

The structuring effects of light on the deep-water scyphozoan
Periphylla periphylla

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“The ethologist wants to watch behaviour whereas the animals do not want to be seen.”

Hamner, W.M. (1985). The importance of ethology for investigations of marine zooplankton; keynote address. *Bulletin of Marine Science*, 37:414-424

Preface

This dissertation is submitted in partial fulfilment of the requirements for the degree of Philosophiae Doctor (Ph.D.) at the Faculty of Biosciences and Aquaculture (FBA), Nord University, Bodø, Norway. The presented original research was carried out as part of my Ph.D. project, funded by the Norwegian Government.

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Special gratitude goes out to three dear friends: Melissa Burke, Cesilie Røtnes Amundsen, and Kanchana Bandara. Your ever-present emotional support during periods of frustration and joy will always be dear to my heart.

And finally, to my family, Binai, Wiggo, and the Bozizerses to come. Thank you for all that you do. Teamwork makes the dream work.

Malmø, October 2018

Andrea Bozman

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List of Papers

This thesis is based on the following papers that will be referred to in the text by their Roman numerals.

Paper I **Bozman, A.,** Titelman, J., Kaartvedt, S., Eiane, K. & Aksnes, D.L. (2017). Jellyfish distribute vertically according to irradiance. *Journal of Plankton Research*, 39: 280-289. DOI 10.1093/plankt/fbw097

Paper II **Bozman, A.,** Aksnes Dag, L. & Eiane, K. (2018). First reports of a mass mortality event across multiple life stages in a mesopelagic jellyfish in high latitude coastal waters. *Marine Ecology*, 0: e12498. DOI 10.1111/maec.12498

Paper III **Bozman, A.,** Eiane, K., & Aksnes Dag, L. Photoperiod and retention constrain the distribution of a light-sensitive mesopelagic jellyfish in high latitude fjords. Manuscript

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Abstract

Field observations revealed that the migratory behaviour of the jellyfish *Periphylla periphylla* (Péron & Lesueur 1810) is an emergent response to ambient light levels. In Lurefjorden, *P. periphylla* distributed within a 'light comfort zone' (LCZ) in where all of the observed jellyfish avoided light levels above $0.02 \text{ mWm}^{-2} \text{ nm}^{-1}$ (at 500 nm) and most of the larger *P. periphylla* population preferred light levels above 10^{-6} mWm^{-2} while some were recorded at depths with darker illumination. The response of individual jellyfish to light as a directional cue may have implications for the geographical distribution of this jellyfish. In fjords above 65°N , *P. periphylla* population are dominated by smaller individuals and reported at lower abundances compared to the mass occurrence levels resident year-round in some western Norwegian fjords. Modelling of the underwater light field shows that there is a decrease in the vertical extension of suitable habitat available to *P. periphylla* during periods of increasing duration and intensity of solar irradiance levels. During midsummer, the decreased habitat availability increases with northwards progression and by $66^{\circ}38'\text{N}$ the upper 50 m of the water column appears to be completely inaccessible to migrating *P. periphylla* during day and night. However, for the smaller non-migratory stages of *P. periphylla*, a refuge from too high illumination levels is found in fjords with substantially deep basin depths that provide an enlarged dark environment at depth thus mitigating the constraints of light on habitat availability. This thesis contributes to evidence that marine processes that govern the behaviour and distribution of mesopelagic fish may also be applicable to jellyfish and contributes to improving our understanding of mesopelagic ecology.

Introduction

The interactions between a species biology and its environment will shape life histories, distribution, behaviour, and ultimately species success. On the population level, variation can be observed on a regional basis as localized groups react to environmental variations, such as temperature, salinity, oxygen level, food availability, and predation risk. In the mesopelagic, however, temperature, and salinity variations are small from a biological perspective compared to the surface-near waters. In addition, environmental heterogeneity is provided by mesopelagic light levels that can vary on a range of temporal and spatial scales. As such, underwater light levels are drivers behind the vertical distribution of species (Prihartato et al., 2015, Norheim et al., 2016, Røstad et al., 2016b, Røstad et al., 2016a, Paper I, Frank and Widder, 1997, Williamson et al., 2011, Warner et al., 1979). A global analysis of the deep scattering layer (DSL) provides empirical evidence of a global pattern of a standard range of light levels in which most mesopelagic species appear to distribute within (Aksnes et al., 2017). Here, the authors show that the DSL varies with depth, in a way that keeps light levels experienced by the animals within a set range.

The optical regime has been shown to influence the mesopelagic ecosystem structure including regimes shifts (Aksnes et al., 2009), species distribution and population structure (Sørnes et al., 2007), and behaviour (Frank and Widder, 1997). Diurnal vertical migration is the most common behaviour to the extent that it represents the largest biomass of animal migration on earth (Irigoien et al., 2014, Klevjer et al., 2016, Barham, 1966, Hays, 2003, Williamson et al., 2011). Theoretical frameworks suggest that an individual migrates on a diurnal pattern in order to balance the gain of the access to food rich environments with the risk of meeting their own demise, primarily due to increased visual predation risk in surface-near waters (Clark and Levy, 1988). For some species, the avoidance of light levels may be a result of the harmful, if not fatal, effects of light exposure (Herring, 1972, Bonnett et al., 1979). Zones of preferential light levels that offer optimal trade-off for species survival have been termed “light comfort zones” LCZ (Dupont et al., 2009).

One main driver behind the variations in the depth and width of an LCZ has been attributed to fluctuations in solar irradiance levels (Roe, 1983), which itself may be impacted by environmental factors. Weather patterns, for example, have been shown reduce incoming solar irradiance levels during stormy periods, leading to migratory behaviour in the lower mesopelagic that mimics the vertical migrations observed during the dark periods (Kaartvedt et al., 2017). In unclear waters, the vertical extension of the LCZ decreases and the maximum light level will be recorded at a more shallow depth than in less clear waters (Røstad et al., 2016b, Røstad et al., 2016a). Under conditions of prolonged solar irradiance levels, such as during midsummer in northern latitudes where sunlight extends to near 24-hours, photoperiod can constrain access to the upper productive waters (Norheim et al., 2016), and thus theoretically constrain population success and distribution (Kaartvedt, 2008).

The majority of studies that have included light levels in their sampling methodologies have focused on photosynthesis and few studies have investigated responses to ambient light levels at or below mesopelagic depths (e.g. Matsuura et al., 2012, Prihartato et al., 2015, Paper I). The difficulties with interpreting model outputs and, in some cases, the lack of technology with resolution adequately sensitive to sample light levels at great depths has resulted in underrepresentation of advanced bio-optical approaches in ecosystem models (Frank and Widder, 1997). The use of proxies, correlated with light attenuation, such as oxygen and salinity, enables addressing the issues with sampling by utilizing data that is more easily collected, and have proven advantageous for studies of coastal water light regimes (e.g. Aksnes, 2015). The combination of using a proxy to estimate the non-phytoplankton attenuation coefficient and models that estimate the downwelling irradiance can be used to present results when sampling equipment is inadequate and LCZ values are known from previous studies (Paper II and III, with results from Paper I).

Visual adaptation in the mesopelagic realm is wide-ranging (Cronin, 1986, Warrant and Locket, 2004). Typically, photoreception is achieved through ocular detection, either primitive or advanced (Warrant and Locket, 2004) but also through extraocular means such as pigment cups (Yamasu and Yoshida, 1973) and light-sensitive cells on

specific ganglia (Wilkins and Larimer, 1976). Hence it has been assumed that mesopelagic species other than visual predators such as fish are also sensitive towards fluctuation in the optical regime (Sørnes et al., 2007). A similar scenario to that of the light related distribution of mesopelagic fish has also been hypothesised for a lesser studied group – mesopelagic jellyfish (Dupont et al., 2009, Dupont and Aksnes, 2010, Paper I).

Mesopelagic light levels and jellyfish

Our understanding of the population dynamics and distribution of some of the common epipelagic jellyfish species is insufficient and the gaps are even greater for mesopelagic species (Mills 2001). Suggested drivers of population growth in jellyfish includes temperature increase or decrease (Boero et al., 2016, Mills, 2001); global ocean sprawl (Duarte et al., 2012) and anthropogenic effects (Purcell et al., 2007); climate effects (Purcell, 2005); and overfishing (Parsons and Lalli, 2002). Jellyfish research has faced limited resources with few to no long-term time series, the lack of which hampers conclusions on the possible changing states and sizes of jellyfish populations. Globally, environmental correlations have been presented for some common species with multi-decadal fluctuations linked to climate oscillations (Condon et al., 2013). Abiotic factors, such as advection and retention are also influencing population growth and distribution and likely work in conjunction with biotic factors (Schmedler-Meyer et al., 2018, Sørnes et al., 2007, Dupont and Aksnes, 2010).

Researchers have stressed caution when interpreting data with shifting baselines and the lack of historical baselines (Condon et al., 2012, Boero et al., 2008). Specifically, Sanz-Martín et al. (2016) highlight articles claiming a global increase in jellyfish numbers published prior 2012 are gross misinterpretations of previous publications for the simple reason that the first global review of jellyfish numbers was by Brotz et al. (2012). While the community of gelatinous researchers have not reached a consensus on the validity of a global jellyfish paradigm, the importance of additional research on population dynamics and distributions in order to provide baseline data is unanimously recognized

(Condon et al., 2012, Sanz-Martín et al., 2016, Mills, 2001, Gibbons and Richardson, 2013, Condon et al., 2013).

The term jellyfish is wide-reaching and encompasses everything from salps to stalked jellies to scyphozoans, sometimes referred to as “true jellies.” With high species numbers found in all marine (and some freshwater) environments, it can be hypothesised that environmental factors in addition to temperature, salinity, and oxygen affect the success of jellyfish populations. The distribution of jellyfish may be formed by less recognized mechanisms and understudied behaviours. Eiane et al. (1997), Eiane et al. (1999) suggest that water column darkening alters the environment to one that negatively impacts visual feeders, such as fish, thus positively impacting tactile predators, such as jellyfish, through decreasing the predation competition between visual and tactile predators. Further evidence of this phenomena was presented by Aksnes et al. (2009), whose study on a series of fjords found evidence of coastal water darkening that could promote mesopelagic regime shifts in these locations. For one species in particular, the coronate jellyfish *Periphylla periphylla* (Péron & Lesueur 1810), the darkening of shallow fjords has promoted population retention to mass occurrence levels in some western Norwegian fjords (Sørnes et al., 2007).

Important questions that pertain to this thesis include (1) Do the ambient irradiance levels of the water column provide a structuring force that affects the vertical distribution of a mesopelagic jellyfish? and (2) does the increasing duration and intensity of seasonal photoperiod with northwards progression affect the habitat available to of mesopelagic light-sensitive jellyfish?

Periphylla periphylla biology and ecology

Periphylla periphylla is a cosmopolitan mesopelagic coronate scyphozoan (Russell, 1970) that typically occurs in nominal densities (Pagès et al., 1996, Dalpadado et al., 1998, Donnelly et al., 2006, Knutsen et al., 2018). This jellyfish is the only known species of jellyfish with true direct development, i.e., development is direct from egg to medusa

and lacks benthic, planula, and ephyra stages (Jarms et al., 2002, Jarms et al., 1999, Tiemann and Jarms, 2010) (Fig. 1 and 2). Gonads of female *P. periphylla* have oocytes at varying stages of maturity regardless of season, suggesting that spawning is not limited to seasonal reproductive periods (Lucas and Reed, 2010, Jarms et al., 2002, Tiemann and Jarms, 2010, Larson, 1986). *Periphylla* populations in the open waters have a wide range of medusa size and sexually maturity, irrespective of sampling season, which is indicative of ongoing reproduction (Lucas and Reed, 2010, Mauchline and Harvey, 1983). Medusa longevity is suggested to span decades (Youngbluth and Båmstedt, 2001, Tiemann and Jarms, 2010). *Periphylla*'s reproductive ability over a long life span likely contributes to the build-up of mass occurrence populations in Norwegian fjords (Sötje et al., 2007, Tiemann and Jarms, 2010).

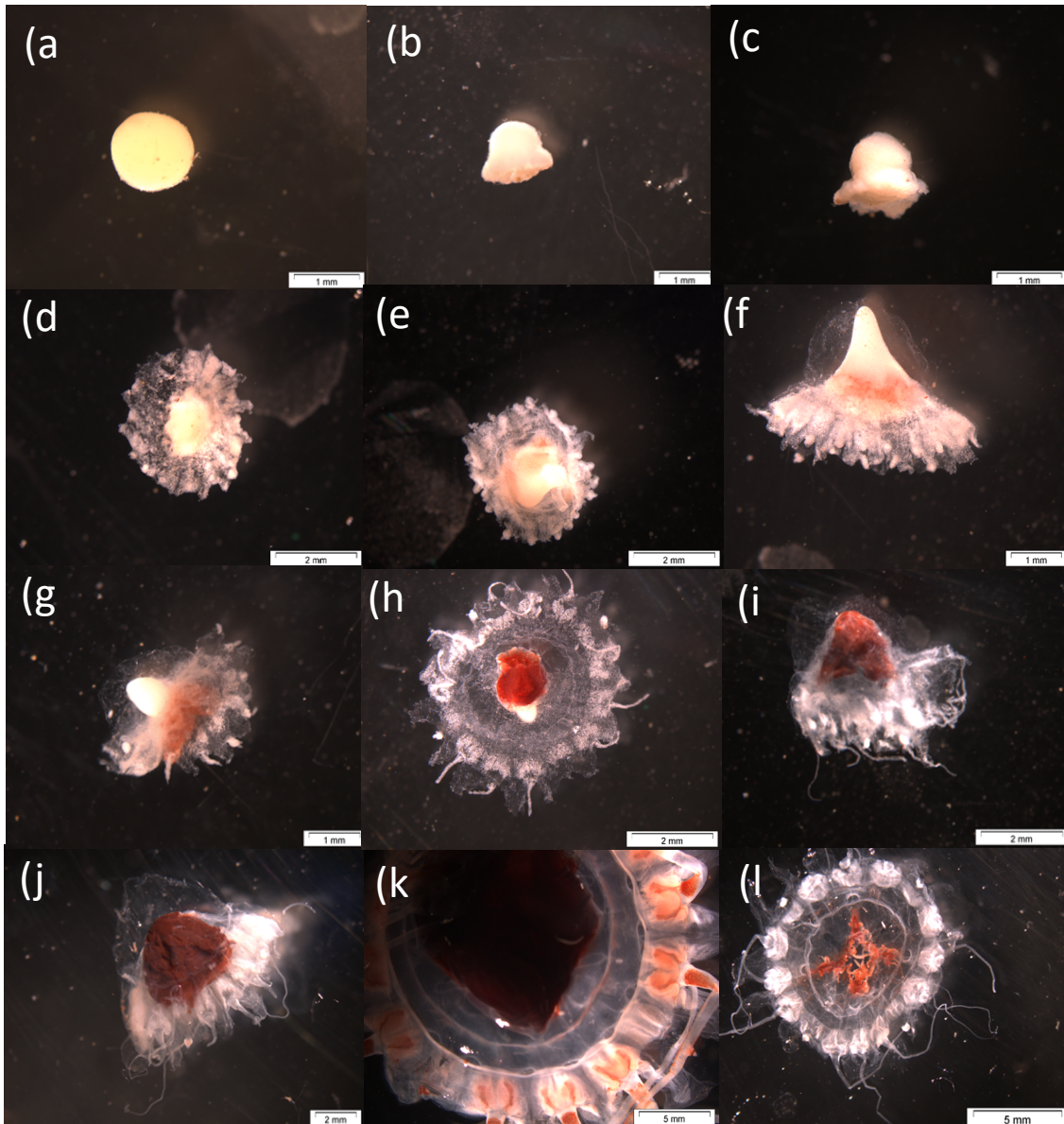


Fig. 1: Fig. 2 Selected developmental stages of *Periphylla periphylla* collected from Vefnsfjorden including (a) stage 2 , (b) stage 3, (c) stage 4, (d) stage 5, oral view, (e) stage 6, aboral view, (f and g) stage 7, (h) stage 8, (i) stage 9, (j) stage 10, (k) stage 14B where gonadal folds are present yet sexual dimorphism is not apparent. A dead and decaying *P. periphylla* (L) is presented for references purposes. For a detailed description, refer to Jarms *et al.* (Jarms *et al.* 1999; Jarms *et al.* 2002).

Periphylla's distinct red-brown colouration is due to the presence of the pigment protoporphyrin, which degrades into toxic compounds upon light exposure (Herring, 1972, Bonnett *et al.*, 1979). Protoporphyrin is not visible on the initial developmental

stages of this jellyfish, including eggs to stage 6, but development likely begins ectodermally during stage 6 (Jarms et al., 1999, Jarms et al., 2002). The extent of pigmentation increases with jellyfish development, with adult *P. periphylla* having fully pigmented stomachs, lappets, and tentacles (Jarms et al., 1999, Jarms et al., 2002). Jellyfish with protoporphyrin pigments, including *P. periphylla*, are restricted to darker waters due to the phototoxic nature of protoporphyrin (Herring, 1972, Bonnett et al., 1979). Intrinsically, *P. periphylla* is considered to be a negatively phototactic species (Youngbluth and Båmstedt, 2001, Herring, 1972, Bonnett et al., 1979).



Fig. 2: Definition of size class measures taken on individual *Periphylla periphylla*.

Periphylla periphylla in Norwegian coastal waters

Periphylla periphylla is an ubiquitous member of the gelatinous zooplankton community along the Norwegian coast (Lid, 1979) with the distribution stretching up to and including Arctic waters (Havnø, 1918, Hognestad, 1969, Fosså, 1992, Hognestad,

1962, Dalpadado et al., 1998, Geoffroy et al., 2018)(Table 1 in Paper III). The first historical reports of high abundances of *P. periphylla* in Norwegian fjords came in the early 1900s (Broch, 1913) and in the 1970s onwards there was renewed interest, possible as the jellyfish disrupted fishing practices (Sneli, 1984, Fosså, 1992, Gjelsvik Tiller et al., 2014). Mass occurrence level populations appeared to be confined to a handful of fjords in western Norway, although Fosså (1992) reports reoccurring apparent aggregations in some fjords above 65°N.

Local fishermen are often the first to notice indications of growing *P. periphylla* populations as large by-catches of medusae clog fishing nets (Sneli, 1984, Fosså, 1992). Similar reports in higher latitude locations have been extensively covered by local media since 2012 (Tiller et al., 2017). However, the status and history of these populations were not clear as there had been limited records on *P. periphylla* in high latitude fjords (e.g., Fosså, 1992).

Still, *P. periphylla* has established mass occurrence populations in at least four fjords in Norway where year-round abundances range from 20 – 320 ind m⁻² (Sørnes et al., 2007, Gjelsvik Tiller et al., 2014, Sneli, 1984, Fosså, 1992). Originally, J. Hjort (as discussed by Fosså, 1992) theorized that mass occurrences of *P. periphylla* in Norwegian fjords are found in systems with shallow sills and relatively deep basins and Broch stressed the biophysical factors, such as low predation rate, minimal competition for food, and stable ocean-like basin waters in regards to temperature and salinity, may promote population growth. Subsequent research by Aksnes and colleagues worked to develop these hypotheses further. Sørnes et al. (2007) provide a simple framework suggesting that the build-up of mass populations of *P. periphylla* in relatively shallow areas requires both high water column light attenuation levels and adequate retention of individuals, which is promoted by shallow sills relative to basin depth (the “optically conditioned retention” (OCR) hypothesis. According to this hypothesis, deep fjords do not require increased light attenuation levels as dark basins are achieved by depth alone, i.e., as observed in Sognefjord (Sørnes et al., 2007). Simulations by Dupont and Aksnes (2010) suggest that the ambient light preferences and ontogenetic shifts in

vertical behavioural strategies may work in conjunction to shape the population structure in individual fjords.

The basin waters in shallow fjords with mass occurrence levels of *P. periphylla* are characteristically Norwegian Coastal Water (NCW) (salinities < 34.5) Sørnes et al. (2007). NCW attenuates light more higher than North Atlantic Water (NAW) (Eiane et al., 1999) and the basin waters in these fjords become “darker,” shifting towards an environment more similar to the deep oceanic habitat native to *P. periphylla* (Sørnes et al., 2007). Fjords with elevated light attenuation create environments where tactile predators have the competitive edge over visual predators (Eiane et al., 1997, Eiane et al., 1999). Water mass characteristics are not static properties but rather fluctuate temporally and spatially. Therefore, in theory, a fjord once preferable to *P. periphylla* may undergo a shift in light attenuation and switch to a system with conditions unsuitable for large numbers of the jellyfish (Dupont and Aksnes, 2010).

