

PRELIMINARY INVESTIGATION OF LIGHT REGIME AND THE POPULATION DYNAMICS
OF A DEEP SEA SCYPHOZOAN, *PERIPHYLLA PERIPHYLLA*, IN A NORTHERN
NORWEGIAN FJORD

BY

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Absract

Jellyfish blooms have been reported worldwide and have ecological and economical consequences. Causes of mass abundances have suggested and include eutrophication, climate change and overfishing. The deep-sea medusa *Periphylla periphylla* has colonized fjords of western Norway in mass numbers since the 1970s and more recently there have been reports of high population numbers in fjords of northern locations. The species experiences fatalities when exposed to light as the medusa pigment is photodegraded. The extended daylight hours of the summer months in northern Norway may be a factor limiting the northern distribution of the *P. periphylla*. Vefsnfjorden is the northernmost fjord with reported mass abundances. Samples were collected from the fjord over a four month period from February to May of 2010 specimens were sorted by developmental stage. Here I present a decrease in both overall numbers of individuals and age classes in Vefsnfjorden, which was most likely caused by a flushing event in the fjord. The lack of early developmental stages collected in the later sampling trips suggest the Vefsnfjorden population may have seasonal reproduction rather than year round as is the case with more southern populations.

Introduction

Periphylla periphylla is a deep-water coronate scyphozoan (Arai 1997) found world wide in nominal numbers (Russell 1970). The exception to this distribution has been observed in Norwegian fjords where mass abundances have been reported over the last decades to present day (Fosså 1992; Sørnes et al. 2007). Populations in Lurefjordnen, Halasfjorden, and Songefjorden have been studied (Jarms et al. 1999, 2002; Tiemann *et al.* 2009; Sørnes et al. 2007; Youngbluth and Båmstedt 2001; Sötje et al. 2007), but there has been little investigation into northern populations (Eiane and Aksnes, unpublished data). Eiane and Aksnes (unpublished data) predict an increase in the northern distribution range *P. periphylla* blooms in the coming years.

Vefsnfjorden is the most northern location with reports of mass abundances of jellies. Population numbers are high enough to prevent fishermen from trawling the area as medusae clog fishing gear (local newspaper, Geir Edvardsen pers. comm.). Limited research has investigated this population and as a result little is known about the population dynamics, status and any possible effects the summer 24-hour light regime may have on the behaviour and adaptations of the species.

Development of *P. periphylla* is direct without a polyp stage and younger age classes are neutrally buoyant in intermediate water column (Jarms *et al.* 1999, 2002; Sötje et al. 2007). Immature and mature medusa have a reddish-brown pigmentation that develops at stage 7 (Jarms et al. 2002). A study by Jarms et al (2002) determined the phototoxic effect light has on the pigment, with both immature and mature medusa suffering lesions and fatalities after exposure to light. Alive *P. periphylla* are rarely found at the surface during daylight hours, and occasions when observations have been made were following storms. Therefore migration of *P. periphylla* can then be assumed limited by light penetration (Jarms et al. 2002). As populations in northern Norway will be exposed to a different light regime than their southern counterparts, distribution throughout the water column may differ seasonally from between southern and northern counterparts. There is limited knowledge of the reproductive behaviours of periphylla, but Tiemann et al. (2009) suggests the surface aggregations observed during night may be a deep sea reproductive strategy now continued into the fjords.

Literature suggests two requirements must be met before mass abundances of *P. periphylla* will colonize a fjord: the presence of and that the optical retention hypothesis and that the system must retain an adequate amount of mature individuals (Eiane et al. 1999; Sørnes et al. 2007; Aksnes et al. 2009). Local fishermen have reported high numbers of *P. periphylla* in Vefsnfjorden and the “optically conditioned retention hypothesis” in the fjord has been discussed by Eiane and Aksnes (unpublished data).

Here I present the population dynamics of Vefsnfjorden *P. periphylla* from samples collected in 2010 and discuss the possible reasons for the observed changes in individual numbers and developmental stages.

Methods

Located at 65 degrees north, Vefsnfjorden is the northernmost fjord with reported mass populations of *P. periphylla*. The fjord is 50-60 km in length with approximate maximum and sill depth of 480m and 85m, respectively. The rivers Vefsna, Fusta and Drevja rivers empty into fjord. Vefsnfjorden was sampled on three separate occasions with cruise dates of February 16, March 20 and April 19 all of 2010 (figure 1). Each cruise began at noon on the sampling day and finished at approximately 2400 hours. Differences in the sampling methods for each trip are explained further in this document. The location of the sample sites were recorded with GPS coordinates as were the starting points of each tow at each site. A Bongo net equipped with a 200 μ m and a 500 μ m nets and closed cod ends. Net diameter was 0.6m and each had a sampling area of 0.28m².

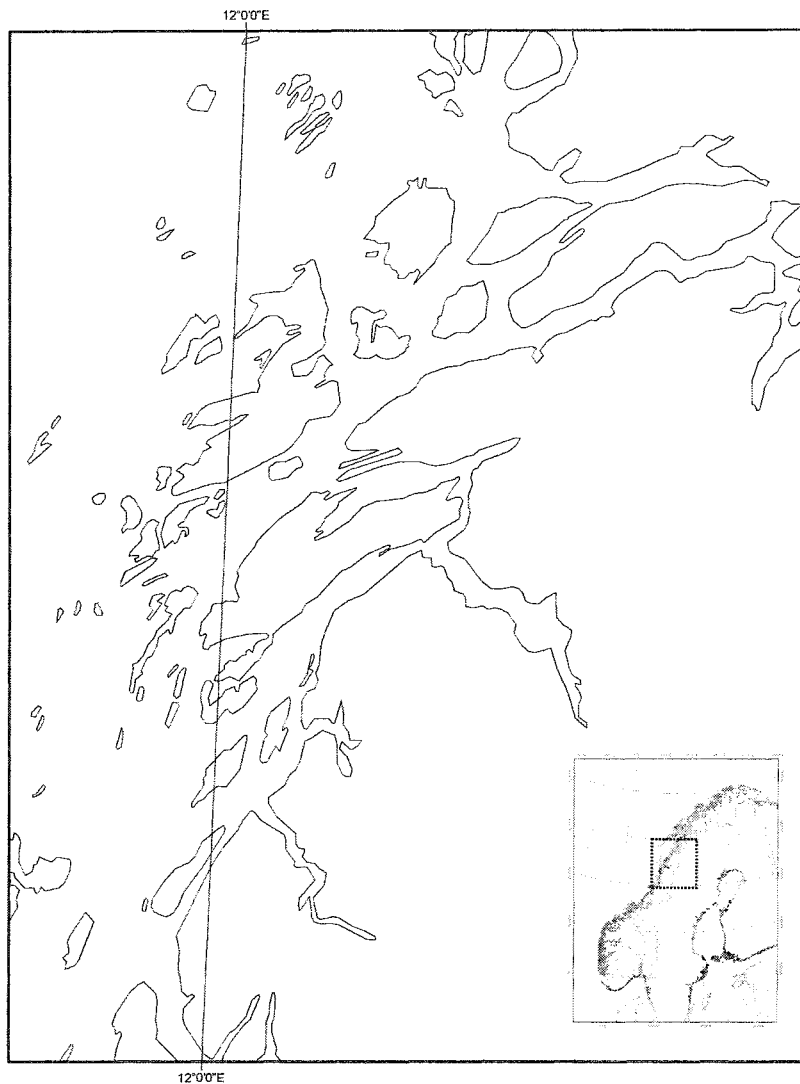


Figure 1: Location of Vefsnsfjorden, northern Norway, the northern most fjord with mass abundance reports of *Periphylla periphylla*. The fjord was sampled in 2008 (Eiane and Asknes, unpublished) and again in 2010.

A salinity, temperature, and density profiler (SAIV AS, Bergen) measured water parameters and was attached to the Bongo net for all samples. In addition, hydrographic profiles were constructed for each cruise using a similar STD fitted with a Turner design fluorometer (figure 2). To ensure the desired depths were sampled, STD data was analyzed on board after the samples for the February cruise only while March and May data was analyzed after cruise completion (Appendix A). At each sampling interval, the Bongo net was towed at specified

depths for a period of approximately 10 minutes before being raised to the next sampling depth in the interval.

