Secchi disk depths) in Norwegian fjords is responsible for decrease in whiting stocks since whiting is a visual feeder in contrast to the Periphylla which benefits from a darker environment. Norvard (2008) examined whiting stomachs for Periphylla in Lurefjorden, but found no traces of Periphylla.

A mass occurrence of the sea anemone *Actinostola collosa* (Verrill 1882) is thought to be correlated with the high abundance of Periphylla in the Lurefjord (Jarms and Tiemann 2004). The anemone is medusivorous, and a video was recorded of this anemone devouring a big Periphylla specimen. Whether this predator affects the Periphylla stock in the Trondheimsfjord is unknown. On the other hand very large specimens of a different sea anemone (*Urticina felina*) have often occurred in bottom trawl together with Periphylla in recent years (J. Mork, pers. comm.).

4.7 Conclusion

This study indicates that the annual reproduction cycle of Periphylla in the Trondheimsfjord is continuous, but with a higher reproduction intensity during autumn and winter. The adult population seems to thrive and proliferate behind the thresholds in the inner parts of the fjord (the Beitstadfjord and the Ytterøya basins), which also seem to be the main spawning areas. In the innermost parts of the fjord (Verrasundet and Verrabotn), Periphylla seems to be trapped under unfavorable conditions; they are weakened and attacked by a parasitic amphipod during winter and spring, and do not seem to reproduce there. The abundance of early developmental stage individuals was low in the coastward part of the fjord (Røberg), possibly because the bottom water masses there have a higher exchange rate and thus lower residence time than in the inner basins. The eggs found on the outermost station, Røberg, are likely transported from the inner parts of the fjord.

As indicated by the documented recent episodes of mass deaths and a leveling-out of the adult specimens as well as egg abundances, the Periphylla population in the Trondheimsfjord seems to have reached the carrying capacity of the local environment. According to the historical pelagic egg records as well as those from bottom trawl surveys, the population growth until this stage has taken approximately 10-12 years. The most recent results indicate that the main population is healthy and still able to withstand its competitors for a top predator position.

Reference list

Aksnes, D.L. (2007) “Evidence for visual constraints in large marine fish stocks” *Limnology and Oceanography* 52(1): 198-203

Aksnes, D.L., Dupont, N., Staby, A., Fiksen, Ø., Kaartvedt S. and Aure, J. (2009) “Coastal water darkening and implications for mesopelagic regime shifts in Norwegian fjords” *Marine Ecology Progress Series* 387: 39-49

Arai, M.N. (2001) “Pelagic coelenterates and eutrophication: a review” *Hydrobiologia* 451:69-87

Avian, M. and Rottini Sandrini, L. (1991) “Oocyte development in four species of scyphomedusa in the northern Adriatic Sea” *Hydrobiologia* 216/217: 189-195

Berrill, N.J. (1949) “Developmental analysis of scyphomedusae” *Biological Reviews* 24(4): 393-409

Bozman, A. (2010) “*Preliminary investigation of light regime and the population dynamics of a deep sea Scyphozoan, Periphylla periphylla in a northern Norwegian fjord*”. Bachelor’s thesis. University of Nordland, Bodø.

Båmstedt, U., Fåsså, J.H., Martinussen, M.B. and Fosshagen, A. (1998) “Mass occurrence of the physonect siphonophore *Apolemia uvaria* (LESUEUR) in Norwegian waters” *Sarsia* 83(1): 79-85

Dupont, N. and Aksnes, D.L. (2010) “Simulation of optically conditioned retention and mass occurrences of *Periphylla Periphylla*” *Journal of Plankton Research* 32(6): 773-783

Eckelbarger, K.J. and Larson, R. (1992) “Ultrastructure of the ovary and oogenesis in the jellyfish *Linuche unguiculata* and *Stomolophus meleagris*, with a review of ovarian structure in the Scyphozoa” *Marine Biology* 114: 633-643

Eiane, K., Aksnes, D.L. and Ohman, M.D. (1998) “Advection and zooplankton fitness” *Sarsia* 83: 87-93

Eiane, K., Aksnes, D.L., Bagoien, E. and Kaartvedt, S. (1999) "Fish or Jellies- A Question of Visibility?" *Limnology and Oceanography* 44(5): 1352-1357