Light and *Periphylla periphylla* behaviour and distribution

With the exception of cubozoans that use imaging forming eyes (Coates, 2003), jellyfish use extraocular photoreception to detect light (Martin, 2002). Light sensory structures are found on the rhopalia (Arai, 1997) as pigment-cup and pigment-spot ocelli (Yamasu and Yoshida, 1973) and simple eye spots (Martin, 2002). *P. periphylla* lack ocelli, but may be able to detect light levels through protoporphyrin (Herring, 1972, Bonnett et al., 1979).

Jellyfish with protoporphyrin pigments are limited to “dark” habitats and surface migrations during periods of low solar irradiance (Herring, 1972, Bonnett et al., 1979, Benfield and Graham, 2010). When exposed to light these jellyfish have been recorded exhibiting active swimming described as a “fight or flight” response (Youngbluth and Båmstedt, 2001) and may suffer potentially lethal lesions (Jarms et al., 2002) describe to be similar to those suffered by humans with porphyria disease (Herring, 1972). Light exposure has also proven harmful for development as reported in mortalities of lab-reared young stages (Jarms et al., 2002).

Periphylla's light tolerance probably differs with medusa size and biological needs (Jarms et al., 2002, Sørnes et al., 2007). The exact level of light that is harmful to *P. periphylla* is unknown. For larger *P. periphylla*, results in Paper I suggest this level is suggested to be at a total irradiance above $5 \times 10^{-3} \mu\text{mol quanta m}^{-2} \text{s}^{-1}$. It has been suggested that coastal water darkening in some shallow systems has led to a darkening that promotes *P. periphylla* retention (Sørnes et al., 2007, Aksnes et al., 2009) in waters that would otherwise have illumination levels presumably too high for protoporphyrin jellyfish.

Studying fjord populations of *P. periphylla* make it is possible to access with relative ease an otherwise open ocean species (Fosså, 1992, Sneli, 1984, Klevjer et al., 2009, Kaartvedt et al., 2011, Ugland et al., 2014, Jarms et al., 1999, Jarms et al., 2002, Sötje et al., 2007, Tiemann et al., 2009, Tiemann and Jarms, 2010). Topographical and hydrographical characteristics result in individual fjord systems representing unique environments along a latitudinal range, which enables comparison across systems to test factors influencing species ecology (Sørnes et al., 2007, Aksnes et al., 2009, Aksnes et al., 2004, Bagøien et al., 2001). Studies on the drivers of population dynamics of deep-dwelling organisms are important pathways for building a new understanding of the environmental variability in mesopelagic ecosystems.

It does seem reasonable that *P. periphylla* mass occurrences should not be restricted to certain areas in Norway. The jellyfish has a historical presence in Norwegian coastal waters (Fosså, 1992 and citations within) and the coastal water darkening of the Norwegian Coastal Water has been suggested as a factor behind the increased retention of *P. periphylla* (Aksnes et al., 2009). However, persistent populations have not yet occurred at higher latitudes, which leads to the question: why are perennial mass population levels of *P. periphylla* apparently restricted to lower latitudes in Norway?

Kaartvedt (2008) suggests the lack of mesopelagic fish at high latitudes can be explained by the constraining effect of high light during summer. It has been suggested that at high latitudes, the 24-hour sunlight limits the waters available for safe foraging behaviour of mesopelagic fish (Kaartvedt, 2008). Empirical evidence of this hypothesis was found by Norheim et al. (2016) in a study of the ambient irradiance levels of the

mesopelagic scattering layer along a latitudinal gradient. Here, the night time depth of the mesopelagic species was located at greater depths with increasing latitude (Norheim et al., 2016). The incoming light at night increased two to three orders of magnitude along a latitudinal gradient from 63°N to 67°N (Norheim et al., 2016).

Objectives

The main objective of this thesis is to investigate how the light levels affect the distribution of the light-sensitive jellyfish, *Periphylla periphylla*. Here I,

- tested the hypothesis that *P. periphylla*'s vertical distribution is a response to changes in absolute light intensities in the water column (Paper I).
- describe a mass mortality event across multiple life stages of *P. periphylla* in a high latitude fjord and presents the hypothesis that the high light levels of the summer night limit the distribution and retention of *P. periphylla* (Paper II).
- test two hypotheses for *P. periphylla* populations at higher latitudes: (1) fjords at high latitudes are not sufficiently dark to promote high numbers of *P. periphylla* due to the long photoperiod in summer; and (2) that basin depth in substantially deep fjords compensates for the lack of vertical habitat in the upper water layers by providing an enlarged dark habitat at depth (Paper III).

Main findings

Paper I – *Periphylla periphylla* distributes vertically according to light levels

Paper I tested the previously proposed hypothesis that *P. periphylla*'s vertical distribution emerges from individual responses to absolute light intensities (Dupont et al., 2009). Paper I was achieved by analyzing video profiles from a series of remotely operated vehicle (ROV) deployments under three different light regimes during which simultaneous continuous measurements of the surface irradiance levels were recorded. ROV profiles were analyzed for records of individual *P. periphylla*, and depth and time of day were noted, which enabled assignment of the corresponding surface irradiance value. These data were used to calculate the ambient irradiance levels of individual jellyfish from the surface to the benthos (0 – 440 m). The observations demonstrate that active selection in *P. periphylla* emerges as a behavioural response to light. At least part of the *P. periphylla* population appears to inhabit a “light comfort zone” (sensu Dupont et al., 2009) avoiding light levels that are too high but also avoiding levels that are too low. *Periphylla periphylla* were never observed above ambient irradiance levels of $0.02 \text{ mWm}^{-2} \text{ nm}^{-1}$ (at 500 nm) but mostly preferred light levels above $10^{-6} \text{ mWm}^{-2} \text{ nm}^{-1}$ (corresponding to total irradiance levels of $5 \times 10^{-3} \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ and $10^{-7} \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$), although some were located at depths with darker illumination. Migrating jellyfish were observed hovering below the upper light level limit, only to ascend into the upper waters when the solar irradiance decreased. Results suggest that *P. periphylla* migrates in asynchrony rather than in synchrony, which is consistent with the different migration modes documented during a three-month continuous study (Kaartvedt et al., 2011). The results also indicate that jellyfish may distribute by mechanisms similar to those of fish. There was no evidence that *P. periphylla* distributed according to other environmental variables such as the distribution of common mesozooplankton prey items.

Paper II - Mass mortality during periods of increasing duration and intensity of solar irradiance levels

A mass mortality occurring across multiple stages of the early developmental stages of *P. periphylla* was studied during an 11-month field campaign in a Norwegian fjord at 65°N. The mortality rate increased with the increasing intensity and duration of solar irradiance levels and was highest in the period with near 24-hours of sunlight. Modelling of the underwater light field on each sample date and over the year suggested a decrease in the access to the upper waters during the summer period because the maximum upper irradiance level that *P. periphylla* avoids (represented by total irradiance and estimated from Paper I) is located at deeper depths and for a longer duration around midsummer. These results illustrated a decrease in vertical habitat suitability in the summer months. The findings suggest that the high light intensity of the summer night at high latitudes limits *P. periphylla* populations through solar irradiance induced mass mortality events on the young developmental stages and by reducing the amount of suitable vertical habitat available.

Paper III - Photoperiod and retention constrain the northwards progression of *Periphylla periphylla* populations

This study was initiated during a period when local fishermen and media reported increasing numbers of *P. periphylla* in northern locations. These reports were documented through field sampling in nine Norwegian fjords between 65°N and 67°N during 2007-2015. Two previously suggested hypotheses were applied: the photoperiod constraint hypothesis previously suggested for mesopelagic fish (Kartvedt, 2008, Norheim et al., 2016) and the optically conditioned retention hypothesis for the mass occurrences of *P. periphylla* (Sørnes et al., 2007). Paper III tested that (1) the midsummer photoperiod limits the distribution of *P. periphylla* at higher latitudes through constraints on vertical habitat and (2) that substantially deep fjords can provide refuge from light for the non-migratory members of the population. A mass occurrence phenomenon at the same levels as in Lurefjorden, Halsafjorden,

Sognefjorden (Sørnes et al., 2007), and Trondheimsfjorden (Gjelsvik Tiller et al., 2014) was not detected in the nine sampled fjords. Modelling of the underwater light field along a south to north latitudinal gradient revealed a temporal and spatial change in the vertical habitat available to *P. periphylla* during midsummer. This is because the maximum upper irradiance level that *P. periphylla* avoids (represented by the total irradiance and estimated from Paper I) is located at deeper and for a longer duration with northwards progression during the summer. During midsummer in fjords at higher latitudes, the water column in shallow fjords (< 500 m) appears not to be substantially dark enough to promote retention of *P. periphylla*. However, in deeper fjords (> 500 m), the enlarged dark habitat may compensate for the increased latitudinal light exposure in the upper waters. In addition, the amount of time during increasing photoperiod in which upper surface waters are available to *P. periphylla* decreases with increasing latitude during midsummer.

Discussion

Light levels and mesopelagic jellyfish

The compilation of work in this thesis describes the importance of solar irradiance levels on the structuring effects of the mesopelagic jellyfish, *P. periphylla*. The findings in this thesis suggest light levels are one main driver behind the distribution and population retention of *P. periphylla* (Paper I-III). Evidence suggests *P. periphylla* is able to actively select its distribution through responding to the ambient light levels (Paper I). Photoperiod may have a constraining effect on *P. periphylla* in locations above 65°N during midsummer (Paper II and III). Mass mortality across multiple developmental stages of *P. periphylla* increased with increasing strength and duration of solar irradiance levels (Paper II). The amount of vertical habitat available to *P. periphylla* decreases with northwards progression, but deep basined fjords provide an extension of vertical habitat at deeper depths thus providing refuge for the smaller *P. periphylla* (Paper III).

The relationship between light levels and the distribution of jellyfish has been studied previously (Hamner et al., 1994, Hamner and Hauri, 1981, Dawson and Hamner, 2003) and hypothesised for *P. periphylla* (Eiane et al., 1997, Eiane et al., 1999, Sørnes et al., 2007, Dupont et al., 2009, Dupont and Aksnes, 2010, Aksnes et al., 2009). The work in this thesis, however, was the first to report on the active migratory response of individual jellyfish to ambient irradiance levels from the surface waters to 440 m. The ability of jellyfish to deliberately respond through swimming behaviour to their surrounding environment and seek out preferential conditions has implications for species distribution. The findings in this thesis are therefore relevant not only for the understanding of the factors structuring behaviour and populations of mesopelagic jellyfish but also as further evidence for the inclusion of bio-optical approaches in ecosystem research.

Light comfort zone, the photoperiod constrain hypothesis and *Periphylla periphylla*

At least part of the *P. periphylla* population in Lurefjorden distributes within an LCZ range of total irradiance values between 10^{-7} $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ and 5×10^{-3} $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ (Paper I). All *P. periphylla* avoided light levels above the latter value, while some individuals were located outside the lower total solar irradiance value. Presumably, *P. periphylla*'s vertical habitat in other fjords will also be found within the same LCZ levels, but the depths of which may be affected by local water quality conditions and latitude (Aksnes et al., 2009, Aksnes et al., 2017, Røstad et al., 2016b, Røstad et al., 2016a, Norheim et al., 2016). In locations above 65°N, the available habitat for *P. periphylla* decreases to the extent of a complete restriction to the upper waters (ca 50 m) during midsummer (Paper III). Restrictions on access to upper waters may, in theory, limit a population success by preventing efficient feeding (Fosså, 1992) or reproduction (Tiemann et al., 2009), both of which have been suggested to occur in the upper water layers during periods of low solar irradiance.

The hypotheses in Papers II and III take root in the body of literature providing evidence of the effects of light on *P. periphylla* population success and survival (Eiane et al., 1997, Eiane et al., 1999, Sørnes et al., 2007, Aksnes et al., 2009, Dupont et al., 2009, Dupont and Aksnes, 2010, Jarms et al., 2002, Herring, 1972, Bonnett et al., 1979, Youngbluth and Båmstedt, 2001). Firstly, mass populations have been recorded in fjords with elevated light attenuation levels, and in fjords with great basin depths that provide substantially dark environments (Sørnes et al., 2007). Secondly, *P. periphylla* vertically migrates within an LCZ (Dupont et al., 2009, Paper I), and upper water migrations have only been reported during periods of low solar irradiance (Sötje et al., 2007, Fosså, 1992). Thirdly, exposure to light has resulted in stress responses (Youngbluth and Båmstedt, 2001), lesions and, in at least the smaller stages, death (Jarms et al., 2002, Herring, 1972, Bonnett et al., 1979). Only the upper limit of *P. periphylla*'s light avoidance was considered for the Papers II and III because, from a biological standpoint and in regards to the phototoxic properties of protoporphyrin, very low light levels do not appear to cause physical harm to *P. periphylla* (Herring, 1972, Bonnett et al., 1979).

In addition, in the absence of light *P. periphylla* distributes throughout the water column due to the lack of a directional cue (Paper I, Dupont et al., 2009).

Jellyfish are able to search the water column in a manner similar to fish (Hays et al., 2012, Paper I). The environmental heterogeneity provided by underwater irradiance levels is further pronounced with latitudinal progression and season. During the summer months, mesopelagic fish face constraints on habitat availability due to the decreasing depth of the maximum upper limit of their LCZ (Kaartvedt, 2008, Norheim et al., 2016). It can be presumed that during summer periods populations of light-sensitive jellyfish that distribute within a specific range of light levels will face similar constraints on habitat availability and population success at higher latitudes (Paper II and III) as described for mesopelagic fish. In our hypothesis, the trade-off between predation behaviour and predator avoidance is not the reason for vertical distribution as *P. periphylla* is a tactile rather than visual predator, and is presumed to have minimal predators in the fjords (Fosså, 1992). Instead, the work in this thesis assumes the physiological restrictions related to the phototoxic degradation of protoporphyrin is connected *P. periphylla's* avoidance of light levels above $5 \times 10^{-3} \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ observed in Paper I.

Paper II considers the increasing duration and intensity of the solar irradiance levels during summer nights as a factor behind the mass mortality observed. The presence of initial developmental stages indicated ongoing recruitment or reproduction within the fjord during the autumn and winter period (Paper II). Large *P. periphylla* are able to migrate freely throughout the water column yet the motility of the smaller *P. periphylla* in develops as they phase through stages of neutral buoyancy, limited swimming capabilities, to a medusa with fully developed muscles yet not large enough to complete the vast migrations observed in *P. periphylla* with a CD > 4cm (Jarms et al., 1999, Jarms et al., 2002). It was these early developmental stages (including those that morphologically resembled the adult medusa) that dominated the mass mortality event documented in Paper II. The jellies that suffered mortalities were at the pigmented stage, and so at a point in their life cycles during which light can either harm or cease development (Jarms et al., 2002, Herring, 1972, Bonnett et al., 1979).

Active response to the surrounding environment

Documented thus far in scyphozoans, deliberate movement patterns in jellyfish are behaviour advantageous to aggregations and life history. For example, *Rhizostoma octopus* displays current-orientated swimming in order to remain in or move position towards an aggregation thereby increasing mate encounter rate (Fossette et al., 2015). Both *Cyanea capillata* and *Phacellophora camtschatica* differ in their horizontal swimming speeds in response to tidal flow and time of day, keeping these jellyfish within the same location regardless of current direction (Moriarty et al., 2012). Deliberate responses by *Aurelia* spp to current shear and turbulence drive orbital swimming patterns, resulting in hollow aggregations which induce currents at the bottom of the aggregation and promote mixing at the pycnocline (Churnside et al., 2016). Most surprising is the evidence of social interactions described as possible coordinated hunting behaviour displayed by *P. periphylla* during migrations in the upper 100 m (Kaartvedt et al., 2015). Larger jellyfish are able to locate each other and form groups. Mechanisms are unclear, but light as a common directional cue (Paper 1) may be one possibility. That *P. periphylla* displays migration behavior similar to mesopelagic fish (Paper I), is further evidence that jellyfish are active migrators able to respond to a common cue.

The larger *P. periphylla* display a diverse range of migration behaviour (Kaartvedt et al., 2011), which may reflect switching between different searching pattern behaviours between day and night possibly hunting scarce prey (Ugland et al., 2014). Results in this thesis (Paper I) suggest an additional, but not exclusive, interpretation of the searching pattern during the night: that *P. periphylla* has lost its directional cue (light) during dark periods, and the searching pattern is the result of searching the water column for the desired LCZ or just randomly.

If, as argued here, jellyfish respond to environmental conditions by choosing vertical habitat (Fossette et al., 2015, Moriarty et al., 2012, Hays et al., 2012, Paper I), there is reason to believe they will tend to avoid depths outside of the suitable range of said environmental variables. *Periphylla's* emergent response to light levels may, therefore,

partly explain the lower population numbers of *P. periphylla* at latitudes above 65°N (Paper III).

Optical controlled retention hypothesis and *Periphylla periphylla*

In fjords, sufficient basin depth (> ca 500 m) can mitigate habitat constraint by providing refuge from light levels at depth (Paper III) which is in agreement with the findings in the OCR hypothesis (Sørnes et al., 2007). Deeper basin depth was found to promote the presence of *P. periphylla*, although the ratio between sill and basin depth had no apparent effect on *P. periphylla* abundance (Paper III).

In Paper III, the *P. periphylla* populations were dominated by the smaller jellyfish (73-97%, with the exception of Sørfolla at 33%). This size class structure may be a reflection of the habitat preference and swimming behaviour of smaller *P. periphylla* (Sørnes et al., 2007, Dupont and Aksnes, 2010). Vertically migrating *P. periphylla* can be removed from a fjord through advective forces if the jellyfish migrate above the sill depth and into the advective layer (Eiane et al., 1998, Dupont and Aksnes, 2010). The large *P. periphylla* regularly migrate to depths within the advective layer (Dupont et al., 2009, Dupont and Aksnes, 2010) while the smaller jellyfish seem to prefer the deeper, darker habitats of the fjord basin and do not migrate above sill depth (Youngbluth and Båmstedt, 2001, Kaartvedt et al., 2011).

The basin depth preference and minimal swimming abilities of the smaller developmental stages (Jarms et al., 1999, Jarms et al., 2002) suggests that the rate of advection into the fjord for these stages is minimal. The range of early developmental stages (Paper II) and populations skewed towards smaller size classes (Paper III) suggests reproduction was occurring within the fjords. A topic of special interest is if *P. periphylla*'s migration response to light as a common cue of the larger jellyfish (Paper I) and the ability to locate and group with other members of the population (Kaartvedt et al., 2015) is related to deliberate migration towards locations that optimize mate encounter and population growth (Fossette et al., 2015, Moriarty et al., 2012). Such a study would consider if the larger *P. periphylla* migrate into the fjords during favourable irradiance conditions, for example during winter, a period that coincides with the

increased presence of initial developmental stages (Paper II), only to migrate out or lost by advection at some point after reproduction (for a similar suggestion see Geoffroy et al., 2018).

The effect of photoperiod on water column light attenuation results in regional differences and fluctuations in irradiance levels become more extreme with northwards progression (Kirk, 2011, pg. 42-44, Norheim et al., 2016). Paper II and Paper III suggest that the suitability of a fjord for population growth of *P. periphylla* (Sørnes et al., 2007) might shift (Dupont and Aksnes, 2010) on a seasonal basis according to the extreme changes in photoperiod experienced between seasons (Paper II) and latitude, respectively. The status of the Vefsnfjorden population from 2008 to 2015 had significantly decreased from a mass to a low occurrence level (Paper III). In 2008 and 2015, the largest individuals had a CD of 9.1 and 2.9 cm (a sexually immature jellyfish), respectively (Paper III). The presence of the larger *P. periphylla* had been in decline since ca 2013 according to local fishermen (pers. comm. G. Edvardson). The development stage classes ranged in summer 2011 and 2015 ranged from 7 – 14D (14D is the sexually mature stage) and 9 – 14C (unpub. data), respectively.

If sufficiently frequent, local mass mortality events are one mechanism that would reduce the ability to promote population retention (OCRH; Sørnes et al., 2007). Although local changes in optical conditions may be sufficient to foster *P. periphylla* population growth, such changes likely will lead to overall ecological changes and mesopelagic regime shifts (Aksnes et al., 2009, Haraldsson et al., 2012).