Secchi disk readings and weather conditions were recorded at the beginning of each sampling trip. KLUX levels were recorded with a Hanna HI 97500 LUX meter at approximately 10-minute intervals. Readings were converted into photosynthetically active radiation (PAR) units ($\mu\text{mol m}^{-2} \text{s}^{-1}$) (LI-COR 1982; Enoch and Kimball 1986) and graphed for all three sampling days (figure 3).

February 9

Samples were collected from depths of 450-300m, 300-225m and 200-50m during the day and at depths of 450-300m, 275-225m and 200-50m during the night. At Vefsnfjorden site 2, a clean tear in the net of the 200 μm was noticed, which was attributed to errors when lifting the net on board. After this point the cod end was removed for the 200 μm from the rest of the samples of this trip.

MARCH 16

Samples were collected from depths of 450-350m, 300-200m and 150-50m during the day and night.

May 19

Samples were collected from depths of 450-350m, 325-225m and 200-50m during the day and 450-300m, 250-150m and 100-25m during night.

Vertical hauls with a large plankton net were undertaken to compare both the effectiveness of sampling methods and any changes in the *P. periphylla* population with a previous study by Eiane and Aksnes (2009) (table 1). Triplicate hauls with a net 1.25m in diameter with a mesh size of 0.2mm at a speed of approximately 0.5m/s were collected from the bottom to the surface on three different occasions during the trip.

Periphylla collection

Adult specimens captured during the sampling were measured on board for coronal dome height (CH) and coronal width (CD) on all three trips. Those collected from the March 16 and May 19 trips were recorded for sex as male, female or immature on board the vessel. Unfortunately, individual sex data was not collected for the initial sampling trip, February 9. Other observations such as damage to individual jellyfish, differences in colour and scent were recorded.

Samples from plankton trawls were brought back to the lab and examined under a dissecting microscope for size, pigmentation and structural development to be staged as previously described in literature (Jarms *et al.* 1999, 2002). Medusae larger than 10mm were sized without the aid of a microscope. Developmental stages were selected from the entire sample were photographed (Appendix B).

Results

Hydrography

There was a cooling of the water system in Vefsnfjorden over the sampling period from a minimum temperature of 5.6 °C in February to a minimum of 4.7 °C in May (figure 2a). The least amount of variation in temperature was observed in March. Water density varied little across all months with values in the upper water column around 26.0-26.5 and increasing to 28.5 – 28.9 in the deep (figure 2d). The salinity in February was near constant at 33 psu from the surface to the deepest measured waters (figure 2c). March salinity was similar with 33 psu from 11m to the deepest measured waters. In May, the salinity hovered around 33 from 10m to 85m. The greatest variation in the measured water parameters was observed with the dissolved oxygen values (figure 2b). In February, dissolved oxygen hovered around 11.5 mg/l in the first 200m after which the amount gradually increased to 13.47 at the deepest point. In March, the upper water column down to 70m had dissolved oxygen readings of 11.5 in the upper water column and 8.5-9.3mg/L to the deepest measured point. At depths of approximately 50m in the May sample, the dissolved oxygen was 9.05 mg/L and gradually decreased to 8.6 mg/L at the deepest depths. The fluorometer readings in February were all 0.02 µg/l. In March the readings were less than

0.2 $\mu\text{g/l}$ at the surface and gradually decreased to 0.02 $\mu\text{g/l}$. More of a change was apparent in May with the highest reading of .88 $\mu\text{g/l}$ around the 6m mark.

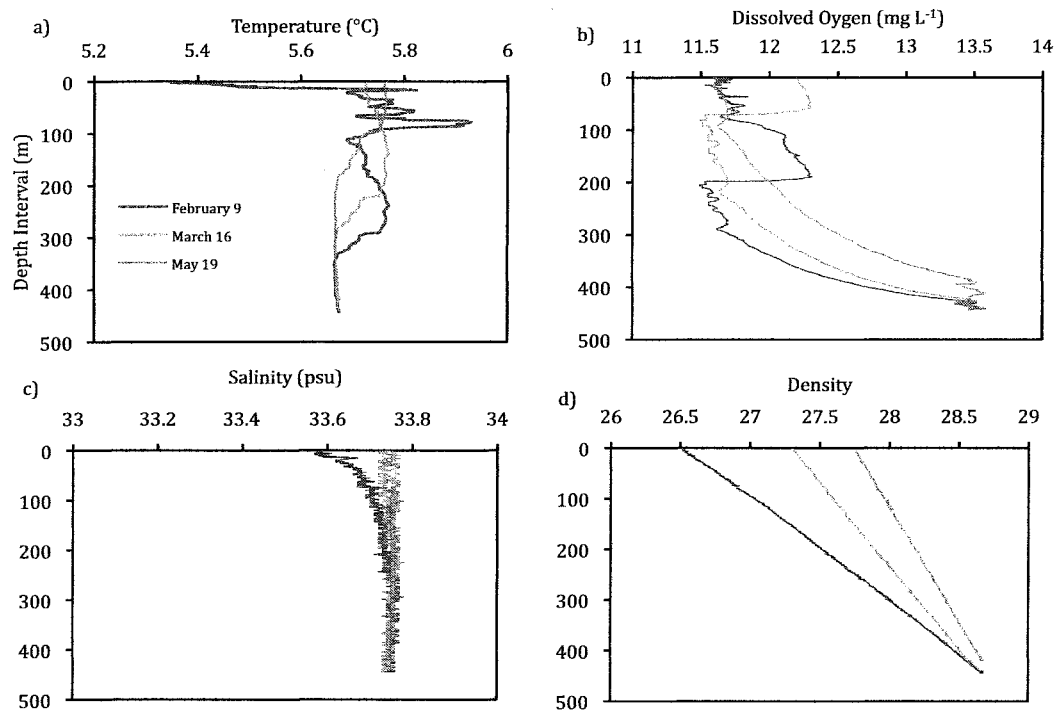


Figure 2: Hydrographic profiles of (a) temperature, (b) dissolved oxygen (c) salinity and (d) density in Vefsnfjorden on sampling dates of February 9, March 16 and May 19 of 2010.

Secchi disk readings changed over the sampling period with a value of over 17m in February (reading was limited by rope length), over 20 m in March (reading was limited by rope length) and 1.5m in May.

Light Levels

The irradiance increased in both intensity and hours available to measure through the sample period (figure 3).

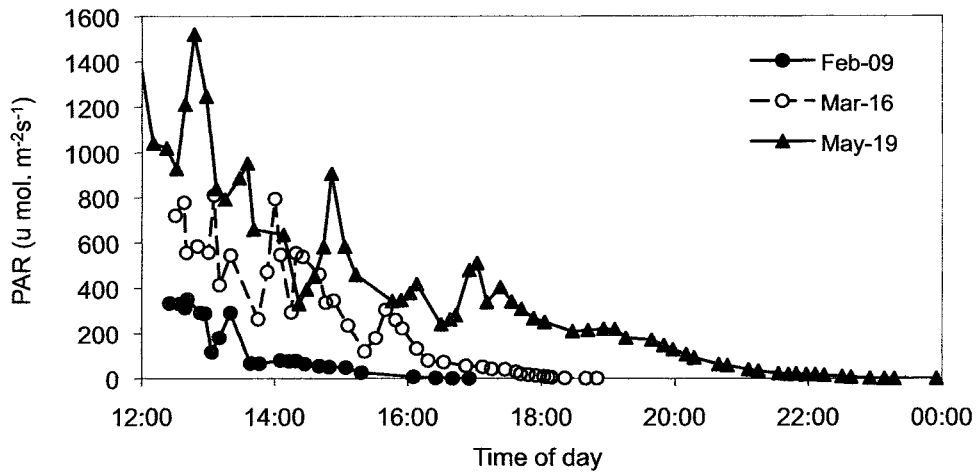


Figure 3: Photosynthetically active radiation readings from Vefsnfjorden during sampling trips on February 9 March 16 and May 19 of 2010.

Abundance Estimates

Density estimates were calculated for the large net samples to compare to data gathered from a previous study by Eiane and Aksnes (forthcoming). There was decrease in density of the 2010 population *P. periphylla* when compared to the 2008 data (table 1). The mean abundance was 2.17 ± 1.24 individuals per m^2 .