Farmer, D.M. and Freeland, H.J. (1983) "The Physical Oceanography of Fjords" *Progress in Oceanography* 12: 147-220

Fosså, J.H. (1992) "Mass occurrence of *Periphylla periphylla* (Scyphozoa, Coronatae) in a Norwegian fjord" Sarsia 77: 237-251

Gorsky, G., Flood, P.R., Youngbluth M., Picheral M. and Grisoni J.M. (2000) "Zooplankton Distribution in Four Western Norwegian Fjords" *Estaurine, Coastal and Shelf Science* 50: 129-135

Hay S.J, Hislop J.R.G. and Shanks A.M. (1990) "North Sea Scyphomedusae; summer distribution, estimated biomass and significance particularly for 0-group Gadoid fish" *Netherlands Journal of Sea Research* 25(1/2): 113-130

Hay, S. (2006) "Marine Ecology: Gelatinous Bells May Ring Change in Marine Ecosystems" *Current Biology* 16(17): 679-682

Hetland, K. (2008) "*Vertical distribution, Abundance and Ecology of Periphylla periphylla (Scyphozoa, Coronatae) in Trondheimsfjorden, Norway*" Master's thesis. NTNU, Trondheim

IPCC, 2001: Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change [Hougton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Dai, X., Maskell, K. and Johnson, C.A. (eds)] "Cambridge University press, Cambridge, United Kingdom and New York, NY, USA

Jacobson, P. (1983) "Physical Oceanography of the Trondheimsfjord" *Geophysical and Astrophysical Fluid Dynamics* 26: 3-26

Jarms, G., Båmstedt, U., Tiemann, H., Martinussen, M.B. and Fosså, J.H. (1999) "The holopelagic life cycle of the deep- sea medusa *Periphylla periphylla* (Scyphozoa, Coronatae)" *Sarsia* 84: 55-65

Jarms, G., Tiemann, H. and Båmstedt, U. (2002) "Development and biology of *Periphylla periphylla* (Scyphozoa: Coronatae) in a Norwegian fjord" *Marine Biology* 141: 647-657

Jarms, G. and Tiemann, H. (2004) "*Actinostola collosa* (Verrill, 1882) (Actionostolidae, Anthozoa), a medusivorous sea anemone and its mass occurrence in the Lurefjord, Norway" *Helgoland Marine Research* 58: 15-17

Kramp, P.L. (1968) "The scyphomedusae collected by the Galathea expedition 1950-52" *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* 131:67-98

Larson, R.J. (1986) "Pelacic Scyphomedusae (Scyphozoa: Coronatae and Semaeostomeae) of the Southern Ocean" In Kornicker, L.S. (ed.) *Biology of the Antarctic Seas XVI, Antarctic Research Series* 41: 59-165, AGU, Washington, D.C

Laval, P. (1980) "Hyperiid amphipods as crustacean parasitoids associated with gelatinous zooplankton" *Oceanography and Marine Biology: An Annual Review* 18:11-56

Lewis, C. and Long, T.A.F. (2005) "Courtship behaviour and reproduction in *Carybdea sivickisi* (Cnidaria: Cubozoa)" Marine Biology 147: 477-483

Lind, M.J. (2008) "*Vertikalfordeling og - svømmeatferd hos Periphylla periphylla i Lurefjorden*" Master's thesis. University of Oslo, Oslo

Lucas, C.H. (1996) "Population dynamics of *Aurelia aurita* (Scyphozoa) from an isolated brackish lake with particular reference to sexual reproduction" *Journal of Plankton Research* 18(6): 987-1007

Lucas, C.H. and Reed, A.J. (2010) "Gonad morphology and gametogenesis in the deep- sea jellyfish *Atolla wyvillei* and *Periphylla periphylla* (Scyphozoa: Coronatae) collected from Cape Hatteras and the Gulf of Mexico" *Marine Biological Association of the United Kingdom* 90(6): 1095-1104

Lynam, C.P., Hay, S.J. and Brierley, A.S. (2004) "Jellyfish abundance and climatic variation: contrasting responses in oceanographically distinct regions of the North Sea, and possible implications for fisheries" *Journal of Marine Biology Association of the United Kingdom* 85:435-450

Maas, O. (1897) "Reports on an exploration of the west coasts of Mexico, Central and south America, and of the Galapagos Islands" *Die Medusen, Museum of Comparative Zoology at Harvard College* 23:9-92