Past, present, and future reports of *Periphylla periphylla* at higher latitudes

This thesis confirms the presence of *P. periphylla* in fjords above 65°N (Paper II and III). Tiller et al. (2017) analysed the media reports from 2012 onwards that suggested this jellyfish was colonizing new environments northwards along the Norwegian coastline as an invasive species. Historical literature on *P. periphylla* distribution in Norwegian waters (Havnø, 1918, Havnø, 1926, Fosså, 1992) suggest a further discussion on fluctuating populations, both increasing and decreasing, is warranted. This is not to say that the catches of *P. periphylla* reported by fishermen were not in high abundances

or constituting an apparent bloom. Jellyfish aggregations can, by definition, disappear as quickly as they appear (Graham et al., 2001). The results presented in this thesis apply to year-round multi-year population growth and do not contest the episodic presence of high population numbers of *P. periphylla* in high latitude locations nor devalue the reports from fishermen.

Purposely, the hypotheses in Paper II and III does not dispute the current and continued presence of *P. periphylla* as a member of the gelatinous community in Norwegian coastal waters, including at higher latitudes (Gulliksen and Svendsen, 2004, Geoffroy et al., 2018, Fosså, 1992, Dalpadado et al., 1998) or at shallow depths in polar regions (Larson, 1986). A future scenario, however, of increased population growth is one possibility. The coastal water darkening due to freshening (Aksnes et al., 2009) and increased amounts of light absorbing dissolved organic matter of terrestrial origin, which in boreal regions is predicted to increase with a changing climate (Larsen et al., 2011) may be a precursor to increased population growth in some fjords at higher latitudes.

Jellyfish have received an increase in scientific and media attention in recent years due mainly in regards to a perceived global increase in population numbers and the negative associated economic losses (tourism, fisheries, aquaculture). With a lack of long-term datasets it has been difficult to define common factors for population growth (Purcell et al., 2007) and if populations are actually increasing globally (Condon et al., 2012). Misinterpretations of newsworthy regional media and scientific reports propagate negative “paradigms,” contributing to an inaccurate portrayal of local situations being wide-ranging factual events (Duarte et al., 2015). For gelatinous zooplankton, this can, and has, led to an incorrect misinterpretation of a species deviations from typical distribution ranges population and numbers (Condon et al., 2012, Sanz-Martín et al., 2016). In some cases, the apparent onset of increasing jellyfish numbers may be the adaptive response of the species to fluctuations in the availability of advantageous resources (Boero et al., 2008, Mills, 2001). For *P. periphylla* in particular, the changing optical conditions in some Norwegian fjords results in an environment less favourable to visual predators, such as fish, and better suited for

tactile predators such as jellyfish (Sørnes et al., 2007, Eiane et al., 1997, Eiane et al., 1999).

P. periphylla's historical distribution along the Norwegian coastline (as reviewed by Fosså, 1992) and the mass mortality in Vefsnfjorden (Paper II) followed by a continued decrease in abundance (Paper III) led to the consideration that the reports of increased numbers in the fjords could be naturally occurring fluctuations. The fluctuations in abundance observed in the Vefsnfjorden population (Paper III) appear to support the theory of episodic populations at higher latitudes, while the mass mortality event provides evidence of population fluctuation on a yearly basis (Paper II). Cyclic fluctuations in jellyfish abundance levels occur on a 20-year timeline that has been associated with global oscillations (Condon et al., 2013). With the current data, it is not possible to assess to what extent *P. periphylla* occurrences also oscillates on a similar timescale. As gelatinous zooplankton cover a wide range of habitats and species, applying findings as a generalization should be taken with caution (Sanz-Martín et al., 2016, Duarte et al., 2015, Condon et al., 2012).

Continued work on the ecological and biological interactions of *P. periphylla*, including on predator/prey interactions, fecundity, and dispersal patterns, needs to be undertaken in order to attain a more cohesive understanding on retention and distribution. Caveats aside, the work in this thesis further strengthens the previous hypotheses on the strong effects of the underwater light field and *P. periphylla* success (Eiane et al., 1999, Eiane et al., 1997, Sørnes et al., 2007, Aksnes et al., 2009), and for the mesopelagic realm (Aksnes et al., 2017, Aksnes et al., 2009, Frank and Widder, 1997, Warner et al., 1979, Martini and Haddock, 2017, Williamson et al., 2011).

Distribution of mesopelagic jellyfish in a changing climate

Reports of perennial mass occurrence populations are rare and include *Mastigias sp.* in Palau marine lakes (Cimino et al., 2018, Hamner and Hauri, 1981) and the Black Sea *Mnemiopsis leidyi* populations (Kideys, 2002). The first instance occurs in aseasonal landlocked marine lakes (Dawson et al., 2001, Hamner et al., 1982) and the latter occurred in the Black Sea during a period of extensive eutrophication (Kideys, 2002).

While unclear, a common theme for the persistent presence of jellyfish populations seems to be the presence of at least one (relatively) constant environmental factor or, in the very least, at levels that never cross over that of the species' tolerance level.

This thesis studies one factor that may constrain *P. periphylla* distribution at higher latitudes, which is in a region predicted to experience changes in species distribution and biomass with a changing climate. For gelatinous zooplankton, current dogma predicts that warming temperatures will result in an increase in population numbers and dispersal. But while evidence suggests that increasing temperatures will promote jellyfish growth at mid-latitudes there is limited evidence similar growths will be reported at low- and high-latitude coastal areas where species may already be close to or at their thermal maximum or where reproductive output is restricted to low temperatures ranges, respectively (Boero et al., 2016, Purcell et al., 2012, Purcell, 2005). In Norwegian fjords, *P. periphylla* resides mainly in the basin waters where temperatures are relatively homogeneous below the sill depth year-round (Sørnes et al., 2007, Youngbluth and Båmstedt, 2001). Correspondingly, differences in temperatures in fjords with mass occurrences of *P. periphylla*, low population numbers of *P. periphylla*, and no sampled *P. periphylla* are minimal (Paper III) (see also Sørnes et al., 2007).

P. periphylla mass occurrence populations are found in relatively shallow fjords where water masses show negative correlation between oxygen levels and increased light attenuation (Aksnes et al., 2009, Sørnes et al., 2007, Eiane et al., 1999). In boreal areas, this may be an indirect result of warming temperatures (Larsen et al., 2011). A predicted shallowing of the DSL with warming temperatures has been hypothesized to result in an increase in the mesopelagic biomass at higher latitudes with the expansion of species ranges and an increase in food resources (Proud et al., 2017). Such a change in water quality may open up more habitat for *P. periphylla* if the distribution of this jellyfish is related to the migratory behaviour of following light levels as a directional cue (Paper I). The light regime, however, will not change and during midsummer, the upper limit of the vertical extent will still on some level be constrained by the photoperiod (Kartvedt et al., 2018). Meaning that the increase in *P. periphylla* numbers at higher latitudes will still face photoperiod related restrictions that increase with northwards progression

(Paper II and III) but this constraint may weaken if environmental conditions alter to promote a darker water column. For example, an increased supply of light absorbing DOM of terrestrial origin (to NCW) is a potential scenario associated with climate change (Larsen et al., 2011, Wolf and Heuschele, 2018) that may promote growth of *P. periphylla* populations (Aksnes et al., 2009).

At what threshold will the vertical extent shallow to a level that promotes perennial populations of *P. periphylla* is of research interest not only for the distribution of this jellyfish but also for mesopelagic regime shifts (Aksnes et al., 2009). More turbid waters may reduce feeding rates of fish due to a decrease in the efficiency of visual predation, resulting in a decrease in competition for food resources between visual and tactile predators thus providing a scenario for increased numbers of jellyfish (Eiane et al., 1997, Eiane et al., 1999). Such an environmental condition coupled with the relatively high medusa longevity (ca up to 30 years (Tiemann and Jarms, 2010, Youngbluth and Båmstedt, 2001) and the high reproductive output (Tiemann and Jarms, 2010), have made for a prime scenario for high levels of population numbers in some fjords.

Concluding remarks and future directions

This thesis contributes to the understanding of jellyfish behaviour in the mesopelagic, specifically to the structuring effects of irradiance levels on vertical distribution (Paper I) and limitations on species distribution (Paper II and III). These studies build upon previously developed hypothesis for the success of *P. periphylla* in relations to light levels (Eiane et al., 1999, Sørnes et al., 2007, Aksnes et al., 2009, Dupont et al., 2009, Dupont and Aksnes, 2010) and goes further by providing evidence that marine processes that govern the behaviour and distribution of mesopelagic fish may also be applicable to jellyfish. Taken together, *P. periphylla* distribute vertically through an active response to absolute light levels and as a result face limitation on species distribution. However, as not all of the individuals in the population distributed within the same LCZ further research should investigate who is light sensitive and who is not, and why. The findings in this thesis highlight a behavioural response by jellyfish to their surrounding environment, which has implications for species distribution. This thesis also supports the further need for the inclusion of bio-optical measurements that are sufficiently sensitive to measure mesopelagic light intensities in ecosystem studies, something that is not adequately addressed through today's commercially available equipment that is for the daytime use in the epipelagic zone.

This thesis provides further evidence that jellyfish are capable of deliberate and active behaviour; behaviour that is potentially more common than generally presumed. The ability of jellyfish to select preferential habitats (Hays et al., 2012, Fossette et al., 2015, Moriarty et al., 2012), social behaviour (Kaartvedt et al., 2015), and migration patterns that result in the concentrations of prey items (Churnside et al., 2016) opens more research avenues for consideration. For example, if jellyfish are actively selecting their distribution in response to the physical or biological environment, are the distributions of jellyfish populations a reflection of these actions? Are jellyfish able to migrate long distances and between localities while following changing preferential conditions?

There is a series of questions specific to *P. periphylla*'s apparent ability to respond to the ambient irradiance levels. Do large *P. periphylla* utilize fjords as nursery grounds and migrate during periods with suitable photoperiod? Additionally, could decreased water

clarity in higher latitude fjords promote retention of *P. periphylla*? If so, do optical conditions fluctuate on a scale that limits multi-year mass occurrence populations? All of these questions suggest behaviour at a level of complexity not previously appreciated for gelatinous zooplankton.

Investigating that jellyfish make deliberate choices that affect their distribution would be a complicated endeavour. Methods similar to the tagging practises undertaken in studies on the migration patterns of other scyphozoans (Fossette et al., 2016, Hays et al., 2008) could be one component. Other points to consider include but are not limited to, species anatomy and swimming abilities, environmental tolerances, and life histories. The term “jellyfish” is wide-ranging and covers gelatinous zooplankton in all marine depths and zones as well as some freshwater locations. Naturally, with the range of species that comprise the term jellyfish, it can be expected for there to be a range of behavioural patterns and responses within the group.

Jellyfish have an aspect of an enigma: multiple factors may promote increased population numbers, which can occur in what seems a rather sudden timeline. Understanding what drives jellyfish distribution and populations would be beneficial not only to the scientific community but also to industries. Evidence presented in this thesis indicates that an organism we previously have (mis)conceived as simple has the ability to actively respond to its environment and that this ability helps to shape both the vertical and local distributions. Indeed, jellyfish are capable of migratory responses to their surrounding environment. For the jellyfish *P. periphylla*, it appears that ambient irradiance levels go a far way in shaping the behaviour, distribution, and population structure. The structuring effects of light in the mesopelagic realm warrants continued and further research not just for jellyfish but for the members of this zone as a whole.

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Paper I

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Jellyfish distribute vertically according to irradiance

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We tested the hypothesis that the coronate jellyfish *Periphylla periphylla* distributes vertically according to a preferential range of absolute light intensities. The study was carried out in Lurefjorden, Norway, a fjord characterized by mass occurrences of this jellyfish. We collected data on the vertical distribution of *P. periphylla* medusa during day, dusk and night periods from video observations by a remotely operated vehicle in relation to estimated ambient light levels. Our results suggest that large *P. periphylla* (average size in catches ~9 cm diameter) avoided total irradiance levels above $5 \times 10^{-3} \mu\text{mol quanta m}^{-2} \text{s}^{-1}$. Nearly two-thirds of the population stayed above irradiance of $10^{-7} \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ during daytime, while some individuals occupied much darker water. Thus, part of the population appeared to distribute vertically and undertake diel vertical migration (DVM) according to a preferential range of light intensities.

KEYWORDS: *Periphylla periphylla*; light attenuation; diel vertical migration; jellyfish behavior

INTRODUCTION

Light-mediated migration is widespread in jellyfish and numerous mesopelagic species undergo nocturnal ascents from depths of hundreds of meters and below to then descend with sunrise (Graham *et al.*, 2009). Yet diel vertical migration (DVM) is not the sole migration pattern in jellyfish (Graham *et al.*, 2001). Directionally specific migrations are triggered by detection of the onset and offset of surface light levels (Garm *et al.*, 2012).

Sun-compass migration exists in at least one *Aurelia* spp. population where individuals orientate at the water's surface in accordance to the position of sunlight (Hamner *et al.*, 1994). Species that lack light-sensing ocelli also may perform DVM (Schuyler and Sullivan, 1997; Graham *et al.*, 2001) by detecting light through extraocular photoreception (Garm and Ekström, 2010). For example, medusa with porphyrin pigments, including *Stygiomedusa gigantea* (Benfield and Graham, 2010),

Atolla spp. and *Periphylla periphylla* (Bonnett *et al.*, 1979), are limited to waters with low light levels due to the phototoxic effects of light exposure on the pigment (Herring, 1972; Larson, 1986).

In situ studies on downwelling irradiance and mesopelagic vertical migrations can present methodological challenges, yet provide results that are more realistic than data solely extrapolated from surface irradiance measurements (Frank and Widder, 1997). Few studies have investigated an organism's sensitivity to ambient light levels in relation to vertical distribution (eg. Matsuura *et al.*, 2012; Prihartato *et al.*, 2015), and the potential effects of ambient irradiance levels on jellyfish migration patterns have received little attention. Such interactions are potentially important in a changing climate as altered optical conditions may result in mesopelagic regime shifts (Aksnes *et al.*, 2009). The darkening of water columns could alter environments toward habitats more suitable for tactile predators, such as jellyfish, rather than for visual predators such as fish (Eiane *et al.*, 1999). Sørnes *et al.* (2007), for example, details altered optical environments in some Norwegian fjords as a criterion for mass abundances of the coronate scyphozoan *P. periphylla*.

The migration patterns of *P. periphylla* are complex (Fosså, 1992; Youngbluth and Båmstedt, 2001; Jarms *et al.*, 2002; Kaartvedt *et al.*, 2007, 2011, 2015; Ugland *et al.*, 2014). Surface aggregations are confined to dark periods (Fosså, 1992; Sötje *et al.*, 2007), yet at greater depths *P. periphylla* displays individual variation with distinct migration patterns related to depth and medusa size (Kaartvedt *et al.*, 2011). Recent evidence has documented deliberate responses by *P. periphylla* to the surrounding environment, including social behavior (Kaartvedt *et al.*, 2015) and the switching of search patterns between day and night periods (Ugland *et al.*, 2014), but the mechanisms and preferences behind *P. periphylla* migration behavior remain unclear.

Light has been suggested to play a role in the life history and behavior of *P. periphylla* (Jarms *et al.*, 1999, 2002; Youngbluth and Båmstedt, 2001; Jarms *et al.*, 2002; Kaartvedt *et al.*, 2007; Sötje *et al.*, 2007). The rhopalia of *P. periphylla* lack ocelli (Sötje *et al.*, 2011); however, protoporphyrin develops with age and becomes entodermally visible with the onset of rhopalia development (Jarms *et al.*, 1999, 2002). Light exposure related lesions, due to the phototoxic reactions of protoporphyrin (Herring, 1972; Bonnett *et al.*, 1979), may lead to fatalities and development ceases in young jellyfish exposed to light (Jarms *et al.*, 2002). Accordingly, *P. periphylla* exhibits stress response behavior when exposed to light (Youngbluth and Båmstedt, 2001).

The increased light attenuation in some Norwegian fjords promotes, in part, the growth of *P. periphylla* mass populations by altering the basin waters toward an environment that better mimics the deep open ocean from which *P. periphylla* originates (Sørnes *et al.*, 2007). It has been hypothesized that the larger members of the *P. periphylla* population have the highest tolerance for light intensities and that it is this tolerance that enables individuals to migrate to shallower depths during day periods (Dupont *et al.*, 2009). However, previous studies have not related *in situ* observations of *P. periphylla* depth distribution to ambient irradiance levels.

We tested the hypothesis of Dupont *et al.* (2009) that *P. periphylla* distribute vertically according to a specific range of preferential light intensities. We collected *in situ* vertical distribution data of the medusa through video recordings using a remotely operated vehicle (ROV) during periods of day, dusk and night. We recorded downwelling irradiance at the surface and underwater irradiance to 83 m simultaneously with the ROV deployment. We obtained an estimate of the attenuation coefficient by exponential regression of the observations of downwelling between 5 and 80 m at 500 nm. To obtain an estimate of the attenuation coefficient below 80 m, we applied absorption measurements on unfiltered water samples as a proxy (Aksnes *et al.*, 2009). We could then relate *P. periphylla*'s vertical distribution to ambient light levels experienced by the different individuals in the water column.

METHOD

Sampling was carried out in Lurefjorden, Norway, (60° 41' 14" N; 5° 10' 16" E), on 7–9 February 2010 aboard the RV "Håkon Mosby" (University of Bergen and Institute of Marine Research). Temperature, salinity, oxygen and chlorophyll fluorescence were profiled from the surface to close to the seabed by a conductivity, temperature and density (CTD) profiler (Seabird Electronics). We also sampled *P. periphylla*, their mesozooplankton prey and irradiance (see below).

Description of study area

Lurefjorden has a maximum basin depth of 440 m and a sill depth of 20 m. Due to the shallow sill depth the water column consists of Norwegian Coastal Water (NCW) (Sørnes *et al.*, 2007). NCW is characterized by lower salinity and higher light attenuation than the surrounding North Atlantic Water (Aksnes *et al.*, 2009). Lurefjorden's elevated light attenuation and fjord

topography promote population retention and growth of *P. periphylla* (Sørnes *et al.*, 2007). Increased numbers of the jellyfish were first reported in 1970s (Fosså, 1992) and have persisted to the present day, with values ranging from 25 to 50 individuals m^{-2} (Sørnes *et al.*, 2007). Compared to adjacent systems, mesopelagic fish are virtually absent in Lurefjorden (Fosså, 1992; Bagøien *et al.*, 2001), a scenario hypothesized to be attributed to the constraints a darker water column places on the feeding success of visual predators (Eiane *et al.*, 1997, 1999; Aksnes *et al.*, 2009). Consequently, the lack of mesopelagic predation pressure has promoted the population growth of mesozooplankton in both individual sizes and abundance levels, both of which are higher than in nearby fjords (Bagøien *et al.*, 2001; Eiane *et al.*, 2002). The stable water masses and semi-enclosed system of Lurefjorden and the exceptionally high abundances of *P. periphylla*, which migrate vertically to the surface, provide unique opportunities for studies on a deep water and otherwise oceanic jellyfish (e.g. Fosså, 1992; Jarms *et al.*, 2002; Sötje *et al.*, 2007; Tiemann and Jarms, 2010; Kaartvedt *et al.*, 2011; Ugland *et al.*, 2014).

Periphylla

We used a ROV, ROV “Aglantha”, fitted with a Sony Hi8 video system and red light to record the depths of individual *P. periphylla*. Ten vertical transects were recorded under red light during four dives between 7 and 9 February 2010. Nine hours and thirty minutes of film footage were analyzed by recording each individual *P. periphylla* encountered in a field of view according to depth and time. We selected three of the ten ROV dives for further analysis. Our criteria for the selected transects were profiles that were without disruptions (i.e. no

hovering of the ROV, out of focus DVDs) and fell under one of three categories of surface irradiance conditions: day, dusk, night (Table I). The ROV footage of individual *P. periphylla* under the three different surface irradiance conditions was then used to calculate the ambient irradiance levels of *P. periphylla* (see details below). Additionally, individual *P. periphylla* observations were grouped into 25 m depth bins for each dive profile to plot the vertical distribution under the different surface irradiance conditions. To compare profiles, we calculated the median, quartiles depth and the interquartile range (IQR) (m) for the *P. periphylla* distribution from the ROV observations under the three different surface irradiance conditions.

The ROV was not equipped to determine the size of the medusa (Youngbluth and Båmstedt, 2001) and so trawl samples were used to indicate the coronal dome (CD, cm) range of *P. periphylla*. We used a Harstad trawl 320 equipped with a Multisampler cod-end to sample during day and night (Table I). The mesh size of the Multisampler cod-end ranged from 200 mm in the front to 10 mm in the rear part. The Multisampler can be opened and closed on demand, thereby permitting depth-stratified sampling (Engas *et al.*, 1997). A Scanmar depth sensor provided information on trawl depth. The depth-specific sampling comprised 8 depth intervals from 350 to 20 m (Table I). All *P. periphylla* caught were counted and measured for CD width (CD, cm).