Replicate	Net area (m^2)	Size class (CDH, mm)			Abundance (ind m^{-2})
		>10mm	10mm-50mm	50mm-100mm	
1	1.23	1			0.81
2	1.23	1		2	2.44
3	1.23	3		1	3.26

Table 1: May 19 2010 *Periphylla periphylla* net catches in Vefsnfjorden with density estimated assuming 100% filtering efficiency by the nets.

Vertical Migration

Vertical migration patterns between size classes were estimated by comparing the numbers of individuals collected per sampling period at each depth interval at both day and night (figure 4,5,6). Size classes were grouped to form three larger classes of mature medusa (those with a CD of at least 50mm), immature pigmented medusa (with a CD less than 50mm and with

pigmentation) and juveniles (with no pigmentation), of which were only represented in the February samples.

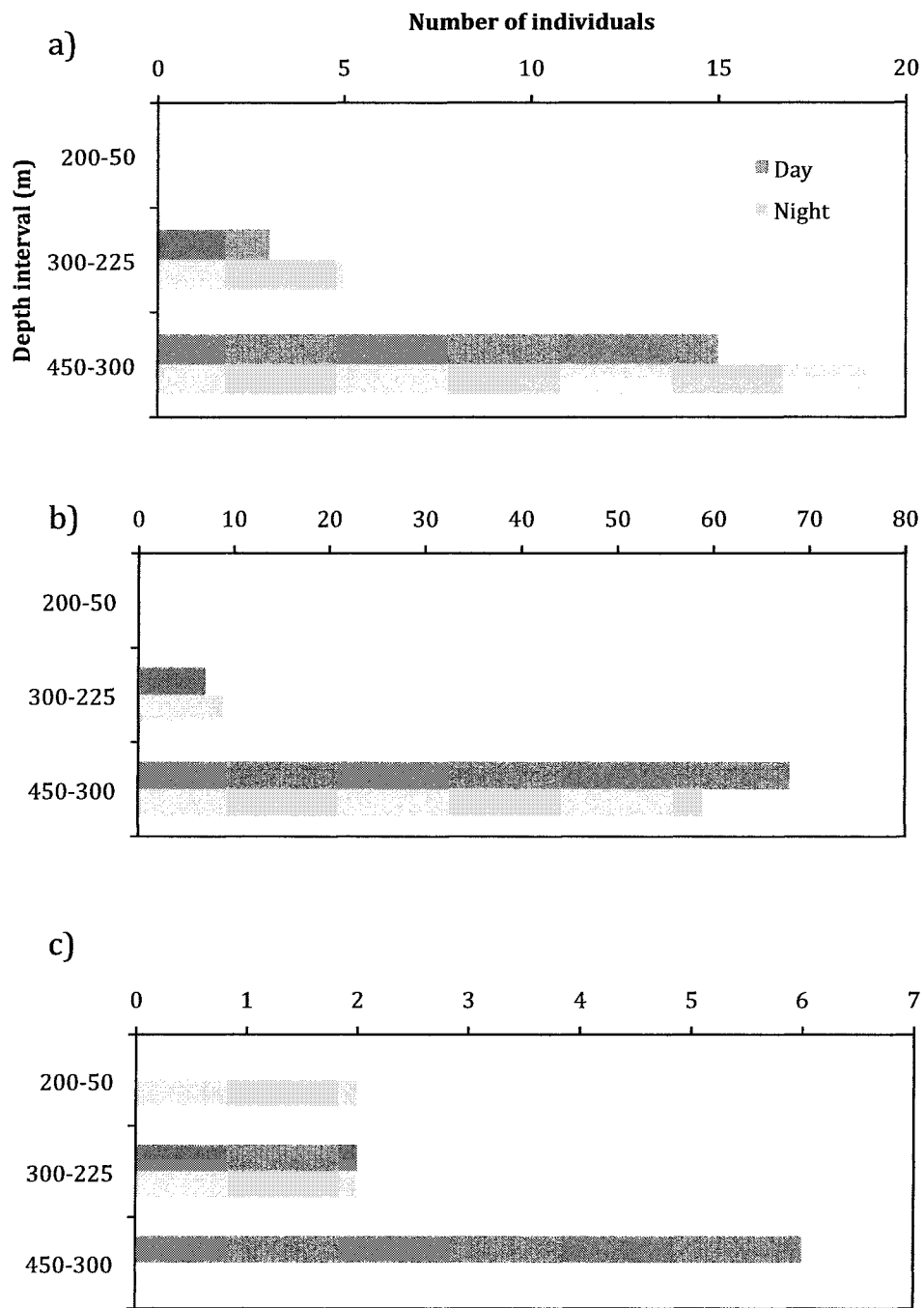


Figure 4: Vertical migration of collected *Periphylla periphylla* during a cruise on February 9 2010 in Vefsnfjorden, Norway, over a 12 hour period. From top, (a) juvenile stages with no pigment; (b) immature pigmented medusa under 50mm in CD; (c) mature medusa with CD greater than 50mm.

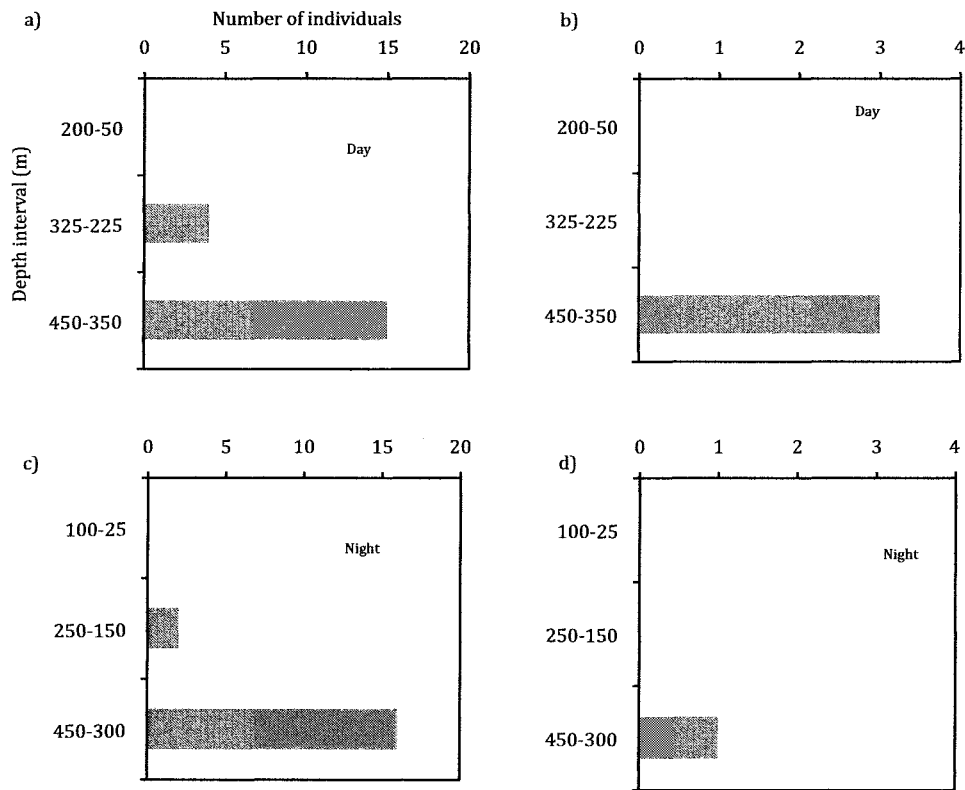


Figure 5: Vertical migration of *Periphylla periphylla* collected during the March 16 2010 cruise in Vefsnfjorden, Norway, over a 12 hour period. Immature medusa with pigmentation and a CD less than 50mm collected during daylight hours (a) and during night hours (b). Mature medusa with a CD greater than 50mm collected during daylight hours (c) and during night hours (d).