Marsh, J., Youngbluth, M.J. and Båmstedt, U. (2001) "Distribution, abundance, behavior and metabolism of *Periphylla periphylla*, a mesopelagic coronate medusa in a Norwegian fjord" *Hydrobiologia* 451: 321-333

Morandini, A.C. and de Silveira, F.L. (2001) "Sexual reproduction of *Nausithoe aurea* (Scyphozoa, Coronatae). Gametogenesis, egg release, embryonic development, and gastrulation*" *Scientia Marina* 65(2): 139-149

Mauchline, J. and Harvey, P.F. (1983) "The scyphomedusae of the Rockall Trough, northeastern Atlantic ocean" *Journal of Plankton Research* 5(6): 881-890

Norvard, L. (2008) "*Vertikalfordeling og døgnvandring hos Periphylla periphylla i Lurefjorden i forhold til fysiske faktorer, fødefordeling og predasjonsfare*" Master's thesis. University of Oslo, Oslo

Purcell, J.E., Uye, S. and Lo, W. (2007) "Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review" *Marine Ecology Progress Series* 350: 153-174

Reigstadt, M. and Wassmann, P. (1996) "Importance of advection for pelagic- benthic coupling in north Norwegian fjords" *Sarsia* 80: 243-327

Russel, F.S. (1959) "Some observations on the scyphomedusa *Atolla*" *Journal of the Marine Biological Assosiation of the United Kingdom* 38: 33-40

Sneli, J.A. (1984) "Masseopptreden av *Periphylla periphylla*" *Fauna* 37: 167

Sneli, J.A. (2003) "*Marinbiological publications from the Trondheimsfjord 1763- 2000*" Universitetsbiblioteket I Trondheim, Trondheim

Solheim, H. (2012) "Population trend of *Periphylla periphylla* in inner Trondheimsfjord" Master's thesis. NTNU, Trondheim

Sørnes, T.A., Aksnes, D.L., Båmstedt, U. and Youngbluth, M.J. (2007) "Causes of mass occurrences of the jellyfish *Periphylla periphylla*: a hypothesis that involves optically conditioned retention" *Journal of Plankton Research* 29(2): 157-167

Søtje, I., Tiemann, H. and Båmstedt, U. (2007) "Trophic ecology and the related functional morphology of the deepwater medusa *Periphylla periphylla* (Scyphozoa, Coronata)" *Marine Biology* 150: 329-343

Tiemann, H., Søtje, I., Johnston, B.D., Flood, P.R. and Båmstedt, U. (2009) "Documentation of potential courtship- behaviour in *Periphylla periphylla* (Cnidaria: Scyphozoa)" *Journal of Marine Biological Association of the United Kingdom* 89(1): 63-66

Tiemann, H. and Jarms, G. (2010) "Organ- like gonads, complex oocyte formation, and long-term spawning in *Periphylla periphylla* (Cnidaria, Scyphozoa, Coronatae)" *Marine Biology* 157: 527-535

Towanda, T. and Thuesen, E.V. (2006) "Ectosymbiotic behavior of *Cancer gracilis* and its trophic relationships with its host *Phacellophora camtschatica* and the parasitoid *Hyperia medusarum" Marine Ecology Progress Series* 315: 221-236

Wassmann, P., Peinert, R. and Smetacek, V. (1991) "Patterns of production and sedimentation in the boreal and polar Northeast Atlantic" In Sakshaug. E., Hopkins, C. C. E. and Oritsland. N. A. (eds.) *Proceedings of the Pro Mare Symposium on Polar Marine Ecology, Polar Research* 10(1): 209-228, Trondheim

Wendelbo, P.S. (1970) "*Hydrografiske forhold I Trondheimsfjorden 1963-66*". Master's thesis. University of Oslo, Oslo

Youngbluth, M.J. and Båmstedt, U. (2001) "Distribution, abundance, behavior and metabolism of *Periphylla periphylla*, a mesopelagic coronate medusa in a Norwegian fjord" *Hydrobiologia* 451: 321-333

Appendix

Table 12: Abundance of eggs and early developmental stage individuals and average size of eggs from all cruises in years 2012 and 2013.