Mesozooplankton

Following previous studies (Youngbluth and Båmstedt, 2001; Sötje *et al.*, 2007; Sørnes *et al.*, 2008), we assumed that *P. periphylla* prey on the common mesozooplankton in Lurefjorden including *Calanus* spp., Ostracods,

Table I: ROV dives, Harstad trawl and MultiNet sampling parameters for *Periphylla* and mesozooplankton collection for day, dusk and night samplings in Lurefjorden on 7, 8 and 9 February 2010

Date	Start time (local time)	Surface irradiance conditions ($mW m^{-2} nm^{-1}$)	Equipment	Transect/-trawl	Sampling depth or depth interval (m)	Target organisms	Individual observations of <i>Periphylla</i> (#)
9 February 2010	15:05	Day (>245.75)	ROV	1	440–0	<i>Periphylla</i>	107
7 February 2010	17:45	Dusk (0.03–0.21)	ROV	1	440–0	<i>Periphylla</i>	95
9 February 2010	19:00	Night ($<1.00 \times 10^{-3}$)	ROV	1	440–0	<i>Periphylla</i>	76
8 February 2010	10:00	Day	Harstad trawl	1	20, 50, 100, 150, 200, 250, 300, 350	<i>Periphylla</i>	658
7 February 2010	20:00	Night	Harstad trawl	1	20, 50, 100	<i>Periphylla</i>	329
8 February 2010	19:00	Night	Harstad trawl	1	150, 200, 250, 300, 350	<i>Periphylla</i>	358
8 February 2010	12:00	Day	Kiel MultiNet	1	0–50, 50–90, 90–140, 140–170, 170–210, 210–250, 250–310	Mesozooplankton	
8 February 2010	19:00	Night	Kiel MultiNet	1	0–50, 50–90, 90–140, 140–170, 170–210, 210–250, 250–310	Mesozooplankton	

Measured surface irradiance levels are only available for corresponding ROV dives.

Chaetognaths and mysids (Bagoien *et al.*, 2001). Mesozooplankton was sampled during day and night on 8 February 2010 by vertical hauls with a MultiNet (0.25 m² opening, 200 μm mesh size, HydroBios, Kiel) from 310 m to the surface (Table I). Unfortunately, a malfunction of the sampling gear prevented sampling of depths below 310 m. Samples were preserved in a 4% buffered formaldehyde-in-seawater solution for subsequent identification and numeration. *Calanus* spp. dominated the samples, but the numbers reported here are pooled data of the most abundant mesozooplankton species.

We calculated the weighted mean depth (\bar{z}_m , m) and standard deviation (\bar{z}_s , m) for mesozooplankton during day and night sampling periods according to the trapezoid method (Dupont and Aksnes, 2012):

$$A = \sum_{i=1}^n \Delta z_i D_i, \quad (1)$$

$$\bar{z}_m = \frac{\sum_{i=1}^n \Delta z_i D_i \bar{z}_i}{A}, \quad (2)$$

$$\bar{z}_s = \sqrt{\frac{\sum_{i=1}^n \Delta z_i D_i \bar{z}_i^2}{A} - \bar{z}_m^2}, \quad (3)$$

where A is the surface integrated abundance, n is the number of depth strata, Δz_i is the lower sample-upper sample (m) of depth sample interval i , D_i is the abundance of taxon under study and \bar{z}_i is the mid-strata of depth interval i .

Vertical overlap between *P. periphylla* and mesozooplankton

We estimated the degree of overlap between the vertical distributions of zooplankton and *P. periphylla* by use of the overlap coefficient (V) following an adaptation of Williamson *et al.* (1989) and Williamson and Stoeckel (1990):

$$V = \frac{\sum_{z=1}^m (N1_z N2_z) m}{\sum_{z=1}^m (N1_z) \sum_{z=1}^m (N2_z)}, \quad (4)$$

where $N1$ and $N2$ are prey and predator abundances in depth interval “ z ”, and m is the number of depth intervals sampled. As $N1$ we used the seven depth-specific mesozooplankton abundance estimates from the MultiNet samples, and we obtained estimates for $N2$ values from the ROV observations by calculating the abundance estimates of *P. periphylla* from depth intervals corresponding to those of the MultiNet mesozooplankton collections. Units for this are *P. periphylla* individuals in depth interval per second. For a situation with seven depth intervals, it follows from equation (5) that a $V = 0$

represents non-overlapping distributions and a $V = 7$ would reflect identical distributions. A $V = 1$ is indicative of one of the populations having uniform distribution.

Estimation of the ambient irradiance of individual *P. periphylla*

To calculate the ambient light for individual ROV observations of *P. periphylla*, we used a Trios RAMSES ACC hyperspectral radiometer to measure downwelling irradiance (E_0) at 500 nm continuously at the surface (i.e. mounted on the ship deck during ROV deployments) and underwater irradiance down to 83 m depth at midday under a sunny clear sky. Below this depth the sensitivity of the instrument was insufficient. In accordance with previous measurements in NCW (Claes *et al.*, 2010), irradiance at 500 nm was the strongest at 83 m (Fig. 1a) and we used this wavelength to characterize the ambient irradiance, in units of mW m⁻² nm⁻¹, for *P. periphylla*. We have also reported the upper irradiance exposure of *P. periphylla* as total irradiance, i.e. in units of quanta m⁻² s⁻¹, by summing over the spectrum after conversion from watts to quanta for the different wavelengths. The attenuation coefficient for downwelling irradiance at 500 nm, $K_{80} = 0.117$ m⁻¹ was estimated from exponential regression of the observations of downwelling irradiance between 5 and 80 m (Fig. 1b). To obtain an estimate of the attenuation coefficient below 80 m we applied absorption measurements on unfiltered water samples as proxy (Aksnes *et al.*, 2009). Water samples were collected from the surface to 400 m depth. The water samples were acclimatized to room temperature and light absorbance was measured in a 10-cm quartz cuvette with a spectrophotometer (Lambda 2, Perkin Elmer). The blank control contained distilled freshwater purified with a Millipore Simplicity 185 Water Purification System. The light absorption coefficient (Fig. 1c) was calculated according to $a = 2.303A/0.1$ where A is the absorbance at 500 nm. We assumed that the ratio between K and a was the same above and below 80 m and obtained an estimate of the attenuation between 80 and 400 m depth ($K_{400} = 0.102$, Table II).

For each *P. periphylla* observation during a dive, time (t) and depth (z) was noted. The downwelling irradiance at 500 nm at the depth of the individual was calculated according to:

$$E(t, z) = (1 - R)E_0(t)f(K_{80}, K_{400}, z) \quad (5)$$

Here, R is the surface reflectance given as a fraction. This quantity was estimated according to local time and the corresponding zenith angle of the sun, which was calculated according to the NOAA solar position calculator

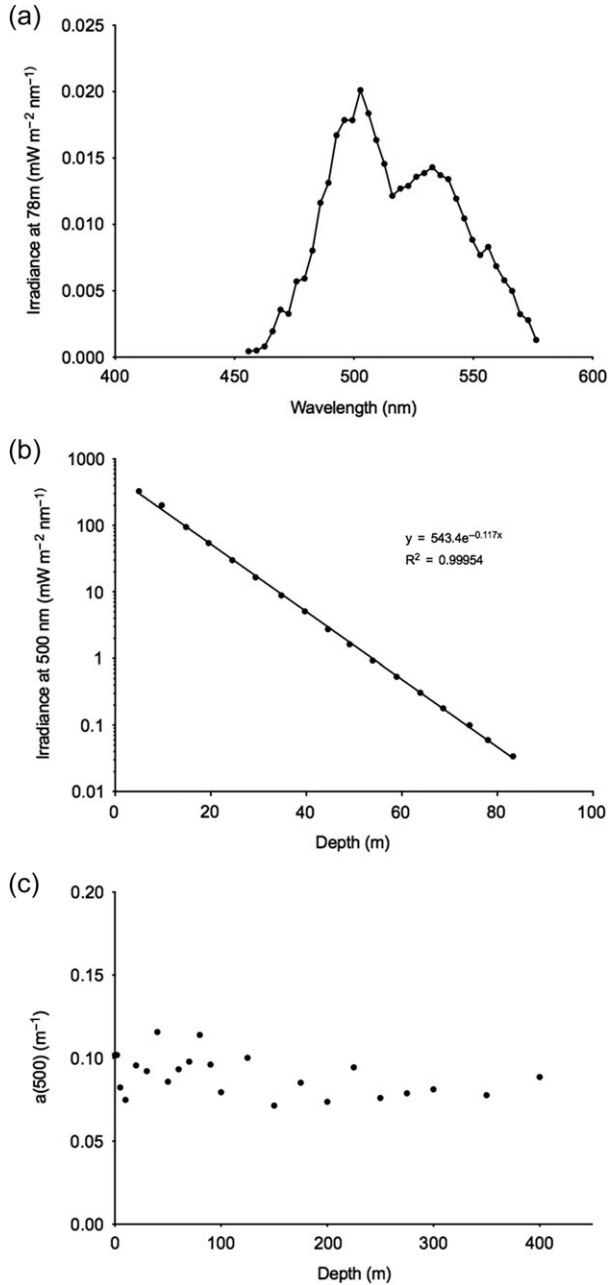


Fig. 1. (a) Downwelling irradiance in Lurefjorden in February 2010 at 78 m depth as a function of wavelength. (b) Downwelling irradiance at 500 nm as a function of depth. The attenuation coefficient ($K_{500} = 0.117 \text{ m}^{-1}$) of downwelling irradiance was calculated by fitting $y = 543.4e^{-0.117x}$, ($R^2 = 0.9995$) where y is observed irradiance at depth (x). (c) Light absorption coefficient calculated according to $a = 2.303A/0.1$ where A is the measured absorbance at 500 nm. We assumed the ratio between K and a was the same above and below 80 m and obtained an estimate of the attenuation between 80 and 400 m depth ($K_{400} = 0.102$, Table II).

(<http://www.esrl.noaa.gov/gmd/grad/solcalc/azel.html>), at the sampling location (60.41.14 N, 5.10.16 E). The wind speed ranged between 2 and 8 m s^{-1} during

*Table II: Estimate of the attenuation of downwelling irradiance (at 500 nm) deeper than 80 m from measurements of light absorption (see text Estimation of the ambient irradiance of individual *P. periphylla* in Methods section).*

	(m ⁻¹)	SD	n
Absorption shallower than 80 m (a_{80})	0.096	0.012	11
Absorption deeper than 80 m (a_{400})	0.084	0.012	11
Attenuation shallower than 80 m (K_{80})	0.117	See Fig. 2B	
Attenuation deeper than 80 m (K_{400})	0.102	$K_{400} = K_{80}a_{400}/a_{80}$	

daylight and a reflectance of 50% was set as the maximal reflectance at high zenith angles (Fig. 2.11 in Kirk 2011). The lowest (i.e. at midday) zenith angle in Lurefjorden during the present study was ~ 76 degrees which corresponds to a minimal reflectance of 23% (table 2.1 in Kirk, 2011). The f -function of equation (5) is the fraction of the irradiance penetrating to depth x as a function of the attenuation shallower and deeper than 80 m, i.e. $f = \exp(-K_{80}z)$ or $f = \exp(-K_{80}80) \exp(K_{400}(z-80))$ for z shallower and deeper than 80 m respectively. This procedure was used to calculate the ambient irradiance of individual *P. periphylla* observations during three ROV profiles obtained under three surface irradiance conditions: during day, dusk and night.

To compare profiles, we calculated the median and quartiles distribution of the ambient irradiance of each individual *P. periphylla* ($\text{mW m}^{-2} \text{ nm}^{-1}$) during day, dusk and night periods.

RESULTS

Hydrography

Surface waters (0–60 m) were well mixed during the study period with temperate $\sim 5^\circ\text{C}$ and salinity of 32.5 PSU (Fig. 2). There was a weak stratification with modest increase in density from 60 to ~ 120 m below which the water column was relatively homogenous with temperatures of $\sim 7^\circ\text{C}$, salinity ~ 33.0 PSU. Oxygen levels declined from surface values of 5.7 to 2.0 mg L^{-1} close to the seabed. The fjord basin was filled with NCW (with salinities < 34.50). Fluorescence levels were low with all Chl a concentrations $< 0.05 \mu\text{g L}^{-1}$ (Fig. 2).

Periphylla distribution

Harstad trawl

In total, 1345 *P. periphylla* were caught in the Harstad trawl. The *P. periphylla* population was predominantly

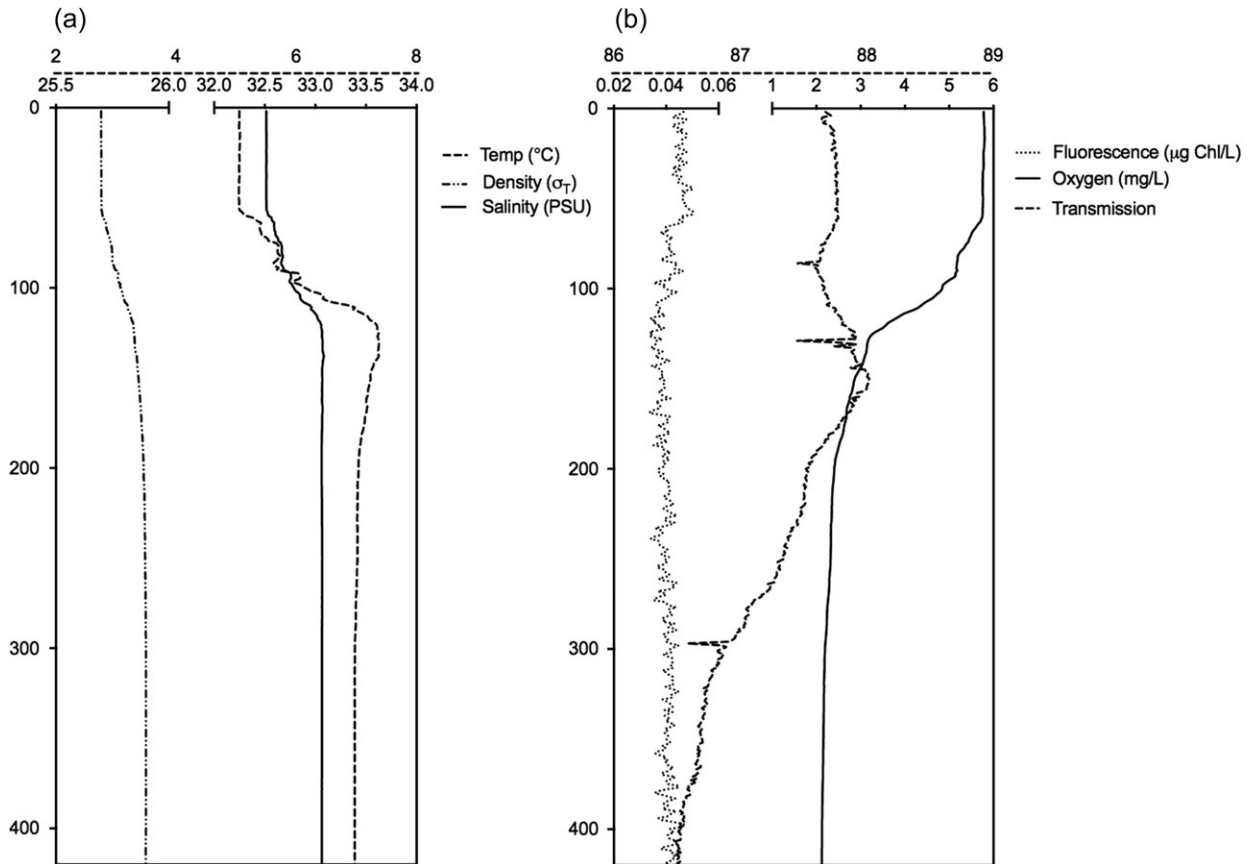


Fig. 2. Lurefjorden vertical water profiles for (a) temperature, density and salinity; and (b) fluorescence, oxygen and transmission on 9 February 2010.

represented by large individuals (*sensu* Sørnes *et al.*, 2007); CD ranged from 4.0–13.5 cm with a mean of 8.8 ± 1.33 cm (Fig. 3).

ROV observations and surface irradiance conditions

Under day (high) surface irradiance conditions (Table I), 30% of the *P. periphylla* population was located between 100 and 125 m (Fig. 4a). At dusk (low) surface irradiance conditions (Table I), the abundance peak had shifted to ~75 m with 45% of *P. periphylla* encountered between 50 and 100 m (Fig. 4b). At night (night surface irradiance conditions; Table I), 20% of the population were recorded above 25 m with the rest of the jellyfish evenly dispersed throughout the water column from surface to ~250 m (Fig. 4c). One-third of the population was observed below 250 m in day, while only ~10 % of the population were observed below this depth for dusk and night. The depth distribution for the day, dusk and night *P. periphylla* ROV vertical distribution observations had a median depth of 155 m (IQR = 114–228 m), 77 m (IQR

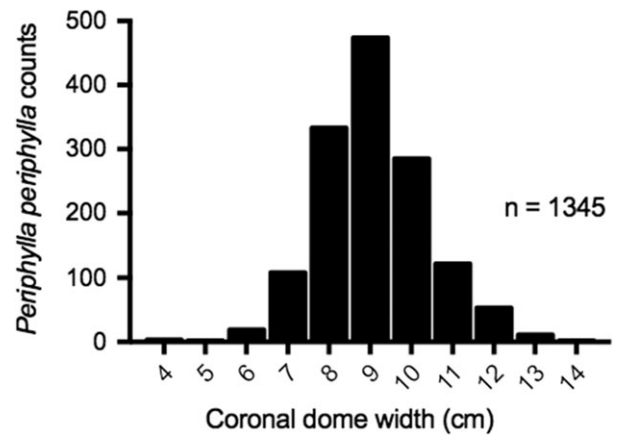


Fig. 3. CD width (cm) of Lurefjorden *P. periphylla* total catch collected with Harstad trawl during day and night on 7 and 8 February 2010 (mean CD = 8.85 ± 1.33 cm). See Table I for sampling parameters.

= 55–124 m) and 36 m (IQR = 15–178 m), respectively. The depth range was widest under the night surface irradiance (Fig. 4).

Ambient irradiance of individual *Periphylla*

Under day (high) and dusk (low) surface irradiance conditions, the bulk of the population aggregated in similar ambient irradiance levels 10^{-4} – 10^{-6} $\text{mW m}^{-2} \text{nm}^{-1}$ (Fig. 5a and b). The mean ambient irradiance of *P. periphylla* \log_{10} for day and dusk was -6.52 ± 4.41 $\text{mW m}^{-2} \text{nm}^{-1}$, -6.60 ± 3.60 $\text{mW m}^{-2} \text{nm}^{-1}$, respectively (Fig. 5). The median depth for the ambient irradiance of individual *P. periphylla* \log_{10} ($\text{mW m}^{-2} \text{nm}^{-1}$) for the day and dusk was -5.08 (IQR = -8.33 to -3.28) and -5.44 (IQR = -7.56 to -4.46), respectively (Fig. 5). *Periphylla* were never observed at ambient light levels above $0.02 \text{mW m}^{-2} \text{nm}^{-1}$ (Fig. 5). This level is the same as the irradiance measured at 78 m (peak irradiance at 500 nm in Fig. 1a), and the total irradiance, obtained by summing over the spectrum after conversion to quanta, corresponds to 5×10^{-3} $3 \text{ mol quanta m}^{-2} \text{s}^{-1}$.

The aggregation observed during daylight lessened at night and the population became distributed over a broader range of calculated light levels (Figs. 4c and 5c). The median ambient irradiance of individual *P. periphylla* \log_{10} ($\text{mW m}^{-2} \text{nm}^{-1}$) at night was -10.02 (IQR = -13.44 to -6.12), respectively (Fig. 5). Note, however, that the low calculated downwelling irradiance levels in most of the water column during night are purely theoretical. Downwelling irradiance is likely lower than bioluminescent light. It is unclear to what extent there is a gradient in light with depth at night.