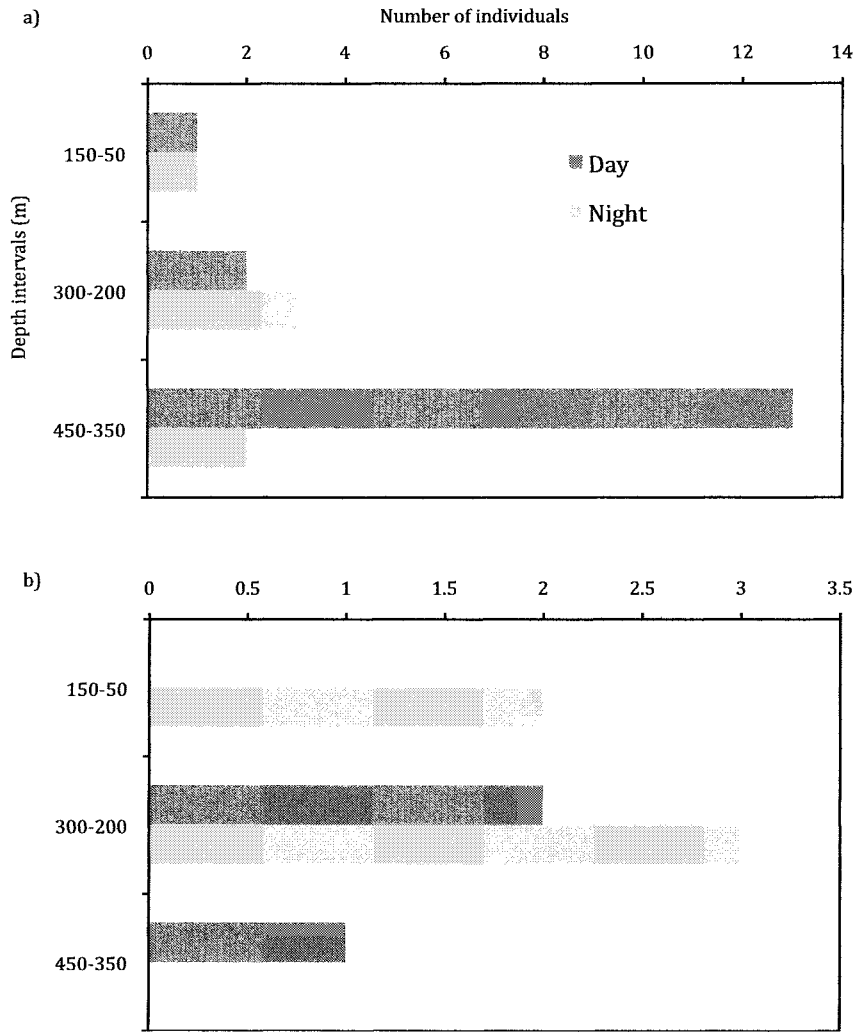


Figure 6: Vertical migration of *Periphylla periphylla* collected during the May 19 2010 cruise in Vefsnfjorden, Norway, over a 12 hour period. Immature medusa with pigmentation and CD less than 50mm (a) and mature medusa with a CD greater than 50mm (b).

February 9

Samples collected in February and processed in the lab had the most damaged specimens.

Atmospheric temperatures during this period were approximately -17°C and tows would freeze when sorted onboard. If the individuals had not suffered damage, and were measureable, the total number of individuals would increase from 188 to 216.

The highest number of individuals was found in the deepest sampling depth across all size groups during both day and night samples (figure Y). Only mature medusa were collected in the upper water column and only for those samples collected at night. All size groups were represented in the intermediate depths for both day and night.

March 16

Immature medusae were collect from both the intermediate and the deepest depths for both the day and the night samples. Mature medusa were only collected in from the 450-300m sampling depth. No size classes were collected in the upper water column for either day or night samples.

May 19

Both mature and immature medusae were collected from all depths during both day and night samples. The highest number of recorded immature medusa was collected from the 450-350 m sampling depth during the day.

Developmental Stages

After stages and measuring all the collected jellies from the three sampling dates a pattern emerged in the progression of developmental stages towards larger medusa and away from the younger stages (figure 7). In February, all stages of *P. periphylla* development were identified and those with a CD less than 5.00mm were the most prominent. Only one out of the 36 specimens collected in March lacked pigment and the highest counts were from the immature pigmented medusae in the two groups with a CD less than 1.00mm and CD of 1.00-5.00mm. Again in the May sample, the group with the highest number of medusae was those with a CD of 1.00mm-5.00mm. The largest mature specimen collected from all cruises was sampled on May 19 and had a CDW of 110 mm and CDH of 175 mm. No unpigmented stages were collected in May.

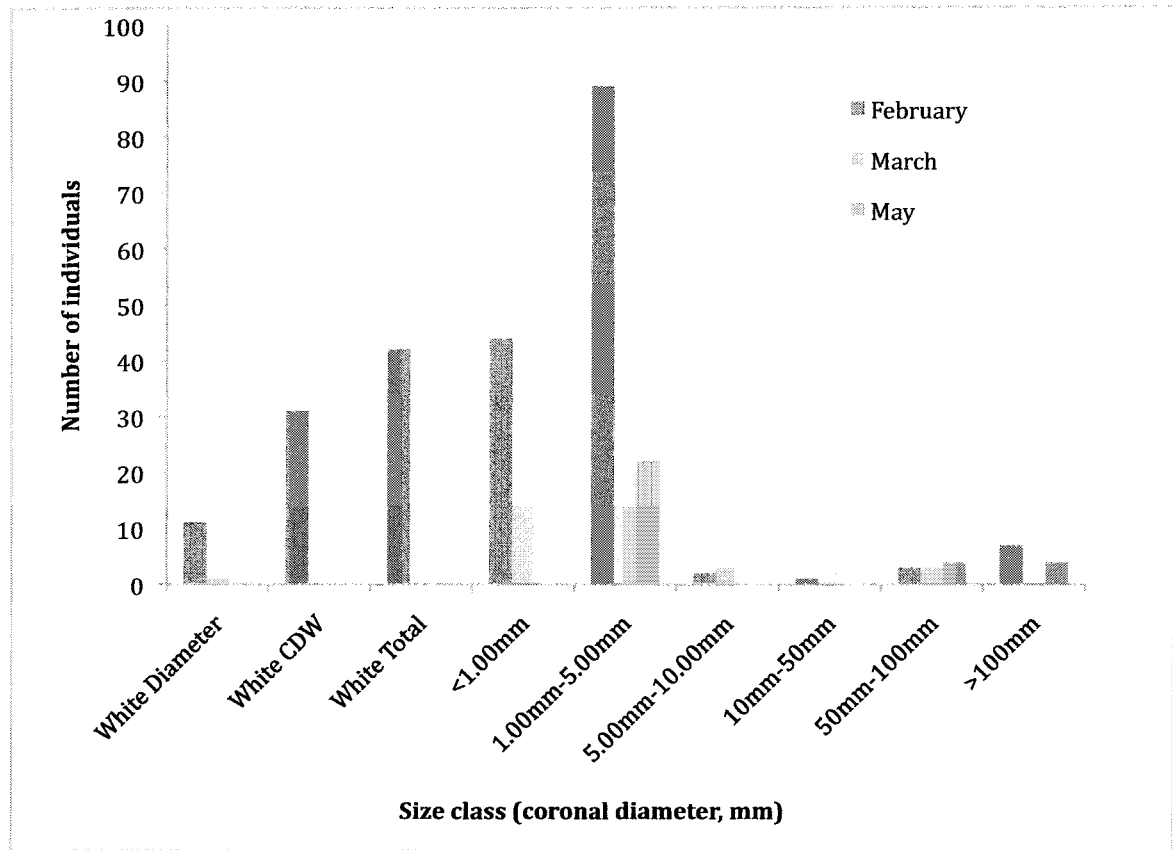


Figure 7: Size distribution of individual *Periphylla periphylla* in Vefsnfjorden, Norway, on three dates, February 9 (n=188), March 16 (n=38) and May 19 (n=30). A total of 28 damaged, and therefore not measured medusa, were found in the February sample and were not included in the graph.

Discussion

Life history

The reproductive behaviours of *P. periphylla* are suited for a deep sea open ocean environment where encounters with the opposite sex may be limited (Tiemann et al. 2009). By migrating to the surface at night, sexually mature medusa lower the dimensional planes from three to two, effectively increasing the chance of encounters (Tiemann et al. 2009). In a relatively closed system, such as a fjord, this method of reproductive behaviour will increase encounters as the surface area of a fjord is much smaller than in the open ocean. An increase in copulation and

reproduction will also increase the population size. With limited or no predators (Søjte et al. 2007), the population of *P. periphylla* has minimal constraints enabling high abundances.