Early stage	Individuals	Eggs	Average size eggs
Station 3	**116**	**0**	**0**
27.03.2012	11	0	0
13.11.2012	13	0	0
05.02.2013	37	0	0
09.04.2013	55	0	0
Station 5	**13**	**22**	**1.39**
20.01.2012	0	2	1.36
26.03.2012	6	7	1.27
20.08.2012	3	5	1.33
16.10.2012	3	6	1.56
12.11.2012	0	2	1.43
15.01.2013	0	0	0
04.02.2013	1	0	0
08.04.2013	0	0	0
Station 1	**3**	**0**	**0**
28.03.2012	3	0	0
14.11.2012	0	0	0
10.04.2013	0	0	0
Station 2	**2**	**0**	**0**
28.03.2012	2	0	0
14.11.2012	0	0	0
10.04.2013	0	0	0
Station 4	**73**	**3**	**1.35**
26.03.2012	18	3	1.35
12.11.2012	37	0	0
04.02.2013	5	0	0
09.04.2013	13	0	0
Total	**207**	**25**	**1.37**

Table 13. Historical plankton hauls samples for the years 1994-2011.

Station	Year	Bottom-up (m)	100-0 (m)	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
5	1994	X	Y	XY	XY	XY	XY	Y	XY	XY	XY	XY	XY	XY	XY
5	1995			XY	XY	XY	XY	XY	XY	XY	XY	XY	XY	XY	XY
5	1998			XY	XY	X	XY	XY	XY	XY	XY	XY	XY	XY	XY
5	2000			XY	XY	XY	XY	XY	XY	XY	Y	XY	XY	XY	XY
5	2001			XY	XY	XY	XY	XY	XY	Y	XY	XY	XY	XY	XY
5	2002			XY	XY	XY	XY	XY	XY	Y	XY	XY	XY	XY	XY
5	2003			X	XY	XY	XY	XY	XY	XY					
5	2004										XY	XY	XY	XY	
5	2005			XY	XY	XY	XY	XY			XY	XY	XY	XY	XY
5	2006			XY	XY		XY	Y			X	XY	XY	XY	XY
5	2007			X	X	XY	XY	XY	XY	XY	XY		XY	X	X
5	2008			XY	XY	XY	XY	XY	XY	XY	XY	XY	XY	XY	XY
5	2009			XY	XY		XY	XY							
5	2010														
5	2011			XY							XY				
4	1994			XY	XY	XY	XY	XY	XY	XY	XY	XY	XY	XY	XY
4	1995			XY	XY	XY	XY	XY	XY	XY	XY	XY	XY	X	XY
4	1998			XY	XY	XY	XY	XY	XY	XY	Y	XY	XY	XY	XY
4	2000			XY	XY	XY	XY	XY	X		Y	XY	XY	XY	XY
4	2001			XY	XY	XY	XY	XY	XY	XY	XY	XY	XY	Y	XY
4	2002			XY	XY	XY	XY	XY	XY	XY	XY	XY	XY	XY	XY
4	2003			XY	XY	XY	XY	XY	XY	XY					
4	2004								XY		XY	XY	XY	XY	
3	1994			XY	XY	XY	XY	XY	XY	XY	XY	XY	XY	XY	XY
3	1995			XY	XY	XY	XY	XY	XY	XY	XY	XY	XY	XY	XY
3	1998			XY	XY	XY	XY	XY	XY	XY	XY	XY	XY	XY	
3	2000			XY	XY	Y	XY	XY	XY	XY	XY	XY	XY	XY	XY
3	2001			XY	XY	XY	XY	XY	XY	XY	XY	XY	XY	XY	
3	2002			XY		XY	XY	XY	XY	XY	XY	XY	XY	XY	XY
3	2003			X	XY	Y	XY	XY	XY			XY			
3	2004											XY	XY	XY	

Table 14. A summary of the 14 developmental stages. Adopted from Jarms et al. 1999.