Mesozooplankton distribution

Mesozooplankton peaked at 90–140 m during day and 140–170 m during night sampling (Fig. 6). Weighted mean depth varied little between day ($\bar{z}_m \pm Z_s = 188.8 \pm 113.4$ m) and night (183.5 ± 119.5 m). The vertical

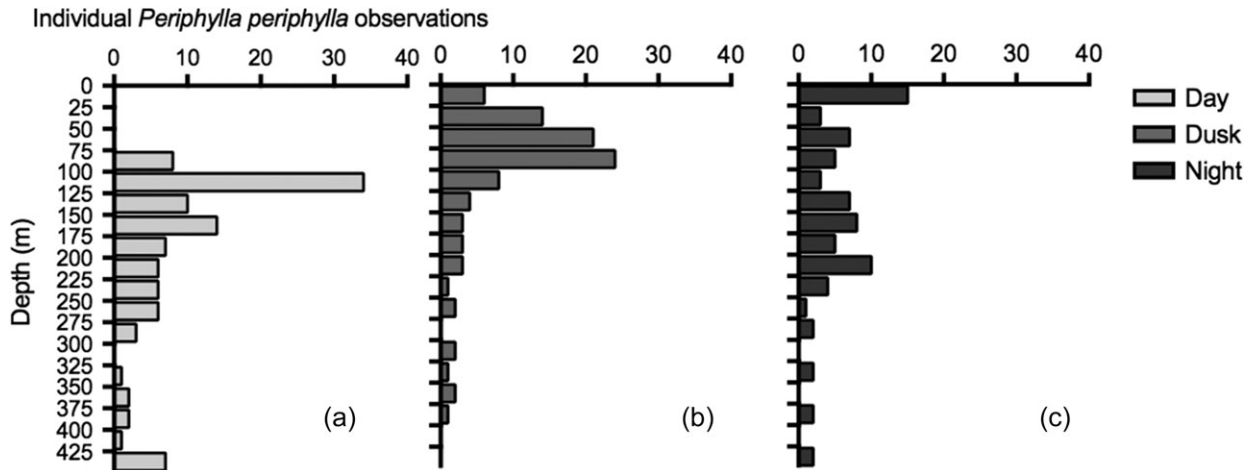


Fig. 4 Depth distribution of individual *P. periphylla* observed during three ROV dives: (a) day under high surface irradiance conditions ($>245.75 \text{mW m}^{-2} \text{nm}^{-1}$); (b) dusk under low surface irradiance conditions (0.03 – $0.21 \text{mW m}^{-2} \text{nm}^{-1}$); and (c) night under night surface irradiance conditions ($<1.00 \times 10^{-3} \text{mW m}^{-2} \text{nm}^{-1}$) in Lurefjorden, Norway, on 7 and 9 February 2010. All times local. See Table I for sampling parameters.

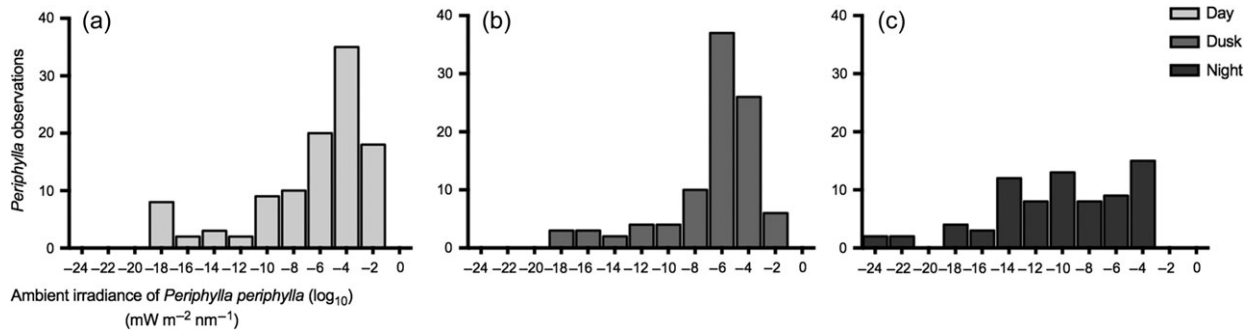


Fig. 5. Ambient light distribution of Lurefjorden *P. periphylla* \log_{10} , in units $\text{mW m}^{-2} \text{nm}^{-1}$, during a dive in (a) day, mean = -6.52 ± 4.41 $\text{mW m}^{-2} \text{nm}^{-1}$; (b) dusk, mean = -6.60 ± 3.60 $\text{mW m}^{-2} \text{nm}^{-1}$ and (c) night, mean = -10.22 ± 4.97 $\text{mW m}^{-2} \text{nm}^{-1}$ on 7 and 9 February 2010. See to Table I for sampling parameters. Ambient light is the calculated ambient downwelling irradiance at the depth where the individual *P. periphylla* were observed from the ROV profiles. Corresponding depth distributions and surface irradiance conditions are provided in Fig. 4.

distribution of the mesozooplankton was likely affected by the low winter Chl *a* values ($<0.05 \mu\text{g L}^{-1}$, Fig. 2), which would render the benefits of migrating minimal. The dominant group was *Calanus* spp. with Ostracods, Chaetognaths and mysids as the other abundant groups. The overlap between *P. periphylla* and total mesozooplankton varied little between day and night periods ($V = 1.03$ and 1.01 , respectively).

DISCUSSION

The vertical migration of large *P. periphylla* (Fig. 4) appears as an emergent property from light-related behavior (Fig. 5). The ambient irradiance of the individual *P. periphylla* suggests that the bulk of the jellyfish have a range of preferential light levels (Fig. 5a and b). The population dispersed throughout the water column (Fig. 4) during the period of lowest calculated ambient irradiance (Fig. 5c), which was expected if light is a cue for migratory behavior (Dupont *et al.*, 2009). Our observations agree with the model predictions that *P. periphylla* asynchronous migrations result from proximate responses to light levels (Dupont *et al.*, 2009).

Perhaps the most prominent feature in the vertical positioning of *P. periphylla* is the distribution peak skewed toward 100 and 75 m present during high and low surface irradiance conditions (Fig. 4a and b), respectively. Few to no individuals were recorded above these depths, presumably due to *P. periphylla* phototoxic protoporphyrin pigment (Herring, 1972; Bonnett *et al.*, 1979). Accordingly, we recorded increased numbers of *P. periphylla* in the upper 20 m only during night (Fig. 4c).

The exact level of when light becomes harmful to *P. periphylla* is unknown (Herring, 1972; Bonnett *et al.*, 1979; Youngbluth and Båmstedt, 2001; Jarms *et al.*, 2002) but our results suggest this light level will be at a total irradiance above $540 \times 10^{-3} \text{ mol quanta m}^{-2} \text{ s}^{-1}$. *Periphylla*'s distribution in the upper waters during day and dusk periods negates an assumption that the negative phototactic behavior of *P. periphylla* (Youngbluth and Båmstedt, 2001; Sötje *et al.*, 2007) would result in a preference for the darkest waters during periods of high surface irradiance. Furthermore, as demonstrated by simulations, vertical migration patterns as seen in *P. periphylla* do not emerge from purely negative phototactic behavior (Dupont *et al.*, 2009).

The relatively constant range of ambient light at individual *P. periphylla* (Fig. 5) suggests that, as long as there is sufficient light present, jellyfish adjust their vertical position in response to changes in ambient irradiance (Figs 4 and 5). For example, there was a well-defined avoidance of depths with high illumination where ambient

irradiance was above $10^{-2} \text{ mW m}^{-2} \text{ nm}^{-1}$, corresponding to a total irradiance of $5 \times 10^{-3} \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$. A large fraction appears to avoid very low light levels and few individuals were observed at depths with the darkest irradiance levels, specifically below 250 m (10^{-10} – $10^{-16} \text{ mW m}^{-2} \text{ nm}^{-1}$, day–night; Figs 4 and 5). This might support the hypothesis (Dupont *et al.*, 2009) that a large fraction, although not the entire, *P. periphylla* population distributes within a certain range of light intensities during day. If that is the case, Fig. 5 indicates the range of light preferences of *P. periphylla*. Most appear to avoid light levels above $10^{-2} \text{ mW m}^{-2} \text{ nm}^{-1}$ (corresponding to total irradiance of $5 \times 10^{-3} \text{ mol quanta m}^{-2} \text{ s}^{-1}$), but also that $>60\%$ appear to prefer light levels above $10^{-6} \text{ mW m}^{-2} \text{ nm}^{-1}$ ($10^{-7} \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$) during day and dusk periods.

During day and dusk, the ambient irradiance of Lurefjorden was darker than $10^{-6} \text{ mW m}^{-2} \text{ nm}^{-1}$ at depths below 173 and 87 m, respectively. If we assume the same proportion between total irradiance and irradiance at 500 nm as in Fig. 1a we arrive at a total irradiance of $10^{-7} \text{ mol quanta m}^{-2} \text{ s}^{-1}$. Two-thirds of the *P. periphylla* were located at irradiances above this level, indicating a preference for some, albeit low, levels of light under these periods. During night, only one-quarter of the jellyfish was located at these same illumination levels. There were observations of some jellyfish in the basin waters (ca 430 m; Fig. 4) with calculated ambient irradiance levels of 10^{-18} – $18^{-24} \text{ mW m}^{-2} \text{ nm}^{-1}$. Such low estimates of downwelling irradiance are purely theoretical and cannot be considered as cues for *P. periphylla*. It rather suggests that some *P. periphylla* occupy what should here be considered as darkness (except from local bioluminescent sources). During the night most of the water column probably had no gradient in downwelling irradiance that possibly could be sensed by *P. periphylla*. Under such circumstances downwelling irradiance provides no guidance and a spread of individuals over the water column is to be expected (Dupont *et al.*, 2009).

The alternative possible explanations of hydrography or the distribution of mesozooplankton prey governing *P. periphylla* distributions could not alone account for our observations. *Periphylla* are the most eurythermic coronate with a temperature tolerance range 4–19.8°C (reviewed by Arai, 1997), implying that the vertical difference from 5 to 7°C in February (Fig. 2) was probably not restricting migrations. In regards to prey availability, zooplankton abundance in Lurefjorden is substantially greater than in adjacent systems (Bagoien *et al.*, 2001). *Calanus* spp., Ostracods, Chaetognaths and mysids are common zooplankton in Lurefjorden (Bagoien *et al.*, 2001) and all have been identified as *P. periphylla* prey

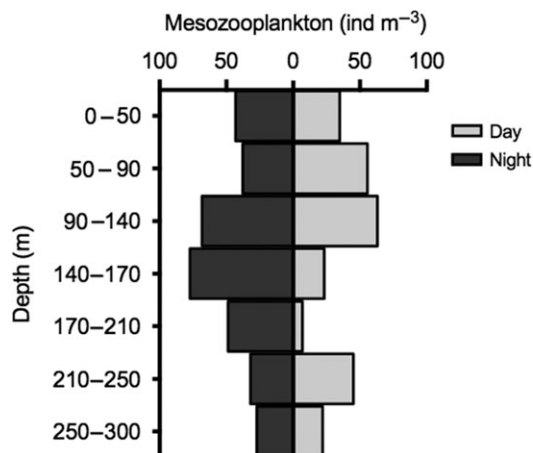


Fig. 6. Depth distribution of Lurefjorden mesozooplankton (ind m^{-3}) collected via a Kiel MultiNet during day (light bars) and night (dark bars) periods on 8 February 2010. Weighted mean depth \pm standard deviation for day and night was 188.8 ± 113.4 m and 183.5 ± 119.5 m, respectively. See Table I for sampling parameters.

items (Youngbluth and Båmstedt, 2001; Sötje *et al.*, 2007; Sørnes *et al.*, 2008), yet it is unclear if the diet of *P. periphylla* in Lurefjorden is a reflection of prey preference or a result of the high abundance of mesozooplankton in this fjord. In our study, potential prey was available throughout the water column (Fig. 6), irrespective of illumination levels (Fig. 5). Thus given that sampled mesozooplankton is representative of the prey availability, prey vertical distribution probably had limited importance for the *P. periphylla* vertical migration (Fig. 4).

Ugland *et al.* (2014) detected a switch in *P. periphylla* search strategies with an increased frequency of long steps from day to night. The authors linked this change in behavior to availability of scarce prey (species not specified) as one possibility to explain the complex migration patterns observed in *P. periphylla* in Lurefjorden (Ugland *et al.*, 2014). Alternatively, as suggested by our results, the spread of *P. periphylla* throughout the water column during very dark ambient light results from the loss of a directional cue.

While our study and Ugland *et al.* (2014) indicate different factors contributing to *P. periphylla* vertical distribution patterns, the two may not be easily separated. Instead, it is likely that the interactions of light levels and prey availability might both act on migratory behavior. An in depth study that also incorporates measurements of actual feeding rates of *P. periphylla* would clarify our understanding of feeding and light associated migratory behavior of *P. periphylla* and other mesopelagic jellyfish.

Light detecting organisms that adhere to a depth distribution where preferential light levels are neither too strong nor too low are said to inhabit a light comfort zone (LCZ) (Dupont *et al.*, 2009). Then the expectation

is that a lower light attenuation will lead to a deeper and wider vertical habitat, while an increased light attenuation will lead to a shallower and narrower vertical habitat. Empirical evidence for this expectation was provided in a study comparing the mesopelagic sound scattering layers (SSLs) in a murky fjord with that of the clear water of the Red Sea (Røstad *et al.*, 2016). Despite large observed differences in the depth distribution of the SSL in the two systems, they found that the organisms making up the SSL distributed at similar calculated ambient irradiance levels. If *P. periphylla* behaves according to a LCZ, we should expect that the vertical distribution in oceanic water with a low light attenuation, which is the common habitat of *P. periphylla*, should be much deeper and broader than in Lurefjorden, which is characterized by a high light attenuation coefficient. Whether or not such behavior is applicable to other jellyfish has not been investigated and warrants further study. Jellyfish are omnipresent in the mesopelagic and are poised to take advantage of ecological changes (Mills, 1995) and an increase of suitable habitat available to jellyfish may contribute to regime shifts at mesopelagic depths (Aksnes *et al.*, 2009).

CONCLUSION

In summary, we demonstrate that ambient light can act as a directional cue for *P. periphylla* migratory behavior. Light associated behavior accounts for the spread of individuals throughout the entire water column during periods of very low ambient irradiance and for the apparent barrier in the upper 100 m during daylight periods. Our study suggests that jellyfish can make use of downwelling irradiance as a directional cue to actively navigate and select where to stay in the water column.

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Paper II

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First reports of a mass mortality event across multiple life stages in a mesopelagic jellyfish in high latitude coastal waters

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Abstract

Mass mortality events can occur naturally and may have important ecological impacts on local populations. The abundance and stage structure of the coronate scyphozoan *Periphylla periphylla* in a Northern Norwegian fjord were studied between October 2010 and August 2011. Developmental stage composition varied for the duration of the study, with early developmental stages only present in the autumn and winter. Records of large number of dead *P. periphylla* across multiple life stages revealed that a mass mortality event occurred towards the end of the study period. The abundance of live medusa increased from 27 to 39 individuals (ind.)·1,000 m⁻³ from October 2010 to February 2011, then fell to <10 ind.·1,000 m⁻³ in August 2011. The estimated abundance of dead jellyfish increased from slightly >1 ind.·1,000 m⁻³ in October 2010 to >34 ind.·1,000 m⁻³ in August 2011, corresponding to an estimated population mortality of >80% on the last sampling date. Mortality increased as the length of high solar irradiance periods increased. Based on previous published evidence that strong light is harmful to *P. periphylla*, we speculate whether the light climate of this high latitude location may have contributed to the mass mortality of *P. periphylla*.

KEYWORDS

Fjord, habitat availability, high latitude, light regime, *Periphylla*, Scyphozoan

1 | INTRODUCTION

Mass mortality events occur when a population has suffered a loss of 50% or greater over a 1-year period (Reed, O'Grady, Ballou, & Frankham, 2003). Although mostly studied in terrestrial systems (Fey et al., 2015), mass mortality events also seem common in marine ecosystems (Eiane & Daase, 2002; Raup & Sepkoski, 1982; Stokstad, 2014). Mass mortality events may have important ecological effects regulating population levels through an impact on all size classes or developmental stages in a population (Fey et al., 2015). This is in contrast to mortalities related to life histories. For example, numerous jellyfish species undergo mass die offs as part of the typical jellyfish life cycle, and therefore do not fit the criteria of a mass mortality events. However, mass mortalities have been observed

in iteroparous jellyfish species, such as reported (Sweetman & Chapman, 2011, 2015) for the larger stages of the mesopelagic jellyfish *Periphylla periphylla* (Péron & Lesueur, 1809). Observations of high mortalities of *P. periphylla* have, so far, only been documented for the larger developmental stages of the jellyfish.

Periphylla periphylla is a mesopelagic cosmopolitan coronate scyphozoan (Russell, 1970) that normally occurs at modest densities in the open ocean (Donnelly, Sutton, & Torres, 2006; Larson, 1986; Larson, Mills, & Harbison, 1991; Pagès, White, & Rodhouse, 1996) including high latitude Norwegian waters (Dalpadado, Ellertsen, Melle, & Skjoldal, 1998; Fosså, 1992; Havnø, 1918, 1926). Since the 1970s, *P. periphylla* has established populations of unusually high abundances in some Norwegian fjords south of 64°N (Fosså, 1992; Gjelsvik Tiller et al., 2014; Sneli, 1984; Sørnes, Aksnes, Båmstedt,

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& Youngbluth, 2007), with some populations reaching mass occurrences levels two to three orders of magnitude higher than reported in oceanic populations (Dalpadado et al., 1998; Donnelly et al., 2006; Pagès et al., 1996). This phenomenon appears to be mostly confined to Western Norwegian fjords (A. Bozman, E. Eiane & D. Aksnes, unpublished data) and in these fjords coastal water darkening has been proposed as a potential cause (Aksnes et al., 2009; Sørnes et al., 2007).

It has been hypothesized that light levels affect *P. periphylla*'s life history (Jarms, Tiemann, & Båmstedt, 2002) and distribution (Sørnes et al., 2007; Sötje, Tiemann, & Båmstedt, 2007). Similarly to other mesopelagic organisms, this jellyfish appears to prefer a dark habitat (Bozman, Titelman, Kaartvedt, Eiane, & Aksnes, 2017; Jarms et al., 2002; Sørnes et al., 2007; Youngbluth & Båmstedt, 2001). This is consistent with properties of the pigment protoporphyrin (Herring, 1972), which gives this jellyfish its distinct red-brown coloration. Protoporphyrin degrades into toxic compounds upon light exposure; thus, *P. periphylla*'s upper water migrations are restricted during periods of high solar irradiance (Bonnett, Head, & Herring, 1979; Herring, 1972). Young *P. periphylla* have an apparent lower level of tolerance for light exposure, residing in deeper and darker fjord basins (Sørnes et al., 2007) and ceasing development when exposed to light in the laboratory (Jarms et al., 2002). The exact level at which light becomes harmful for *P. periphylla* is unknown. However, the species appears to distribute itself within a "light comfort zone" (sensu Dupont, Klevjer, Kaartvedt, & Aksnes, 2009) where at least part of a population avoids light levels that are either too high or too low (Bozman et al., 2017). Such behaviour seems to be common for mesopelagic organisms (Aksnes et al., 2017; Røstad, Kaartvedt, & Aksnes, 2016a, 2016b).

At higher latitudes, organisms face extreme photoperiod regimes with up to 24-hr light in summer and 24-hr darkness in winter periods. For diel migrating mesopelagic organisms, it has been shown that a long photoperiod limits the vertical migration distance and consequently reduces the habitat available for foraging (Norheim, Klevjer, & Aksnes, 2016). The negative effect of photoperiod at high latitudes on the success of mesopelagic species, which are visual predators, has been termed the "photoperiod constraint hypothesis" (Kaartvedt, 2008). *Periphylla periphylla* is not a visual predator and so the premise of the photoperiod constraint hypothesis is not directly applicable. However, solar irradiance levels may constrain jellyfish through factors other than the use of visual predation and there is evidence that individual *P. periphylla* can distribute according to preferential light levels (Bozman et al., 2017). Pitt, Budarf, Browne, and Condon (2014) pointed out that, although not yet studied, solar irradiance levels that constrain diel vertical migration in shallow systems could potentially lead to jellyfish mortality, and thus affect population structures and abundance.

In the present study, we report on a mass mortality event in a sub-Arctic fjord population of the mesopelagic jellyfish *P. periphylla*. We describe changes in the population structure and abundance of *P. periphylla* over an 11-month period, including high numbers of mortalities in the population that increased in periods of increasing

solar irradiance. We discuss our findings in relation to the "photoperiod constraint hypothesis" (Kaartvedt, 2008), i.e. that high solar irradiance during summer nights at high latitudes constrains the vertical habitat available to *P. periphylla*. The observations presented here originate from a larger study on *P. periphylla* in high latitude fjords (A. Bozman, E. Eiane & D. Aksnes, unpublished data).

2 | MATERIAL AND METHODS

2.1 | Study area

The study site was located in Vefsnfjorden, Northern Norway (65°55' N, 13° 06' E; Figure 1). The fjord has a deep basin with a maximum depth of 483 m, a sill depth of 80 m and an area of 60 km². This location has a sub-Arctic light regime with prolonged periods of darkness around the Northern Hemisphere midwinter and extended sunlight hours of near 24 hr sunlight around midsummer. Day length information was retrieved from the Norwegian Meteorological Institute (www.met.no; Table 1).