Jarms et al. (1999, 2002) has described a total of 14 stages with four sub-stages in the last stage for the development of *P. periphylla* (Appendix B). Different stages are distinct and categorized by size, structural development, presence of pigmentation and reproductive maturity. In lab experiments by the same authors, individuals spent five to tens days at the initial stages and development from stage 1 to stage 9 was completed in two to three months, pigmentation was observed at stage 7 and *P. periphylla* from this stage are light intolerant. Stages 1-5 are neutrally buoyant at depths of approximately 230m (Jarms et al. 1999, 2002). *P. periphylla* has direct development, lacking polyp or ephyra forms (Jarms et al. 1999, 2002).

One structural developmental feature used in classification of stages is the extent and progression of pigmentation starting at the tip of the tentacles (Jarms et al 1999, 2002). The samples collected over the sampling period suffered damage to tentacles with pigment from adult tentacles being removed while in the Bongo net. Younger stages also suffered damage to tentacles as some tentacles appeared to be removed all together. Replacing the cod end with a plastic bag may decrease the amount of damage to all stages of medusa, and should be implemented for future sampling trips. Other sampling and transport methods described by Raskoff (2003) will also be considered.

Populations of *P. periphylla* sampled in western Norway have the ability to reproduce year round with females containing many oocytes of different developmental stages present at any time (Tiemann and Jarms 2009). An adult female of 14 cm in coronal diameter can have 2000 mature oocytes at one time and a male of similar size will have more than 800,000 testis vesicles. (Tiemann and Jarms 2009). Previously studied populations contain females with oocytes at varying levels of maturation, drawing to the conclusion that reproduction is not restricted by season (Jarms et al. 1999, 2002; Tiemann and Jarms 2009).

In Vefsnfjorden, eggs were found in the February samples, but as the sex of the adults were not recorded, it is difficult to say how many of the eggs were shed into the net from a capture female

and how many were from the water column. In the March cruise, eggs were only recorded in one sample, and a ripe adult female was also present. Only one individual yet to develop pigmentation was collected in the March sample. The decrease and then lack of early stages of juvenile *P. periphylla*, both with and without pigmentation, collected during the March and May sampling period suggests this population may not experience continuous spawning as observed in other fjords (Jarms et al. 2002; Tiemann and Jarms 2009). Whether this is a result of environmental changes or a characteristic of the population cannot be determined with the short length of this sampling period.

Specimens with a coronal diameter less than 5 cm are immature (Tiemann and Jarms 2009). *Periphylla* of this size have rarely been observed at the surface layers, which lends support to surface aggregation as a reproductive mechanism (Tiemann and Jarms 2009; Tiemann et al. 2008). ROV observations by Tiemann (2008) indicated coupling behaviour during surface aggregations, yet more research into the behaviour needs to be undertaken to confirm fertilization events.

The sex of the mature adults was recorded for both the March and May sampling trips. In both trips, males were only collected at night and females during the day. Unfortunately, the total number of adults collected for March and May was 7 and 11, respectively, and higher numbers should be collected before conclusions are drawn. Females from all trips had mature gonads with oocytes of different sizes and, but more analysis need to be done to confirm reproductive readiness of the oocytes.

Although individuals were recorded at the surface waters during the March sampling trip, no aggregations were observed. Specimens collected in the March and May trips did not have any stages younger than stage 7, whereas all stages were represented in the February trip. If the *P. periphylla* population in Vefsnfjorden only reproduces during the winter months - allowing enough time for the early stages to develop muscles required for swimming behaviour - then no reproductive behaviour should be seen in the later sampling trips.

A possible adaptation to the light regime of northern Norway could be surface aggregation for reproduction. The summer months of 24-hour sunlight may prevent migrations to shallow depths, restricting reproduction in surface waters to winter months. The direct result of which would likely be a slower increase in population size than observed in southern habitats. Analysis of gonad quality throughout the year may shed light into reproductive ability of northern populations. If the distance of vertical migration of adults decreased over the sampling period, and surface aggregation was connected to reproduction, it would also support light regime as a limiting factor for reproductive ability. There were not enough adults in this sample period to draw speculations and surface aggregations were not observed. Also, the literature lacks sufficient studies to conclusively support a relationship between surface aggregation and reproductive behaviour (Youngbluth and Båmstedt 2001; Tiemann et al. 2009).

Stages 1-6 are not affected by light as are 7-14, although laboratory stage 5 individuals displayed aversion to light (Jarms et al. 2002). In the samples collected, there was a distinct development pattern observed as the year progressed. All stages from eggs to adults were collected during the February trip, all pigmented stages in March, and medusa stage 9 or greater during the last of sampling trip in May. As *P. periphylla* in northern climates will be exposed to light in the upper water column for the summer months of the year, a change in the reproductive cycle may be an adaptation. With a two to three month developmental period before the juvenile *P. periphylla* is able to freely swim, spawning in February or earlier provides the juvenile *P. periphylla* with enough time to develop the muscles required to migrate through the water column and away from light penetration. If spawning were to occur later in the year, stage 7 or possibly stage 5 (Jarms et al. 2002), at which *P. periphylla* shows aversion and sensitivity to light, may coincide with the summer and may result in fatalities.

The age of the population in Vefsnfjorden should not be ruled out when considering the apparent lack of year round reproduction. More southern populations were colonized earlier and with have higher number of mature individuals which may be a quality that enables continuous reproduction. This reproductive pattern can be further investigated through gonad quality and oocyte development examination during future sampling trips.

The largest specimen collected had a CH of 11cm and a CD of 17.5cm that corresponds with the larger medusa measured by Youngbluth and Båmstedt (2001) in Lurefjorden, a fjord that experiences a mass abundance of this species. There have been reports of larger individuals caught during trawls by fisherman (Geir Edvardsen, pers. comm.) therefore the sampling method used may be not sampling the whole population. Adult medusae are believed to be long lived (Youngbluth and Båmstedt, 2001) and the increase in CD of the Vefsnfjorden medusa may indicate a population that has been colonized for some time.

Decrease in population numbers and developmental stages

In the March sampling trip, an increased number of mature medusa were observed swimming near the surface during the night sampling, but were not collected. During the day sampling of the same trip, mature medusa were observed at the surface but all were determined to be dead. Just prior to the March sampling trip a local newspaper reported numbers of *P. periphylla* in shallow near shore waters during daylight hours after a storm period (Appendix C). The sampling period from February to May spanned the time when the newspaper article was published. The storm event may have caused a decrease in the population numbers, in both immature and mature medusa as both will suffer phototoxic lesions/fatalities when exposed to light (Jarms et al. 2002). If the population did suffer losses of mature and reproducing medusae, therefore decreasing chance encounters between mates, this could explain the lack of youngest stages in the March and May samples.

Sills restrict exchange between water in the fjords and oceanic water outside of the fjord. A large influx of oceanic water will cause a flushing event in the fjord as water from the basin is forced upwards and out of the fjord. In Vefsnfjorden, a flushing event did occur over the sampling period and supporting evidence can be found in the changes in temperature, dissolved oxygen levels and density of the water column (figure 2).

The sill depth in Vefsnfjorden is approximately 85m and the deepest depth is approximately 480m. In February the highest fluctuation in temperature occurred in the upper 80m of the water column. As the spring progressed, the water column began to warm slightly and the temperatures

in the upper 80m became more stable. In March, temperatures had the warmest levels between the 200m and 100m depths and a continued gradual increase was recorded in May when the warmest waters were seen above the 80m depth.

A similar pattern can be derived from the dissolved oxygen levels (DO). In the deepest measured depths, February had the lowest dissolved oxygen while May had the highest. Levels at the surface were similar between both February and May. Oxygen rich oceanic water would be the reason for the increase in DO observed in May. Even though DO levels increased over the sampling period, the measured water column never experiences anoxic conditions.

Water density also increased over the sampling period. As the temperature in Vefsnfjorden became more stabilized so did the density. As the oceanic water enters the fjord and flushes the system, inhabitants of the water column may also be displaced or removed from the fjord. This may explain the decrease in both individual numbers and developmental stages collected from Vefsnfjorden. As discussed above, numbers of individual medusae were photographed at shallow depths in early March by a local news agency. While this is most likely due to the reported storm that occurred just prior, there is also the possibility that forces related to water exchange moved the medusae to the upper water columns. Once in the shallow depths, medusae may be exposed to daylight, which could result in lesions and/or fatalities due to the phototoxic relationship of the species pigmentation and light penetration (Jarms et al. 2002). Another possibility connected with the forced movement of medusae up the water column would be the removal of individuals from the fjord completely. The most individuals were collected in the intermediate depths below the sill depth and the upper water column does not appear to be an area frequented with high numbers. As water exchange occurred in the fjord, members of the *P. periphylla* population could have been transported up and over the fjord into the open ocean. Individuals that are still developing and lack swimming strength would be more susceptible to such water movements, and the low numbers or lack of young stages collected in this sample may be a reflection of such an event.