1. Eggs; they are spherical and have a slightly yellow color. They have been found to be floating on the surface in culture jars, a useful clue in the identification process.
2. Eggs with a flattened part in the middle of the egg, which is a pore.
3. The specimen looks triangular and develops a collar which is the first sign of the coronal groove.
4. The collar develops wavy structures and the mouth pore is closed. At this stage the medusa can move by short convulsions.
5. The first rhopalia buds are present, and sixteen small marginal lappets appear. Mesoglea is swelling and it is able to contract the marginal zone. The mouth is still closed.
6. Tentacle buds are appearing between the marginal lappets. The animal is spherical and contains whitish yolk. The mouth is now open, and it can swim by pulsations of the bell. There is no pigment present.
7. The mouth lips appear, and pigmentation is developing around the mouth. The tentacles are shorter than the marginal lappets (mean tentacle length of 0.64 +- 0.06 mm).
8. The tentacles are at least as long as the marginal lappets. Its shape is flattening from a ball to a hemisphere. The pigmentation reaches from the mouth to most of the central stomach, only the tip of the stomach is not yet pigmented.
9. At this stage the animal looks like an adult medusa. The lengths of the marginal lappets are at least 0.9 mm.
10. The tips of the tentacles develop pigmentation. The coronal diameter (CD) of the medusa is 6.13 +- 0.84 mm.
11. More than half of the tentacles are pigmented, and the medusa has a CD of 8.26 +- 1.2 mm.
12. The tentacles are completely pigmented, and the medusa has a CD of 12.2 +- 1.5 mm.
13. The pigmentation reaches the tip of the bell, marginal lappets and coronal furrow. The CD is now 21.6 +- 4.4 mm.
14. The last stage is divided into four parts. Stage 14A is when the medusa is completely pigmented, but it has no gonads. The CD is now 38.9 +- 11.4 mm. At stage 14B the medusa has signs of gonads, and the CD is 37.0 +- 6.8 mm. Stage 14C is characterized by sexual dimorphism of the gonads. CD is now 57.3 +- 17.8 mm. At stage 14D the medusa is mature. The smallest CD recorded is 80 mm with egg size 1.25 mm.

Table 15. The number of different early stage individuals found in the project hauls.

Station	Date	Nr. Ind	Stage 1/2	Stage 3	Stage 4	Stage 5	Stage 6	Stage 7	Stage 8	Stage 9	Stage 10	Stage 11	Stage 12	Stage 13	Stage 14A	Stage 14 B	Stage 14 C	Stage 14 D
5	20.01.2012	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	26.03.2012	6	7	0	0	1	1	1	3	0	0	0	0	0	0	0	0	0
4	26.03.2012	18	3	0	0	1	0	1	6	6	2	0	2	0	0	0	0	0
3	27.03.2012	11	0	0	0	0	0	0	3	2	0	1	4	1	0	0	0	0
1	28.03.2012	3	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
2	28.03.2012	2	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
5	20.08.2012	3	5	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0
5	16.10.2012	3	6	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0
5	12.11.2012	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	12.11.2012	37	0	0	1	2	0	1	19	4	4	3	2	1	0	0	0	0
3	13.11.2012	13	0	0	0	0	0	1	4	1	0	3	1	0	1	0	1	1
2	14.11.2012	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	14.11.2012	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	15.01.2013	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	04.02.2013	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
4	04.02.2013	5	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	1
3	05.02.2013	37	0	0	0	0	0	1	8	3	0	3	1	6	5	2	8	0
5	08.04.2013	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	09.04.2013	13	0	0	0	0	0	2	4	6	0	1	0	0	0	0	0	0
3	09.04.2013	55	0	0	0	0	0	1	23	14	6	3	2	1	1	2	0	1
2	10.04.2013	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	10.04.2013	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 16. Temperature, salinity and depths at densities approximately 26 Kg/m³ at Stations 3, 4 and 5 in the Trondheimsfjord in April 2013, February 2013, November 2012 and March 2012.

St. Date	Depth m	Temperature ºC	Salinity PSU	Density Kg/m³
3: 9.4.13	25.500	6.3259	33.0886	26.0018
4: 9.4.13	28.500	4.7413	32.8640	26.0106
5: 8.4.13	4.500	4.9018	32.8793	26.0051
3: 5.2.13	44.500	7.5200	33.2925	26.0025
4: 4.2.13	44.500	7.0254	33.2035	26.0008
5: 4.2.13	24.000	5.9540	33.0290	26.0012
3: 13.11.12	67.500	8.6257	33.5030	26.0053
4: 13.11.12	73.000	8.9941	33.5744	26.0040
5: 16.11.12	66.500	9.1338	33.6006	26.0023
3: 27.3.12	43.78	7.5624	33.3005	26.0028
4: 26.3.12	40.474	7.0059	33.2003	26.0009
5: 26.3.12	29.165	6.9771	33.1957	26.0011