2.2 | *Periphylla periphylla* developmental stages

Periphylla periphylla has true direct development, lacking planula, larval or ephyra stages (Jarms, Båmstedt, Tiemann, Martinussen, & Fosså, 1999; Jarms et al., 2002; Tiemann & Jarms, 2010). Eggs develop straight into medusa (Jarms et al., 2002) and the species is able to reproduce continuously (Tiemann & Jarms, 2010). Fourteen developmental stages have been identified and described (Jarms et al., 1999, 2002) from a population in Lurefjorden, Norway. All references to *P. periphylla* developmental stages used in this study

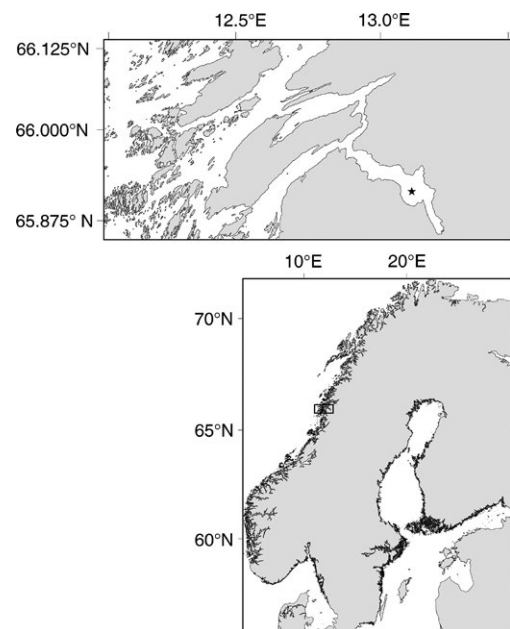


FIGURE 1 Sampling location, Vefsnfjorden, Norway. Star denotes the study site in the deepest section of the fjord basin, where the samples of *Periphylla periphylla* were collected



TABLE 1 Sampling information for Vefsnfjorden *Periphylla periphylla* including tow depth, tow duration, total catch of live and dead jellyfish per tow, and sample date day length for 16 October and 18 November 2010, and 15 February, 3 May and 23 August 2011

Date	Tow depth (m)		Tow time		Total catch <i>P. periphylla</i>	
	Max.	Min.	Start	Stop	Live	Dead
6 October 2010	410	333	10:57	11:31	20	0
Sunrise: 07:33	284	189	12:25	12:58	25	0
Sunset: 18:16	137	45	13:21	13:53	0	0
	404	295	16:49	17:21	53	4
	276	187	18:20	18:50	21	0
	144	18	19:12	19:54	7	1
18 November 2010	423	300	12:15	12:50	55	11
Sunrise: 09:22	263	178	13:25	13:57	9	0
Sunset: 14:25	145	45	14:25	14:56	0	0
	431	319	17:58	18:30	103	4
	274	175	19:24	19:56	10	0
	124	16	20:15	21:00	10	0
15 February	417	337	12:35	13:12	90	18
Sunrise: 07:44	283	185	13:56	14:27	10	0
Sunset: 16:59	136	38	14:51	15:22	0	1
	376	304	17:11	17:56	88	3
	239	150	18:29	18:58	7	0
	109	14	19:22	20:05	21	0
3 May	402	303	11:51	12:30	64	79
Sunrise: 04:20	283	185	13:07	13:44	5	2
Sunset: 21:51	112	36	14:06	14:44	4	47
	368	300	16:53	17:30	35	18
	246	166	18:05	18:37	1	0
	117	18	18:56	19:44	0	0
23 August	375	299	12:48	13:26	24	196
Sunrise: 05:12	216	144	13:58	14:31	0	1
Sunset: 21:06	109	38	14:52	15:25	0	0
	296	226	18:12	18:45	19	51
	247	144	19:23	19:57	7	31
	110	19	20:23	21:07	0	4

are based on the work by Jarms et al. (1999) and (2002). For detailed descriptions and measurements, refer to the work by Jarms et al. (1999, 2002). A brief summary of *P. periphylla*'s developmental stages is provided in the following text. Size at developmental stage according to Jarms et al. (1999, 2002) is provided in Table 2. Fertilization in *P. periphylla* is presumed to be internal (Tiemann & Jarms, 2010; Tiemann, Sötje, Johnston, Flood, & Båmstedt, 2009) and stage 1 jellyfish are neutrally buoyant fertilized spherical eggs. The sphere begins to flatten during stage 2. By stage 3 the shape is triangular and a pit in the anterior end is present. In stage 4 there is a curvature around the margin of the pit, but the coronal groove does not reach full development until stage 5. Stage 5 is also when the 16 lappets and four rhopalia are first apparent as buds. Tentacle buds (12) are present in stage 6. The mouth opens at stage 6; there are no mouth lips. Porphyrin pigmentation is first noticeable at stage 7, yet

only on the mouth lips. At stage 8 the tentacles are at least as long as the lappets. Stage 9 *P. periphylla* resemble mature medusa in morphological portions, but pigmentation is not complete. Stages 10–13 are differentiated by the extent of protoporphyrin pigmentation on the tentacles, stomach and apex. Stage 14 has four sub-stages, A through to D. Stage 14A is a fully pigmented medusa. Gonads are first noticeable as small folds in the adradius in stage 14B. Stage 14C individuals are sexually dimorphic. Medusae are sexually mature at stage 14D.

2.3 | *Periphylla periphylla* sampling

We sampled *Periphylla periphylla* from the deepest section of Vefsnfjorden on five occasions between October 2010 and August 2011 (Table 1) from the Fishing Vessel *Lykken*. Depth-specific

TABLE 2 A brief description of the 14 developmental stages of *Periphylla periphylla* and size at developmental stage in Lurefjorden compiled from Jarms et al. (1999, 2002), and the size at developmental stage of Vefsnfjorden *P. periphylla* pooled from all sample dates during this study (see Table 1 for sampling dates)

Stage	Lurefjorden (Jarms et al., 1999)		Lurefjorden (Jarms et al., 2002)		Vefsnfjorden this study		Stage-specific observations as per Jarms et al (1999, 2002)
	Diameter (mm)		Diameter (mm)		Diameter (mm)		
	Widest dimension	Coronal diameter	Widest dimension	Coronal diameter	Widest dimension	Coronal diameter	
1	1.32 ± 0.28	—	1.17 ± 0.09	—	0.92 ± 0.26	—	Spherical embryo
2	1.44 ± 0.33	—	1.30 ± 0.13	—	1.35 ± 0.32	—	Anterior end somewhat flattened
3	1.52 ± 0.31	—	1.39 ± 0.13	—	1.37 ± 0.60	—	Triangular shape. First signs of coronal groove, and mouth as pit in the anterior end
4	1.92 ± 0.20	1.39 ± 0.12	1.61 ± 0.27	—	—	1.20 ± 0.30	Curvature of margin around pit, coronal furrow development not complete
5	2.34 ± 0.29	1.41 ± 0.22	1.88 ± 0.20	1.19 ± 0.18	—	1.14 ± 0.36	Coronal groove fully expressed
6	2.85 ± 0.36	2.05 ± 0.22	2.90 ± 1.23	2.51 ± 0.89	—	1.74 ± 0.51	Mouth open, no lips
7	4.15 ± 0.82	2.79 ± 0.47	not measured	3.27 ± 0.13	—	1.80 ± 0.47	Mouth lips apparent
8	—	—	not measured	3.40 ± 0.80	—	2.69 ± 0.73	Tentacles at least as long as lappets
9	—	—	not measured	not measured	—	3.98 ± 1.21	Resembles sexually mature medusa, but not fully pigmented
10	—	—	—	6.13 ± 0.84	—	6.79 ± 1.78	Pigmentation on tips of tentacles
11	—	—	—	8.26 ± 1.2	—	8.31 ± 2.98	Tentacle pigmentation reaches 1/2 tentacle length
12	—	—	—	12.2 ± 1.5	—	9.25 ± 1.51	Tentacles fully pigmented
13	—	—	—	21.6 ± 4.4	—	9.71 ± 2.60	Pigmentation reaches lappets, coronal furrow, and almost the apex
14A	—	—	—	38.9 ± 11.4	—	12.90 ± 3.39	Medusa fully pigmented, no sign of gonads
14B	—	—	—	37.0 ± 6.8	—	15.10 ± 13.05	Medusa not sexually dimorphic
14C	—	—	—	57.3 ± 17.8	none present	—	Sexual dimorphism
14D	—	—	—	>80	—	113.20 ± 24.42	Mature medusa

hydrography was measured by using a salinity, temperature and density profiler equipped with an oxygen sensor (SD204, SAIV A/S) on each sampling date. *Periphylla periphylla* displays ontogenetic shifts in vertical distribution (Jarms et al., 1999, 2002; Kaartvedt, Titelman, Røstad, & Klevjer, 2011; Youngbluth & Båmstedt, 2001) and we aimed to sample all development stages and size classes of the jellyfish. To do so, we used a Bongo net (individual net diameter = 0.625 m, mesh size 200 μm and 500 μm , horizontal towing speed = 1 nm/h) fitted with closed cod ends to sample the water column in three depth bins: lower bin, from approximately near bottom – 300 m; intermediate bin, from 250–150 m; and upper bin, from 100 m–surface. Each depth bin was sampled in a stepwise manner in 50-m increments for 10 min every 50 m. Each depth bin was sampled twice per sample date. We used a hydrographic data profiler (above) attached to the net frame to confirm actual sampling depths. Towing depths were within the aimed depth intervals (Table 1) with one exception, the second replicate from the deepest August 2011 haul. The volume of water filtered was estimated with flow meters (Digital flowmeter model 23.091, KC Denmark) in the mouth of each net. All large medusae [coronal dome width (CD) > 50 mm] were measured (CD, mm) immediately upon collection. Gonads from suspected sexually mature medusae were removed and preserved in 4% borax-buffered formaldehyde-in-seawater solution and oocytes were measured at a later date to confirm sexual maturity according to the oocyte size method of Jarms et al. (2002). The remaining water samples were preserved in a 4% borax-buffered formaldehyde-in-seawater solution and brought to the lab where all *P. periphylla* were counted, measured for size class (CD) and identified to developmental stage following procedures described by previous authors (Jarms et al., 1999, 2002).

Neither filtered water volume nor capture of *P. periphylla* differed between the two nets (two-sample *t*-test with Welch's approximation: $t = -0.35$, $df = 57.98$, $p = .72$, and $t = 0.53$, $df = 49.72$, $p = .60$, respectively). Therefore, we estimated *P. periphylla* abundance [n , individuals (ind.) $\cdot 1,000 \text{ m}^{-3}$] by pooling counts from both nets weighted by the volumes filtered by each net, according to:

$$n = 1,000 \cdot (n_{200} + n_{500}) \cdot (v_{200} + v_{500})^{-1}$$

where n_{200} and n_{500} are *P. periphylla* caught (ind), and v_{200} and v_{500} are estimated volume filtered (m^3) by the 200- and 500- μm mesh size nets, respectively.

We identified *P. periphylla* corpses as being in variable stages of decay (i.e. an almost complete lack of pigmentation, with large holes at the aboral surface and some with the stomach pulled through; Figure 2B). Dead jellyfish were counted, measured for CD and assigned developmental stage, where possible. However, some of the corpses were in an advanced stage of degradation, which limited the precision of CD measurement and developmental stage identification. To estimate the developmental stage of the dead jellyfish, we compared the dead jellyfish mean CD to the live jellyfish mean CD at each developmental stage, both from all dates pooled. We calculated the median and quartile distributions of CD for dead *P. periphylla*.

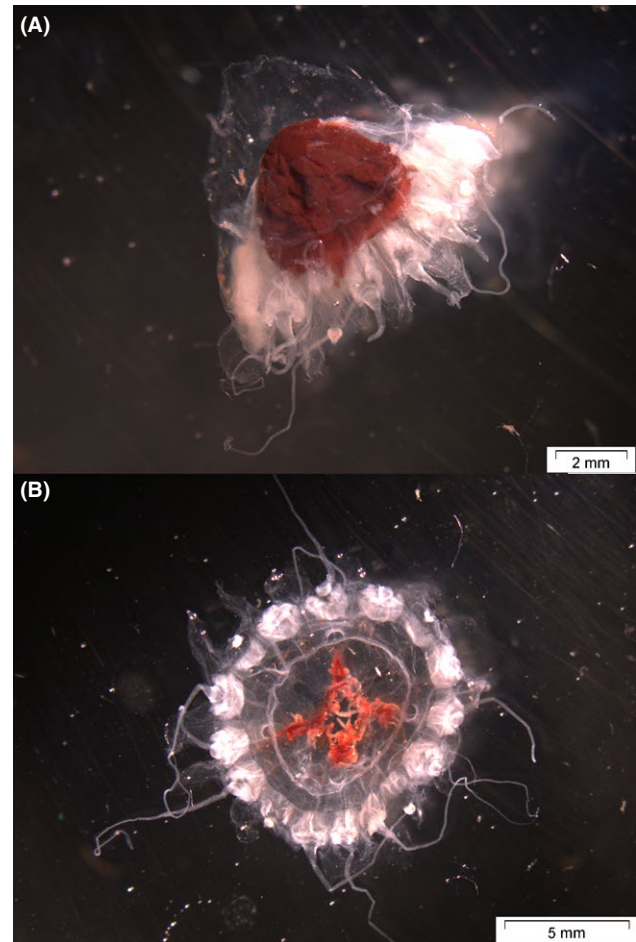


FIGURE 2 An example of young developmental stages of (A) alive *P. periphylla* versus (B) *P. periphylla* corpse collected in Vefsnfjorden during sample dates in the 2010–2011 (see Table 1). The live *P. periphylla* has full stomach pigmentation, whereas the *P. periphylla* corpse not only lacks stomach pigmentation but has also suffered damage to the gastric anatomy, including aboral holes

Data on dead jellyfish were not included in the estimates of developmental stage or size structure.

2.4 | Modelling of the underwater irradiance field

We modelled the underwater irradiance levels for each sample date, midsummer, and annually. The total solar irradiance incident on the sea surface was determined using a global horizontal irradiance model (Robledo & Soler, 2000) assuming clear sky conditions and discounting for Rayleigh scattering and various other measurable atmospheric parameters (e.g. air pressure, temperature, perceptible water, ozone and aerosol concentrations). The estimated irradiance roughly agrees with the field estimates of Norwegian Meteorological Institute (www.met.no).

Sub-surface irradiance was modelled using an exponential function:

$$I_{z,t} = I_{z-1,t} \cdot \exp(-Kp_z)$$

where z is depth (range = 0–209 m), t is time of the day (h) and K_p is the non-chlorophyll light attenuation coefficient at 440 nm for the downward-directed irradiance in the water column. We calculated K_p at 440 nm by use of the proxy developed for winter conditions in Norwegian coastal waters (Equation 7 in Aksnes, 2015). This proxy provides an empirical relationship between the non-chlorophyll light attenuation coefficient on the one hand, and salinity and dissolved oxygen on the other. We used salinity and oxygen data from the same cruise, with R/V *Håkon Mosby* in 2008, that underlies the study of Aksnes (2015). On each modelled underwater irradiance figure, we plotted the total irradiance level that *Periphylla periphylla* avoids, $5 \times 10^{-3} \mu\text{mol quanta m}^{-2} \text{s}^{-1}$, estimated from a previous study (Bozman et al., 2017).

3 | RESULTS

3.1 | Hydrography

The sill (80 m) in Vefsnfjorden ensures communication with the Norwegian Coastal Current containing Norwegian Coastal Water (NCW) (salinities < 34.5 PSU) (Sætre, 2007) and NCW filled the fjord basin for the duration of the study (Figure 3). Basin water temperatures were homogenous with depth at slightly <5°C for the duration of the study (Figure 3). Oxygen levels in the basin were always above 6 mg/L (Figure 3). In October and November 2010, temperature was ~10°C and salinity was ~33.0 PSU above 50 and 80 m, respectively. In February 2011, temperatures for the entire water column were near homogenous at 5°C, and salinity levels ranged from 33.5 to 34.4 PSU from surface to bottom, respectively (Figure 3). A brackish surface layer (<20 PSU) with temperatures of slightly <5°C and slightly >10°C appeared in May and August, respectively (Figure 3).

3.2 | *Periphylla periphylla* abundance

Abundance levels varied throughout the study period. The estimated abundance ($M \pm 1 \text{ SD}$) of live *Periphylla periphylla* ($n = 696$) increased during the early part of the study period for the autumn and winter sampling dates (October and November 2010, and February 2011; 27.3 ± 6.3 , 32.8 ± 16.7 , $39.7 \pm 11.2 \text{ ind.} \cdot 1,000 \text{ m}^{-3}$, respectively; Figure 4). There was an abrupt decrease in abundance of live *P. periphylla* in May, and again in August 2011 (14.9 ± 8.3 and $6.7 \pm 1.1 \text{ ind.} \cdot 1,000 \text{ m}^{-3}$, respectively; Figure 4).

We recorded high numbers ($n = 471$) of dead *P. periphylla* during the study (Table 1; Figures 2B and 4). The relative abundance of dead jellyfish increased as the study progressed (3.8% in October 2010 to >80% in August 2011; Table 1). The estimated abundances of dead *P. periphylla* were initially low in the winter months (0.9 ± 1.3 , 2.5 ± 1.4 and $5.1 \pm 6.1 \text{ ind.} \cdot 1,000 \text{ m}^{-3}$ in October, November and February, respectively), but abundance values sharply increased in the late spring and summer (21.2 ± 23.7 and $34.6 \pm 19.5 \text{ ind.} \cdot 1,000 \text{ m}^{-3}$ in May and August, respectively) (Figure 4).

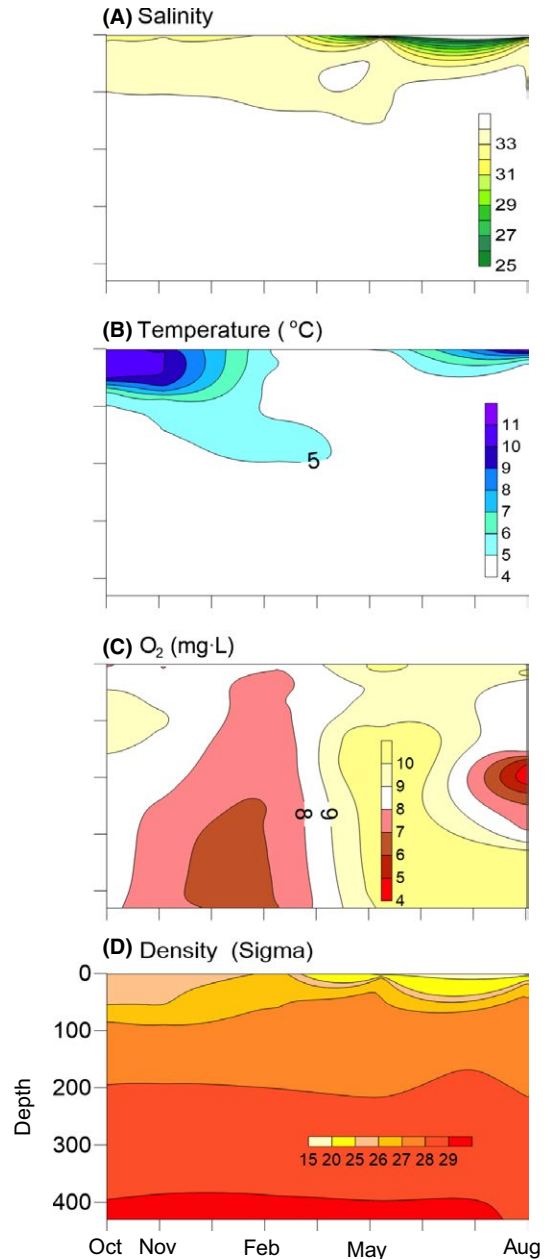


FIGURE 3 (A) Salinity, (B) temperature, (C) oxygen and (D) density depth profiles in Vefsnfjorden on 6 October and 18 November 2010, and 15 February, 3 May and 23 August 2011

There was little variation in the total estimated abundance mean (i.e. the combined abundances of live and dead *P. periphylla*) between sample dates (average over all samplings $\pm 1 \text{ SD}$ was $37.2 \pm 6.9 \text{ ind.} \cdot 1,000 \text{ m}^{-3}$; Figure 4).