The most noticeable difference between water parameters of all the months was the Secchi depths. While the exact difference cannot be determined (as the length of rope was not long

enough during the March sampling) the difference between March and May is at least 18.5m. The May reading is related to seasonal terrestrial and river runoff. Both mature and immature pigmented medusae were collected from the upper water column during this sampling trip, differing from no medusae collected in the same depth interval in March. This suggests the decrease in water clarity may enable *P. periphylla* to migrate vertically through the water column, even when irradiance is still at daylight levels. As with all the samples, the highest number of individuals were collected from depths other than the 150-50m interval.

Further support of a decrease in the population is found when comparing collected specimens from the big net samples of this trip to those collected by Eiane and Aksnes (to be published). Abundances from Vefsnfjorden sampled in 2010 were more similar to samples collected from Ranafjorden in 2009 rather than Vefsnfjorden of the same year. Unfortunately, the Vefsnfjorden 2010 samples with the large plankton net were only collected in May so if decrease in individuals occurred during this year's sampling period or before hand cannot be determined.

Youngbluth and Båmstedt (2001) noted numbers of *P. periphylla* observed by ROV as three times greater than those collected with tows. Discrepancy between sampling methods can lead to inaccurate estimates, and numbers returned from this period should be considered a low reflection of the Vefsnfjorden population. Sötje et al (2007) noted the location in the fjords medusae were found and size versus age distribution can change from year and *P. periphylla* populations may structure changes from year to year. The reason for this is unknown, but the decrease in individual numbers sampled in Vefsnfjorden may be an occurrence the population experiences on a natural basis.

Increase in individual size

While there was a decrease in the overall population numbers of *P. periphylla* in Vefsnfjorden, there was an increase in individual size. Whether such a pattern is a natural occurrence or the effect of a change in the environment cannot be concluded with this one sampling period. As mentioned previously (Sötje et al. 2007), populations in Halsafjorden, Lurefjorden and Songefjorden have recorded changes in population structures, so it is possible that similar events occur in Vefsnfjorden. The fjord also underwent spring storms and adult *P. periphylla* were

observed in shallow near shore waters during daylight hours (Appendix C). Due to the light intolerance of *P. periphylla*, individuals trapped in the upper levels of the water column would most likely suffer lesions that in turn could be fatal. For those individuals that have already reached stage 7, when pigmentation has developed and light intolerance begins, to be washed in shore would be detrimental. With a strong storm and associated water movements, there is a probability that members of the Vefsenfjorden *P. periphylla* population stage 7 and higher were exposed to light levels and succumbed. Numerous dead adult *P. periphylla* were observed at the surface water during daylight sampling hours of the March trip, an occurrence that was not repeated throughout the four month sampling period.

Diel Vertical Migration and light regime in Vefsnfjorden

Individual *P. periphylla* collected during the March cruise suggest the least amount of DVM occurred in this month of the sampling period. Temperatures in the water column in March were beginning to cool, and salinity had decreased slightly. Dissolved oxygen levels had the most variation both within the March cruise and between the other months. Between the 80m to 100m water levels, oxygen levels were supersaturated. No *P. periphylla* were collected at this depth for either the day or night samples. The scyphozoan *Aurelia labiata* has the capability to withstand hypoxic levels if not exposed for a prolonged length of time and will migrate out of the zone to an area with more favorable conditions (Thuesen et al. 2005). As larger *P. periphylla* are strong swimmers, they too may migrate out of zone with critical conditions. Stages that may be affected by hyperoxic or hypoxic levels would be those of yet to develop swimming capabilities and the stages with weak convulsions. None of these stages were collected in the upper water column, but this would not be due to hydrogeographic conditions as these young stages are not found in the upper water layers (Jarms et al. 1999, 2002) and holds true for this study period. A rapid change in dissolved oxygen also occurred the deepest waters, mimicking the levels observed in more shallow waters.

Periphylla have low oxygen consumption intake, which indicates a low energy intake (Youngbluth and Båmstedt 2001). While vertical migration may be a predatory response, it is more likely a reaction to light penetration for migrations out of the upper water column.

Competition between other species for food will be minimal as fjords with mass abundances of *P. periphylla* present tend to experience a change in light optics (Eiane et al. 1999; Sørnes et al. 2007; Aksnes et al. 2009). Sötje et al. (2007) examined *P. periphylla* population in three fjords and determined *P. periphylla* is a predator with a significant effect on the distribution of zooplankton biomass. Planktivorous fish that may share prey sources with *P. periphylla* and rely on visual predation will have difficulty feeding, if at all (Eiane et al. 1999; Aksnes et al. 2004; Sørnes and Aksnes 2006). A combination of a change in light optics that favour tactile predators, competition for food sources, and preying on juvenile fish by *P. periphylla* may establish *P. periphylla* as the dominant predator in a fjord and as a result may also decrease fish populations (Eiane et al. 1999; Sørnes et al. 2007; Aksnes et al. 2009).

With the low numbers of medusae collected that are able to perform the swimming required for vertical migration, it is difficult to determine the effect of light regime of northern fjord on migration patterns as all populations avoid light due to the detrimental phototoxic relationship (Jarms et al. 2002; Sötje et al. 2007). All stages of collected *Periphylla periphylla* avoided the upper water column during daylight hours and the highest number of individuals collected at night was two mature medusae. Interestingly, these two medusae were collected during the May sampling trip, the period with the most daylight hours. Even though the daylight hours were the longest in May, the water clarity was the least clear with Secchi readings of only 1.5m. Such a low Secchi reading indicates a decrease in light penetration in the upper upper column, which may have enabled the mature medusae to migrate to the surface.

Young stages with and without pigmentation dominated the intermediate sampling depths and reflected the populations of other fjords (Jarms et al. 1999, 2002). However, larger medusae may not be represented in this sampling method as they are more effective swimmers and able to detect vibrations and turbulence in the water (Youngbluth and Båmstedt 2001; Sötje et al. 2007) and may be able to avoid the bongo net. Smaller stages may be affected to a lesser extent as strong swimming in younger medusae does not occur until stage 8 (Jarms et al. 2002), therefore these stages lack the ability to avoid the capture if turbulence or vibrations from the net is sensed.

My findings suggest the population in Vefsnfjorden may be limited by seasonal changes such as spring storms and a flushing of the fjord that may remove mature medusa from the population by either forcing them out of the system or by death. The effect of seasonal changes cannot be determined through this sampling period of February to May and subsequent sampling must be undertaken before speculations can be confirmed or denied. Moreover, light regime may not be as strong of a factor as the physical events experienced by the fjord. Fjords with different bathymetry may retain or dispel more medusa, but this can only be determined through the sampling of other fjord systems.

Conclusion

There was an increase in individual sizes may be a natural progression of development within the population or may suggest seasonal spawning of the Vefsnfjorden *P. periphylla* population. Which scenario is more probable cannot be determined from this sampling period. However, both would have been affected by the physical events experienced in the fjord during the sampling period.

There was a decrease in both individual numbers and developmental stages of *P. periphylla* from Vefsnfjorden over the sampling period. From this study I suggest the observed decreases may be a result of two reasons. First, the population may not reproduce continuously throughout the year, instead may have seasonal spawning. Alternatively, other spawning events did occur, but due to the flushing of the fjord and seasonal storms, the younger stages were either pushed over the sill depth and out of the system or forced into the upper water column and exposed to the light leading to fatalities. During the flushing of the fjord, mature medusae may have also been forced out of the system, limiting reproductive activity in the fjord.

Flushing event and seasonal storms do occur in fjords, however, the how these physical effects *P. periphylla* population cannot be determined with the length of this sampling period and in different years there may have different results.

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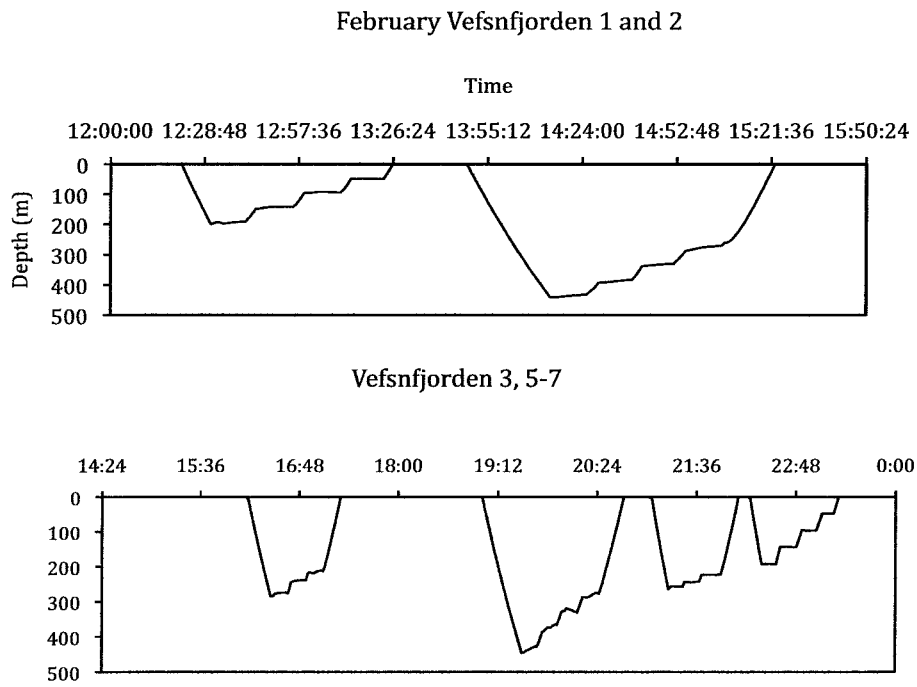
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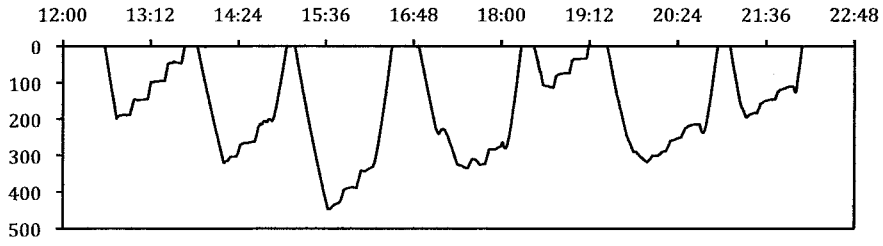
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Appendices

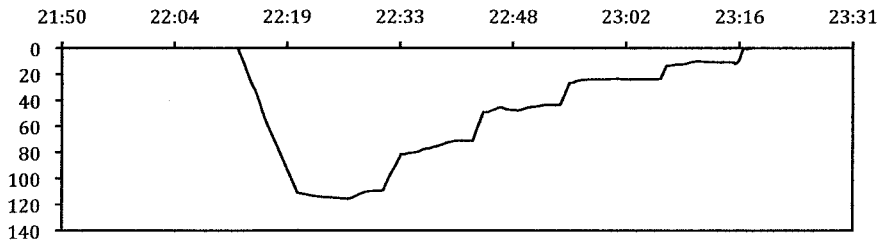
*Appendix A: Depth intervals measured by STD in Vefsnfjorden for *Periphylla periphyllo* collection in 2010.*



March Vefsnfjorden 1, 2, 4, 6, 7

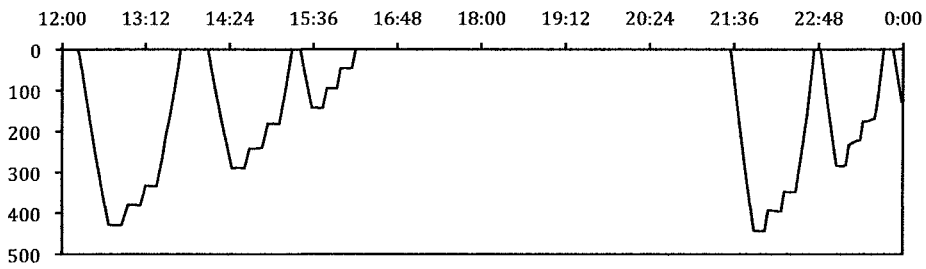


March Vefsnfjorden 8

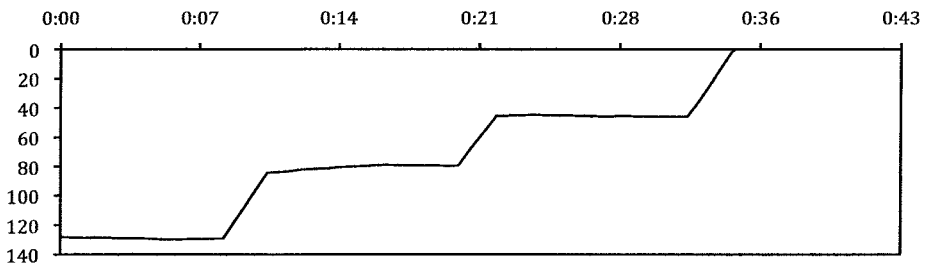


February 9 and March 16 2010 sampling Vefsnfjorden sampling depths measured by STD.

May Vefsnfjorden 1-3, 9, 10

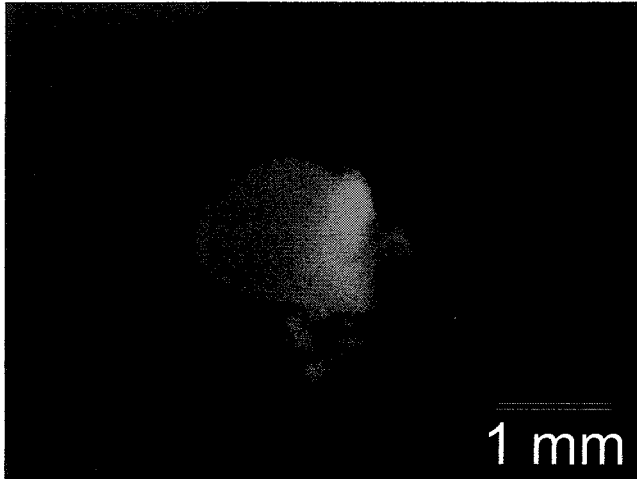


May Vefsnfjorden 11

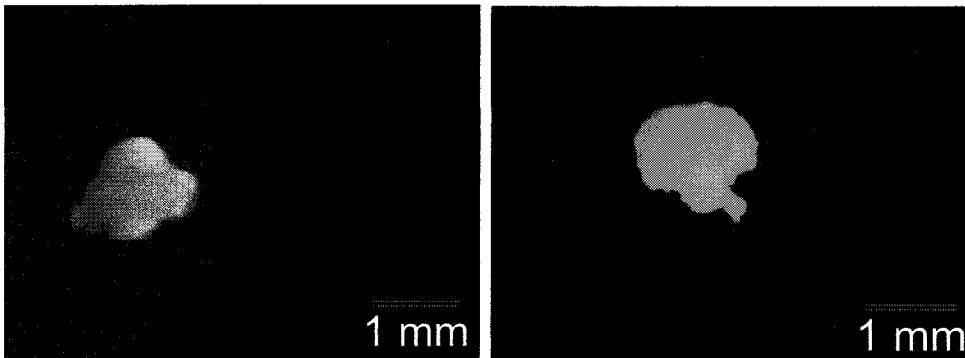


May 19 2010 Vefsnfjorden sampling depths measured by STD.