3.3 | Size class distribution

The size class distribution was dominated by jellyfish with CD < 30 mm (Figure 5A). There were no *Periphylla periphylla* in the 30–70 mm CD size classes on any of the sample dates. The largest size classes belonged to the stage 14D *P. periphylla*, which ranged in CD from 72–159 mm (Figure 5B). With the exception of stage

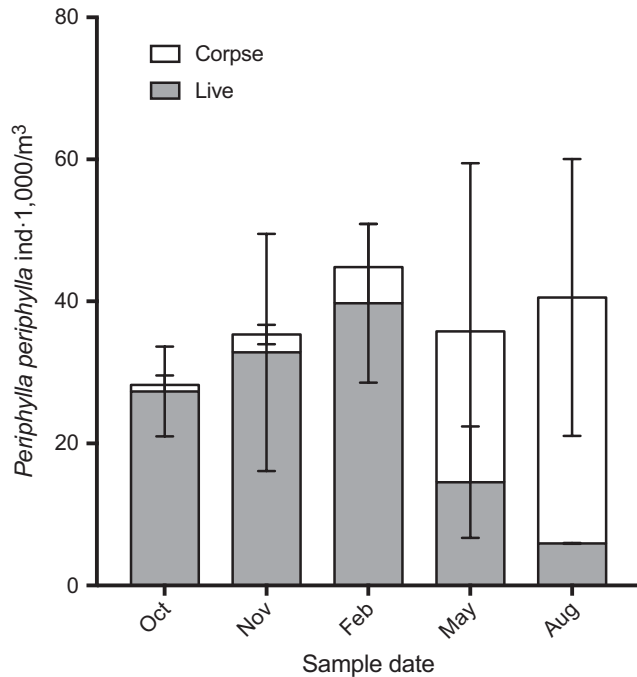


FIGURE 4 Mean abundance and SD for live (grey bars) and dead (white bars) *P. periphylla* collected in Vefsnfjorden on 6 October and 18 November 2010, and 15 February, 3 May and 28 August 2011

14D, *P. periphylla* size at developmental stage was smaller for the Vefsnfjorden (Table 2) population than in the Lurefjorden population (Jarms et al., 1999, 2002).

3.4 | *Periphylla periphylla* population stage structure

The stage structure of live *Periphylla periphylla* differed across study dates (Figure 5C). Early developmental stages (stages 1–3) were recorded only from October to February. In May, the early developmental stages were rare and the majority of the population was at developmental stage 9 or higher (Figure 5C). In August, no individuals below stage 7 were recorded (Figure 5C). Developmental stages 7–9 dominated on all sampling dates, with the exception of August where 14B and 14D were the dominant groups in the population. Sexually mature *P. periphylla* (stage 14D) were present on all dates (Figure 5C). Fifty-three stage 14D *P. periphylla* were collected during the study. Stage 14C *P. periphylla* were not recorded on any of the sample dates.

3.5 | *Periphylla periphylla* corpses

Periphylla periphylla corpses ranged in size (CD) from 1.45 to 14.81 mm (median 4.19 mm; inter-quartile range = 3.81–5.74 mm). Owing to damage and decay, it was not possible to sort all corpses to developmental stage. However, of those that were identifiable ($n = 383$), there was a range in developmental stages from stages 8–14B. Comparing the average CD of *P. periphylla* corpses (4.7 ± 2.1 mm; mean CD \pm SD) to the CD of live *P. periphylla* sorted

to developmental stage indicates that stage 9 was the mean stage of jellyfish corpses (Table 1).

The majority (81.5%) were collected in the deepest nets and only 11.3% and 7.2% were caught in the upper and intermediate depths (Table 1).

3.6 | Fjord irradiance levels

Vefsnfjorden experiences extended hours of fjord illumination during the summer months (Figures 6 and 7). Provided that the *Periphylla periphylla* light threshold of $5 \times 10^{-3} \mu\text{mol quanta m}^{-2} \text{s}^{-1}$, which was reported by Bozman et al. (2017) in Lurefjorden, applies in Vefsnfjorden, *P. periphylla*'s access to upper waters is severely constrained in summer (Figures 6 and 7). During midsummer, there is only a 1-hr window during which the entire water column is available to the jellyfish (Figure 7C).

4 | DISCUSSION

A novel finding in our work was the records of mass mortalities of young developmental stages (Figures 2B and 4). High mortality rates were recorded in at least eight of the 14 developmental stages (Figure 5c). Mortality reached above 50% and 80% in May and August, respectively (Table 1). Medusa longevity is probably high in *Periphylla periphylla*, with some authors suggesting natural senescence occurs after multiple years or decades (Jarms et al., 2002; Tiemann & Jarms, 2010; Youngbluth & Båmstedt, 2001).

Previous studies have observed high numbers of dead *P. periphylla* (mean CD 9.2 ± 0.6 cm) at the bottom by use of photographic bottom transects (Sweetman & Chapman, 2011, 2015; Sweetman, Smith, Dale, & Jones, 2014). We do not know if this occurred in Vefsnfjorden as bottom observations were not included in our study.

Dead *P. periphylla* were found in all depth layers but were concentrated in the deeper depths (Table 1), possibly as a result of passive sinking of the corpses. In situ bacterial breakdown of *P. periphylla* is relatively rapid (Titelman et al., 2006). Empirically fitted temperature dependent decay rate for dead gelatinous zooplankton ($k(T) = 0.14 e^{0.145T}$) (Lebrato et al., 2011) indicates a decay rate of c. 0.25/days at 4°C in the basin in Vefsnfjorden. This value corresponds to a remineralization time scale (i.e. decomposition of 99% of the biomass) for dead *P. periphylla* biomass of c. 18.4 days.

High summer mortality of young stages is likely to affect the population structure. The lack of jellyfish in the intermediate (30–70 mm CD) size classes in the fjord (Figure 5) might reflect an episodic loss of recruits in a previous year.

Assuming an average main basin depth of 450 m, our estimated *P. periphylla* abundances range from 12 to 20 ind./m², which is less than in Norwegian fjords below 64°N where abundances reach mass occurrence levels and range from 20–320 ind./m² (Sørnes et al., 2007; Tiller, Mork, Liu, Borgersen, & Richards, 2015; Youngbluth & Båmstedt, 2001).

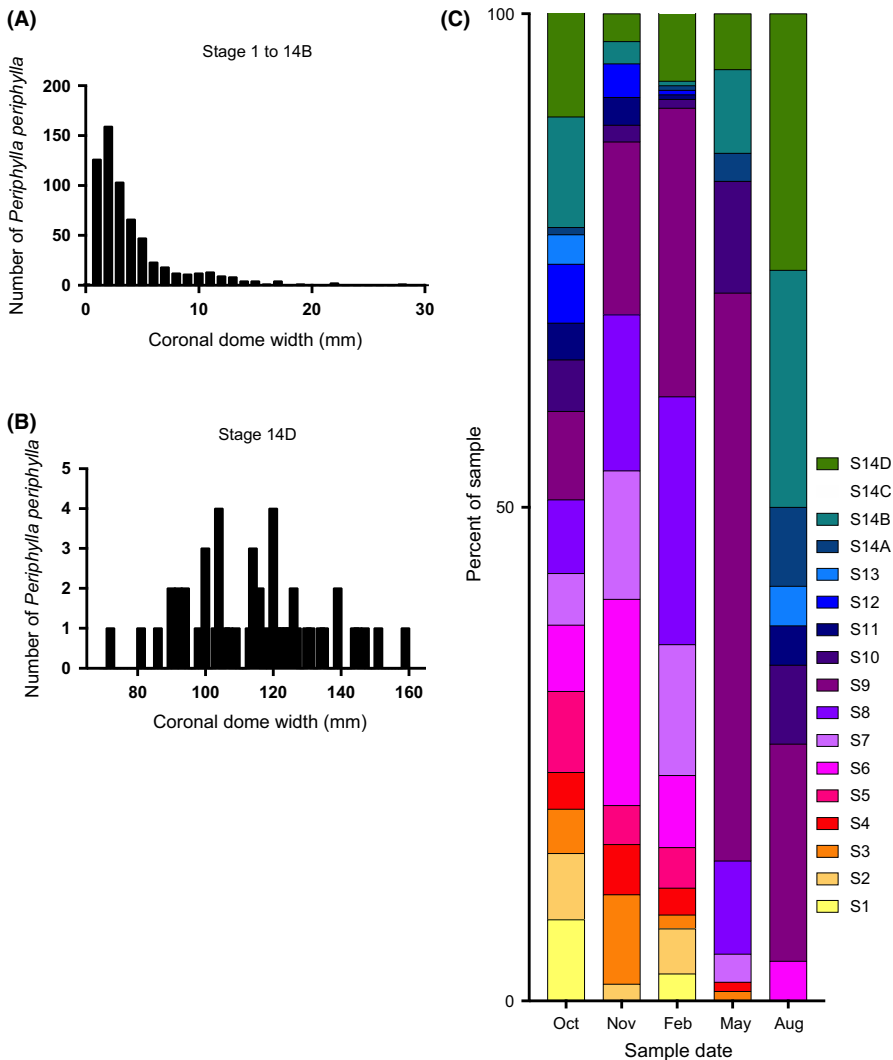


FIGURE 5 (A) Size class distribution for developmental stages 1–14B, (B) stage 14D and (C) the developmental stage composition of the total catch of *P. periphylla* collected in Vefsnfjorden. Stage 14C is left intentionally blank in the legend as no individuals in this developmental stage were recorded on any of the sample dates. Collection dates were 6 October and 18 November 2010, and 15 February, 3 May and 23 August 2011

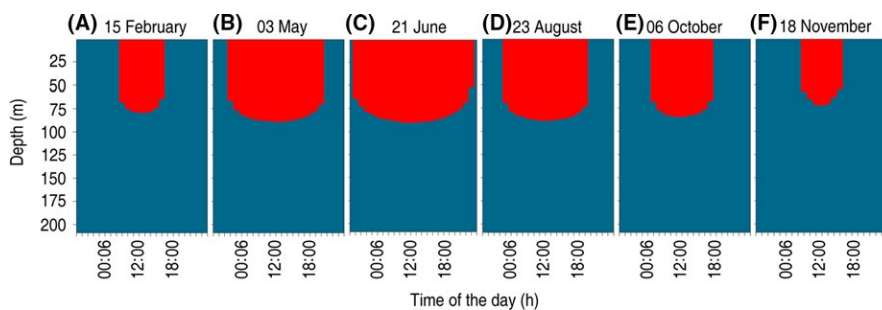


FIGURE 6 Estimated total irradiance ($\mu\text{mol quanta m}^{-2} \text{s}^{-1}$) levels on the sampling dates and midsummer (21 June) in Vefsnfjorden. The red area represents the upper limit of *P. periphylla*'s light comfort zone with total irradiance levels greater or equal to $5 \times 10^{-3} \mu\text{mol quanta m}^{-2} \text{s}^{-1}$. The blue area represents total irradiance levels $< 5 \times 10^{-3} \mu\text{mol quanta m}^{-2} \text{s}^{-1}$. *Periphylla periphylla* avoids total irradiance levels above $5 \times 10^{-3} \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ (Bozman et al., 2017)

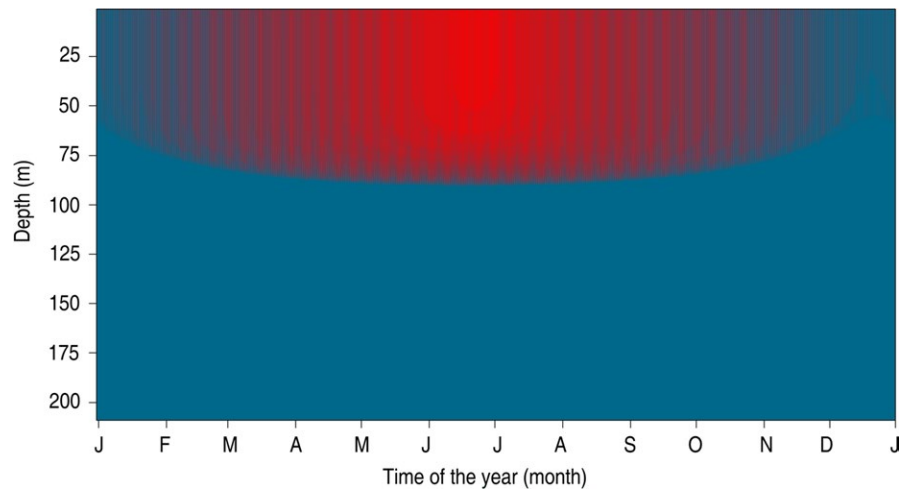
4.1 | Solar irradiance and *Periphylla periphylla* mass mortality

We speculate here as to whether the high levels of solar irradiance during the summer nights in Vefsnfjorden contributed to the high mortalities recorded in the early developmental stages of the

Periphylla periphylla population through either direct mortality or by ceasing growth and development.

Dead *P. periphylla* typically had damaged bells with lesions and gastric cavity injuries with a great loss of pigmentation (Figure 2B), both of which are indicative of damage caused by the phototoxic breakdown of *P. periphylla*'s protoporphyrin pigment (Bonnett et al.,

FIGURE 7 Estimated total irradiance ($\mu\text{mol quanta m}^{-2} \text{s}^{-1}$) levels over the year in Vefsnfjorden and the upper limit of *P. periphylla*'s light comfort zone. The red area represents total irradiance levels greater or equal to $5 \times 10^{-3} \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ whereas the blue area represents total irradiance levels $< 5 \times 10^{-3} \mu\text{mol quanta m}^{-2} \text{s}^{-1}$. *Periphylla periphylla* avoids total irradiance levels above $5 \times 10^{-3} \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ (Bozman et al., 2017)



1979; Herring, 1972; Jarms et al., 2002). Jellyfish are able to heal from injury and regenerate after physical damage or removal of body parts (Pitt et al., 2014). Yet *P. periphylla* exposed to light under laboratory conditions do not develop beyond stage 6, which is the stage at which protoporphyrin development begins (Jarms et al., 2002). It appears that light may be of more importance to the early rather than the later developmental stages. Smaller *P. periphylla* appear to have a lower level of tolerance for light exposure and reside in deeper and darker fjord basins than larger individuals (Sørnes et al., 2007). If we consider the ratio of dead to live *P. periphylla* as a proxy for the mortality rate, this rate appears to increase in concert with seasonally increasing solar irradiance levels (Table 1; Figures 6 and 7).

Pitt et al. (2014) theorized that solar irradiance may alter the population structure and abundance of jellyfish in shallow water locations through imposing limitations on the jellyfishes' diel vertical migration. With a maximum basin depth of 480 m, Vefsnfjorden is not considered deep for a jellyfish that normally resides in the deep ocean (Larson, 1986; Larson et al., 1991; Mauchline & Harvey, 1983; Russell, 1970), and for which too much light exposure may have fatal consequences (Bonnett et al., 1979; Herring, 1972). Located at 67°N , the solar irradiance becomes much stronger from winter to summer in terms of both intensity and hours per day (Figure 7).

Previous reports suggest that *P. periphylla* surface migrations are limited to dark periods (Fosså, 1992; Sötje et al., 2007). *Periphylla periphylla* vertical migrations may be necessary for reproduction (Tiemann et al., 2009), feeding (Fosså, 1992), avoidance of irradiance levels that are too high (Bonnett et al., 1979; Bozman et al., 2017; Herring, 1972; Jarms et al., 2002), or associated with social behaviour related to other biological needs (Kaartvedt et al., 2015). Factors that impose restrictions on vertical migration could negatively affect the success of the population. Strong light exposure during summer (Figures 6 and 7) probably restricted upward migrations (Bozman et al., 2017) and might have caused mortalities.

Food exhaustion has been suggested as a cause of jellyfish-falls in other species (Lebrato et al., 2012) but the dead *P. periphylla* showed no sign of tentacle or lappet shrinkage (Figure 2), both of which are indicators of jellyfish inhabiting food-poor environments (Arai, Ford, & Whyte, 1989; Hamner & Jenssen, 1974; Hatai, 1917).

4.2 | Restricted population growth and the photoperiod constraint hypothesis

The photoperiod constraint hypothesis (Kaartvedt, 2008) predicts that the distribution of mesopelagic fish at high northern latitudes is constrained by high night light intensities during summer, which limit the diel vertical migration and thus access to food in the upper productive water. This hypothesis was later supported by observations from the Norwegian Sea (Norheim et al., 2016). Although *Periphylla periphylla* is not considered to be a visual predator, as was assumed for the mesopelagic fishes (Kaartvedt, 2008), there is some evidence that *P. periphylla* in Lurefjorden distributes according to light in much the same way as mesopelagic fish (Bozman et al., 2017). Mass occurrences of *P. periphylla* have been associated with water column light penetration (Sørnes et al., 2007) and the inclusion of light as a directional cue in a simple mechanistic model (Dupont et al., 2009) was able to explain different observed migration patterns in *P. periphylla* (Kaartvedt et al., 2011; Kaartvedt, Klevjer, Torgersen, Sørnes, & Røstad 2007). The mortality observations in the present study appear consistent with a negative effect of the long photoperiods at high latitudes during summer.

The results of our study do not deny the presence of low numbers of *P. periphylla* in the region but rather suggest that the high summer night light levels limits the population growth in *P. periphylla*. According to the optically conditioned retention hypothesis, a fjord must fulfil two criteria in order to promote the mass occurrence of *P. periphylla* (Sørnes et al., 2007). First, the fjord must have a deep basin relative to a shallow sill in order to enable sufficient retention of individuals. Second, the fjord must be sufficiently dark that the basin waters correspond to the light environment of the deep ocean from which *P. periphylla* originates. The second criterion is satisfied in deep fjord basins such as Sognefjorden, with a depth of 1,380 m (Sørnes et al., 2007). Alternatively, a fjord water column can have high light attenuation, as in Lurefjorden and Halsafjorden (Sørnes et al., 2007). In Figure 6 illustrates the illumination of Vefsnfjorden over the seasons. Modelling of the underwater irradiance level shows that during summer, *P. periphylla*'s light comfort zone (Bozman et al., 2017; Dupont et al., 2009) is predicted to occur at deeper depths for

a longer period of the day compared to other times of year (Figure 7). At midsummer, for instance, waters above 50 m are available to *P. periphylla* for only 1 hr (Figure 6C).

The light climate of Vefsnfjorden may not only cause mortalities in young *P. periphylla*, but may also restrict the recruitment period. In Lurefjorden, recruitment occurs from late summer into the autumn months, and the abundance of early developmental stages is lowest in March/February (Jarms et al., 1999). In Vefsnfjorden, recruitment and composition of developmental stage were highest in the winter months (Figure 5C). Tiemann et al. (2009) suggested that *P. periphylla* reproduction is linked with vertical migration to the upper waters. According to modelled incoming sunlight (Figure 7), upper water migrations in the summer months would not be possible, which may explain the lack of stages 1–6 in the summer months.

In summary, the high light intensity levels of the summer nights at high latitudes may limit vertical migration and the growth of *P. periphylla* populations, and this may be an increasing constraint as one moves northwards.

5 | CONCLUSIONS

We conclude that the observed *Periphylla periphylla* mass mortality event was probably associated with the high and prolonged solar radiation during summer at the high latitude of Vefsnfjorden. This suggests that the photoperiod constraint hypothesis for mesopelagic fishes (Kartvedt 2008; Norheim et al., 2016) might also apply to mesopelagic jellyfishes such as *P. periphylla*. To further test this, and following Kartvedt (2008), we suggest a study of several fjord locations along a latitudinal range of fjords with and without *P. periphylla* so as to address the factors controlling the success and behaviour of this light-sensitive species. Fjord topography and basin water characteristics must also be considered in such a study as both factors have been shown to affect growth of *P. periphylla* populations (Sørnes et al., 2007). Our findings suggest that mass mortality events may often occur undetected, but may be an important feature in jellyfish population dynamics.

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Paper III

Photoperiod and retention constrain the distribution of light-sensitive mesopelagic jellyfish in high latitude fjords

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Abstract

The jellyfish *Periphylla periphylla* distributes within a 'light comfort zone' (LCZ) where light levels are neither too high nor too low. Here, we present a hypothesis that combines this jellyfish's apparent avoidance of too high light levels with the lower abundance levels of *P. periphylla* at higher latitudes. We report on a series of field samples located between 65°N - 67°N during 2007 - 2015 and provide evidence of a photoperiod constraint on *P. periphylla* distribution. Modelling of the conditions of underwater light field during midsummer reveals a decrease in the spatial and temporal components of the vertical extension of *P. periphylla* habitat along a northwards progression. However, a refuge from too high light levels is provided in fjord with substantially deep basins that provide an enlarged and dark habitat. There was no evidence of correlations between *P. periphylla* abundance and environmental parameters other than basin depths. These findings suggest that photoperiod constrains the northern distribution of mesopelagic jellyfish and goes against current dogma that warming temperatures associated with a changing climate will result in increased numbers of jellyfish. Our findings emphasize the structuring effect of light levels on the distribution and populations structure of deep dwelling species.