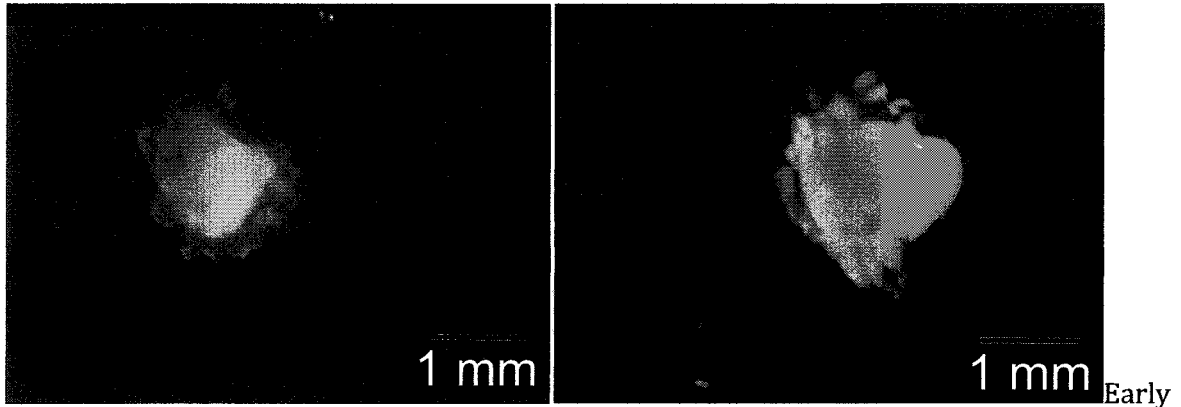
Appendix B: Developmental stages of Periphylla periphylla collected in Vefsnfjorden in 2010.



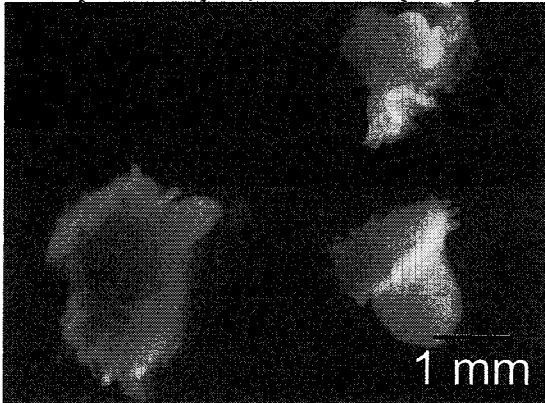
Juvenile Figure X: Juvenile *Periphylla periphylla* from collected from Vefsnfjorden February 9 2010, stage 3. There is no pigmentation, lappets, rhopalia, tentacles or mobility. Red on lower part of juvenile is nematocyte tissue from older *P. periphylla*. Collected during the day at sampling depth of 300-450m. Stage differentiation and descriptions as per Jarms *et al.* (2002).



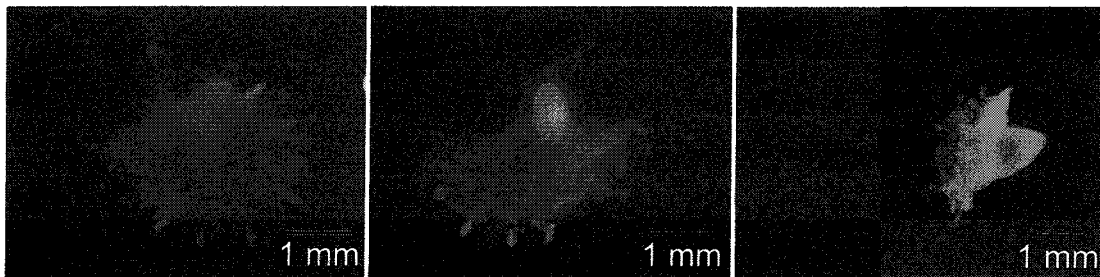
Stage 4 *Periphylla periphylla* collected from Vefsnfjorden February 9 2010 at sampling depth of 300-450m during the daylight hours. Side view (top) and aboral view (bottom). Stage has no pigment, lappets, rhopalia or tentacles but the first convulsions have been observed in lab rearing studies (Jarms *et al.* 2002). Stage differentiation and descriptions as per Jarms *et al.* (2002).



stage 5/late stage 4 juvenile *Periphylla periphylla* collected during daytime cruise at sampling depth of 300-450m on February 9 2010. This stage has no pigmentation or tentacles; lappets are small and rounded, rhopalia are buds. Stage differentiation and descriptions as per Jarms *et al.* (2002).

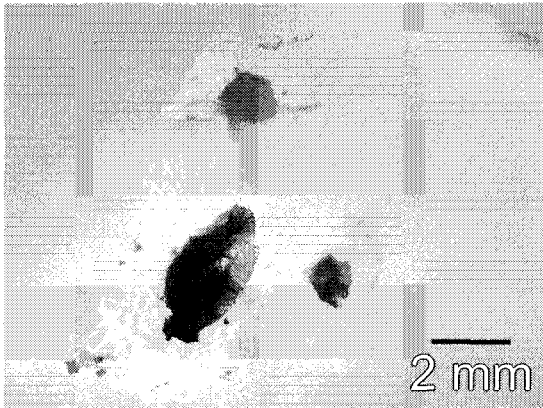


Developmental stages of *Periphylla periphylla* collected during daytime cruise in Vefsnfjorden at sampling depth of 300-450m on February 9 2010. Clockwise from top right: Stage 6 with differentiation of rhopalia as small crystals and tentacles as buds. Pigmentation is not present in this stage and red tissue on specimen is from older *P. periphylla*. Stage 5 has no tentacles, rhopalia are buds and lappets are small and rounded. Stage 7 is the first stage with pigmentation, which can be found around the mouth. All stages have mobility ranging from marginal contractions to regular pulsations. Stage differentiation and descriptions as per Jarms *et al.* (2002).

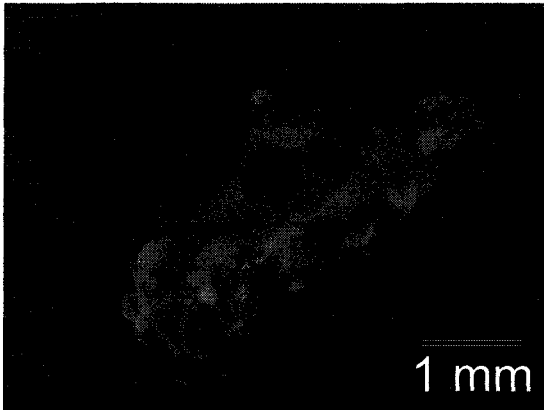


Juvenile *Periphylla periphylla* from cruises of Vefsnfjorden during daylight hours on February 9 2010. From top photograph, oral view and side view both collected from sampling depth of 300-450m and side view (bottom photograph) collected from sampling depths of 225-300m. Early stage 7: with first sign of pigmentation around

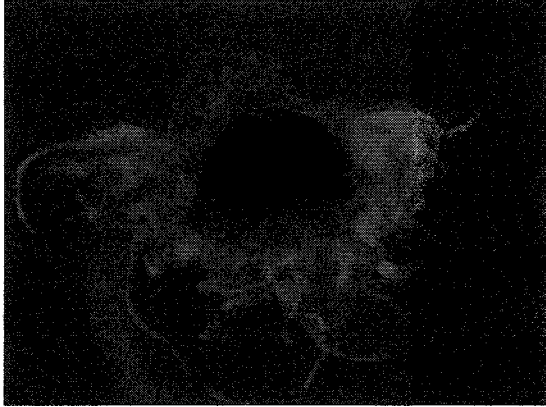
mouth, rhopalium fully developed and tentacles shorter than lappets Stage differentiation and descriptions as per Jarms *et al.* (2002).



Developmental stages of *Periphylla periphylla* collected during daytime cruise in Vefsnfjorden at sampling depth of 225-300m on February 9 2010. Clockwise from top, early stage 7 with first signs of pigmentation; stage 8 with tentacles at least as long as lappets and pigmentation does not yet reach the tip; possible stage 10 but difficult to classify as tentacle pigmentation cannot be seen (which may be a consequence of sampling methods, see discussion for further explanation). Stage differentiation and descriptions as per Jarms *et al.* (2002).



Juvenile *Periphylla periphylla*, stage 8, collected during daytime cruise in Vefsnfjorden at sampling depth of 225-300m on February 9 2010. Pigmentation covers whole mouth area but does not yet reach the tip. Tentacles are at least as long as lappets and stage is strong swimming. Stage differentiation and descriptions as per Jarms *et al.* (2002).



Possible late stage 9 of juvenile *Periphylla periphylla* collected during daytime cruise in Vefsnfjorden at sampling depth of 225-300m on February 9 2010. Resembles to adult form can be seen, without tentacle pigmentation. Stage differentiation and descriptions as per Jarms *et al.* (2002).

Appendix C: Photograph of Periphylla periphylla from local newspaper article