Introduction

The underwater light field can structure the distribution of mesopelagic species, also referred to as twilight species. Most mesopelagic organisms distribute in depth according to a “light comfort zone” (LCZ) where light levels are neither too high nor too low (Røstad et al., 2016b, Røstad et al., 2016a, Dupont et al., 2009, Aksnes et al., 2017, Bozman et al., 2017). Such a comfort zone has also been referred to as an antipredation window (Clark and Levy, 1988, Rosland and Giske, 1994) that determines the depth range in where the risk of predation by visual predators is offset by the access to food. The depth of the LCZ can differ temporally and across geographic locations, which in turn alters the amount of suitable habitat available to a species (Aksnes et al., 2017). Increased solar irradiance during summer at high latitudes results in a deepening of the LCZ (Bozman et al., 2018). The vertical extension of the suitable habitat decreases in locations with increased light attenuation, resulting in LCZ located at shallower depths (Røstad et al., 2016b, Røstad et al., 2016a).

The photoperiod constraint hypothesis (Kaartvedt, 2008) argues that light regime, rather than temperature, regulates mesopelagic fish populations through limiting the habitat available for safe foraging in the productive surface waters during summertime at high latitudes. This view is supported by recent observations of a deepening a mesopelagic sound scattering layer along a latitudinal gradient. This layer appeared to distribute according to a LCZ during night- as well as daytime (Norheim et al., 2016). Increased nightlight levels with increasing latitude caused a successively deeper halt of the upward migration at night so that the organism of the scattering layer did not enter the epipelagic at the highest latitudes.

The photoperiod constraint hypothesis can also be applied to the success of the mesopelagic jellyfish *Periphylla periphylla* (Péron and Lesueur, 1810) in high latitude coastal areas (Bozman et al., 2018). *Periphylla periphylla*'s maximum tolerance for light is presumably due to the pigment protoporphyrin that gives this jellyfish its distinct dark red colouration (Herring, 1972, Bonnett et al., 1979). Protoporphyrin degrades into toxic compounds upon light exposure (Herring, 1972, Bonnett et al., 1979). As a result, upper water vertical migration in *P. periphylla* are limited to periods of with no or low solar irradiance (Herring, 1972, Bonnett et al., 1979, Bozman et al., 2017, Kaartvedt et al., 2011). Such restrictions are common in other jellyfish with protoporphyrin pigments, including *Atolla wyvillei*, *Crossata rufobrunnea*, (Herring, 1972, Bonnett et al., 1979), and *Stygiomedusa gigantea* (Benfield and Graham, 2010).

P. periphylla is a cosmopolitan species found in low numbers in the open ocean (Pagès et al., 1996, Dalpadado et al., 1998, Mauchline and Harvey, 1983, Larson, 1986). This jellyfish is also present in nominal densities along the entire Norwegian coastline up to and including Svalbard (80°N) (Fosså, 1992, Havnø, 1918, Havnø, 1926, Sneli, 1984, Broch, 1913, Gulliksen and Svendsen, 2004, Geoffroy et al., 2018, Knutsen et al., 2018). Unique to Norway, however, are the mass occurrence populations with abundances ranging from 20 – 320 individuals m⁻² in some western Norwegian fjords (Sørnes et al., 2007, Gjelsvik Tiller et al., 2014). These populations have been present year round for multiple decades (Fosså, 1992 and citations

within, Sørnes et al., 2007, Broch, 1913, Sneli, 1984).

Sørnes et al. (2007) promoted the “optically conditioned retention” (OCR) which suggests that the build-up of mass populations of *P. periphylla* in relatively shallow areas requires both high water column light attenuation and adequate retention of individuals, i.e. sufficiently small advective exchange with surrounding waters. According to the OCR, substantially deep fjords do not require increased light attenuation levels and achieve darker basins through depth alone, i.e. as observed in Sognefjord (Sørnes et al., 2007). Dupont and Aksnes (2010) illustrated the OCR mechanism through simulations of *P. periphylla* occurrences in fjords as a function of the water column light attenuation, the fjord topography, and ambient light preferences that were assumed for the individual jellyfish.

Although episodic records of *P. periphylla* have been reported north of 64°N since as early as 1918 (Havnø, 1918, Havnø, 1926), there have not been published reports of perennial mass occurrences at the levels referred to above. The most striking environmental difference between western and northern Norway is the seasonality of the photoperiod: with increasing latitude there is a progression towards 24 – hour sunlight around midsummer. Thus, the increasing duration and intensity of the summer night light levels at high latitude locations may constrain *P. periphylla* distribution through imposing limitations on vertical migrations (Bozman et al., 2018) similar to that observed by Norheim et al. (2016) for a mesopelagic sound scattering layer.

Here, we test the hypothesis that high light intensities of the summer nights at high latitudes constrain the amount of vertical habitat available to *P. periphylla*. We also investigate if this constraint is mitigated by the fjord depth, i.e. if the enlarged dark habitat of a deep fjord compensates for the increased latitudinal light exposure in upper water. To do so, we have used observations of *P. periphylla* abundance, hydrography, and topography of high latitudes Norwegian fjords together with previously published estimates of the upper light limit of *P. periphylla*.

Materials and methods

Periphylla periphylla distribution in northern Norway

Nine fjords located in mid and northern Norway (Fig. 1) (map created with R version 3.5.1, ggplot2 package Kahle and Wickham, 2013) were selected based on one of the following criteria: i) had reports of increased *Periphylla periphylla*, ii) shared bathymetry features similar to other *P. periphylla* fjords yet had no reports of the jellyfish, iii) fjords dissimilar to *P. periphylla* fjords and without reports of the jellyfish (Table 1). STD casts (SD204 SAIV A/S) for salinity, temperature, oxygen were taken at each sampling location from near the seabed to surface.

Periphylla were collected at each study site by triplicate vertical plankton net hauls (net diameter was either 1.5 m or 1.25 m, mesh size = 200 μm in diameter, see Table 1) from 10 m above the seabed to surface in the deepest section of the fjord (Table 1). Medusa stage *P. periphylla* with coronal dome width (CD) > 5mm were measured (CD) upon capture. The remaining specimens were preserved in a 4% borax-buffered formalin-in-seawater solution for subsequent processing in the laboratory. *Periphylla* collected in Vefsnfjorden during 2008 were measured for coronal dome height (CH) instead of CD. We converted CH to CD by using the empirical relationship $CD = 1.399CH + 0.07160$ ($R^2 = 0.98$, $n = 91$, $df = 90$, $p\text{-value} < 0.0001$) from Bozman et al. (2018). Estimates of abundance (ind m^{-2}) was obtained for each 10 mm CD size class for each location by averaging the replicate hauls abundance estimates assuming 100 % filtering efficiency of the net. This assumption may not be met in all sampling events, as elevated concentrations of phytoplankton or gelatinous zooplankton may have led to clogging of the net, and thus under sampling of the *P. periphylla* population. Our abundance estimates, therefore, should be interpreted as reflecting the minimum abundance.

We classified *P. periphylla* abundance levels into three categories according to Sørnes et al. (2007) as: “mass occurrence” ($>10.0 \text{ ind m}^{-2}$), “low occurrence” ($0.1 - 10.0 \text{ ind m}^{-2}$), and “no sampled individuals” (0.0 ind m^{-2}). Note, however, that as *P. periphylla* is an ubiquitous species in Norwegian coastal waters (Fosså, 1992), the last category does not discount the possibility that low numbers of this jellyfish was present in all fjords.

Data was not normally distributed so we applied a non-parametric Spearman’s rank correlation test to determine relationships between *P. periphylla* abundance and fjord environments, including bathymetry and hydrographical features.

Modelling of subsurface irradiance field and *Periphylla periphylla* light comfort zone

Similar to Bozman et al. (2018), we used a global horizontal irradiance model (Robledo and Soler, 2000) to model the total solar irradiance ($\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$) incident on the sea surface assuming clear sky conditions while neglecting effects of Rayleigh scattering and various other measurable atmospheric parameters (e.g. air pressure, temperature,

perceptible water, ozone and aerosol concentrations) to model the underwater irradiance field. Field estimates from the Norwegian Meteorological Institute (www.met.no) roughly agrees with the estimated irradiance.

We used an exponential function to model the subsurface irradiance field during midsummer 2008:

$$I_{z,t} = I_{z-1,t} e^{-K_z}$$

where z is depth (range = 0 – max sample depth), and a one meter interval was used between z and $z - 1$, t is time of the day (h) and K_z is the light attenuation coefficient of downward-directed irradiance between the depth z and $z - 1$. We focus our analysis on midsummer because there is a progression towards 24-hours of sunlight with increasing latitude in the study area. We addressed the lack of *in situ* measurements of downwelling irradiance at the sample locations by using a proxy for K_z (i.e. K_z is set equal to K_p where K_p is the proxy for a particular depth) that provides an empirical relationship between the non-chlorophyll light attenuation on one hand and salinity and dissolved oxygen on the other hand (Equation 7 in Aksnes, 2015). The K_p proxy was developed for Norwegian coastal waters and is based on field measurements along the Norwegian coast in 2008 (Aksnes, 2015). We used data collected from the same cruise as in Aksnes (2015) for the K_p estimations for the locations that overlapped our sampling sites; however, not all of our field locations corresponded with the locations studied in 2008 (Table 2). Note also that since the K_p proxy does not account for chlorophyll attenuation, K_p tends to underestimate K_z , particularly in the surface waters where phytoplankton concentration can be high in summer.

In order to relate the previously reported *P. periphylla* mass occurrence in fjords in western Norway with our sample locations, we also estimated K_p for Lurefjorden and Sognefjorden. For this, we used salinity and oxygen data from Lurefjorden in 2010 that was obtained by (Bozman et al., 2017), and from Sognefjorden that was obtained in 2008 by Aksnes (2015).

The model allows us to quantify the ambient light as a function of depth. From here, using values according to the estimate provided in Bozman et al. (2017), we assumed that total irradiance light intensities higher than $5 \times 10^{-3} \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ are avoided by *P. periphylla*. From the model we were able to locate the estimated depth that corresponds to the total irradiance levels that *P. periphylla* avoids during a 24-hour period, which provided an estimate of how much of the water column was unsuitable for *P. periphylla*. We present values for noon (highest sunlight) and midnight (lowest sunlight), as well as the total number of hours the upper waters are not suitable, if applicable according to latitude.

Results

Periphylla preiphylla were present in five of the nine sampled fjords (Fig. 1; Table 1). Two cases (Sjona and Vefsnfjorden in 2008) qualified as mass occurrence fjords, with abundances of 13.18 ± 2.28 and 41.73 ± 2.86 ind m^{-2} , respectively. Four cases (Bindal, Rana, Sørfolla, and Vefsnfjorden 2015) had low occurrences (Table 1). The remaining fjords (Melfjorden, Mistenfjord, Saltenfjord, and Skjerstadjorden) had no sampled individuals.

Size structure was skewed towards the smaller size groups in all locations with *P. periphylla* (Table 1). In the mass occurrence fjords, the small (CD < 4 cm) *P. periphylla* contributed to 83 and 97% of the population (Table 1). The abundances of large medusa (CD > 4cm) were low in all fjords (range: 0.0 – 2.26 ind m^{-2} ; Table 1).

Fjords with *P. periphylla* had deeper basin depths, ranging from 485-720 m (Table 1) and basin depth correlated with the abundances of both small (Spearman's rank correlation test: $\rho = 0.66$, $p = 0.02$) and large ($\rho = 0.60$, $p = 0.04$; Fig. 2a; 2b) *P. periphylla*. Neither sill depth (Fig. 2 c, d) nor the ratio between sill and basin depths (Fig. 2e, f) correlated with *P. periphylla* abundance (Table 3). Furthermore, no obvious associations with the hydrographical variables were indicated. Results from Spearman's rank correlation test are presented in Table 3.

Irradiance levels

According to the assumed upper tolerance limit for light intensity (Bozman et al., 2017), the part of the water column considered unsuitable for *P. periphylla* differed with time of day and latitude during midsummer.

During the midsummer night, the extension of the unsuitable habitat increased with increasing latitude (Table 2). At 60°N, there was a daily five hour period for when the light environment in the entire water column was suitable for *P. periphylla*. The effect of the midsummer night light became stronger with northwards progression, as a result access to the upper waters was further restricted (Table 2). At 66°12'N, *P. periphylla* access to the upper ca 55m was restricted to 1 hour period. By 66°38'N there was no period during which the upper waters were accessible, i.e. the surface waters at latitudes > 66°38'N was effectively shut down during the entire 24 hours during midsummer.

During periods when solar irradiance is highest (midday), the upper waters (range 70 – 110 m, exact depth was fjord specific) were not available to migrating *P. periphylla* in all locations (Table 2).

Discussion

The combination of fjord depth and photoperiod effects the distribution, abundance, and population structure of *P. periphylla* in fjords above 64°N, which may explain the lower frequencies of regional *P. periphylla* compared to southern fjords. Only two of the fjords, Sjona and Vefsnfjorden 2008, qualified as *Periphylla periphylla* mass occurrence populations with abundances > 10 individuals m⁻² and by 2015 Vefsnfjorden had experienced substantial loss (Table 1). We did not detect mass occurrences as high as those reported at lower latitudes (Table 1) where abundances as high as 320 individuals m⁻² have been reported (Sørnes et al., 2007, Tiller et al., 2015). The abundances of the large size group (> 4 cm) were not extraordinarily high (Table 1), which appears to be common for the large *P. periphylla* found in fjords at high latitudes (Fosså, 1992, Knutsen et al., 2018) and in the northern Atlantic Ocean (Dalpadado et al., 1998).

The photoperiod constraint hypothesis, the optically conditioned retention hypothesis, and *Periphylla periphylla*

Our hypothesis that the light regime at higher latitudes constrains the distribution and retention of *P. periphylla*, originates from the photoperiod constraint hypothesis for mesopelagic fish (Kaartvedt, 2008). Increased intensity and duration of solar irradiance levels, as experienced at higher latitudes, results in a deepening of the upper limit of suitable habitat (Norheim et al., 2016). Based on the study of Bozman et al. (2017) we assumed that *P. periphylla* did not tolerate light intensities higher than $5 \times 10^{-3} \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$. The fact that protoporphyrin degrades into toxic compounds upon light exposure (Herring, 1972, Bonnett et al., 1979) provides a mechanistic explanation for the avoidance of high light in *P. periphylla*.

The photoperiod related restriction on the habitat access of *P. periphylla* during the summertime period in northern latitudes (Bozman et al., 2018) increases spatially and temporally with increasing latitude (Table 2). Photoperiod constraint may have implication for species behaviour and success (Kaartvedt, 2008, Prihartato et al., 2015, Norheim et al., 2016). For *P. periphylla*, the proximate drivers behind migrations into the upper parts of the water column have been suggested to be related to feeding (Fosså, 1992), reproduction or other social behaviours (Tiemann et al., 2009, Kaartvedt et al., 2015). The upper 100 m may be of specific importance to the larger individuals. The results from a continuous acoustic study in a western Norwegian fjord during January through to April show that larger *P. periphylla* constantly migrate within the upper 100m (Kaartvedt et al., 2011). The northward deepening of the light associated tolerance depth prevents *P. periphylla* from entering upper waters relative to locations further to the south, where access to surface exists throughout the year (Table 1).

Habitat preference may explain the dominance of smaller *P. periphylla* in the sample locations as fjord depth appears to influence the habitat and population structure of this jellyfish. A shallow bottom depth restricts the amount of dark habitat available to *P. periphylla*

(Sørnes et al., 2007)(Table 2) yet compensation for the high light exposure at high latitudes during the summer is provided by a sufficiently deep fjord basin (Fig 2; Table 3). Larger *P. periphylla* appear to be better able to tolerate higher light levels and perform longer vertical migrations that expose them to the advective layers in fjords (Sørnes et al., 2007, Dupont et al., 2009, Dupont and Aksnes, 2010, Kaartvedt et al., 2011). Smaller *P. periphylla* do not perform similar migrations and instead prefer deeper, thus darker environments (Sørnes et al., 2007, Jarms et al., 2002) which implies that for these individuals a large bottom depth is more beneficial than decreased light exposure in the upper ca 100 m. At some stage in their life cycle *P. periphylla* apparently benefit from approaching the upper waters; before that stage, however, the strong light exposure in upper water is probably not a constraint.

Light attenuation levels work in parallel with depth as a factor influencing the light exposure in the water column, and elevated light attenuation may compensate for light exposure in shallow systems (Sørnes et al., 2007). Due to low non-chlorophyll light attenuation of Atlantic Water (AW) (defined as >34.95 PSU Sætre, 2007), a fjord with AW must be substantially deeper than 500 m in order to be adequately dark enough to promote sufficient vertical habitat for retention of *P. periphylla* (Aksnes et al., 2009). Both Lurefjorden and Sognefjorden have *P. periphylla* mass occurrence populations at 320 ind and m⁻², respectively. In Lurefjorden, the 440 m deep basin is characterized by NCW, which attenuates light much more than the AW in the 1308 m basin of Sognefjorden (Sørnes et al., 2007, Aksnes et al., 2009). The basin depth of 1308 m in Sognefjorden provides ample dark habitat for the smaller *P. periphylla* and this is ensured by elevated light attenuation in Lurefjorden (Sørnes et al. 2007, Aksnes et al. 2009).

AW fjords shallower than 500 m, such as Saltfjorden, would then not provide a sufficiently dark habitat for mass occurrences. The basins of Bindalsfjorden and Sjøna were deeper than 600 m and contained a mixture of AW and Norwegian Coastal Water (defined as <34.5 PSU Sætre, 2007) (Table 1), which suggests slightly elevated light attenuations (Sørnes et al., 2007, Eiane et al., 1999), and except for the upper water during summer, these fjords might, therefore, be sufficiently dark for *P. periphylla*.

Mesopelagic jellyfish: hiding in plain sight?

The intricate bathymetry as reflected in the many fjords and islands of the Norwegian coastline means the amount of habitat available to jellyfish is potentially high. Our study is not an exhaustive investigation of the higher latitude fjords, and low densities *P. periphylla* are likely present in several deep fjords not investigated here. For example, small *P. periphylla* have been observed in Tysfjord (basin depth: 725 m; 68°12'3.2"N 16°10'7.6"E) (A. Bozman and M. Krogstad, pers. obs). Deep-dwelling jellyfish are subject to undersampling, due in part to sampling methodologies that may not target depth, size, or patchiness. For example, use of an Underwater Video Profiler in Sognefjorden did not return any observations of *P. periphylla* (Gorsky et al., 2000), although a year-round mass occurrence population has been observed in this fjord system since as early as 1910 (Broch, 1913, Sørnes et al., 2007, Aksnes et al., 2009). The same study and methods did observe *P. periphylla* in Lurefjorden (Gorsky et al., 2000),

which may be an artefact of the different size class structures between the two fjords. Both are mass occurrence populations, but while 50 – 80% of the population in Lurefjorden is dominated by *P. periphylla* with CD > 4cm, 90% of the Sognefjorden population has CD < 4 cm (Sørnes et al., 2007).

Our results indicate that the distribution of mesopelagic jellyfish may be influenced by the same forces that shape the latitudinal distribution of mesopelagic fish. Photoperiod imposes a decreasing availability of vertical habitat for mesopelagic fish along a latitudinal gradient (Norheim et al., 2016, Prihartato et al., 2015), and may explain the lower numbers of such fish at higher latitudes (Kaartvedt, 2008, Kaartvedt et al., 2018). Using similar methodologies as for the above studies on mesopelagic fish, our hypotheses, (1) that the high light intensities of the summer nights at high latitudes constrain the habitat available to *P. periphylla* and (2) that this constraint is mitigated by the fjord depth, could be further tested through a study in which the depth distribution of individual *P. periphylla* are recorded with in situ observations of surface and subsurface light intensities in several fjords along a latitudinal gradient.

Variation in mesopelagic species at higher latitudes and in a changing climate

Advection and local jellyfish behaviour may affect temporal shifts in frequencies (Purcell et al., 2018). For fjord populations of *P. periphylla*, fluctuating population numbers may be an indication of changes in the light attenuation levels of the water column. According to the simple mechanistic model outlined by Sørnes et al. (2007) and quantified by Dupont and Aksnes (2010), the suitability of a fjord for *P. periphylla* mass occurrence depends on the interactions between three factors: fjord topography (basin depth and vertical extension of the advective layer), light-related diel vertical migration of the individual jellyfish, and water column light attenuation. Water mass characteristics are not static properties but rather fluctuate temporally and spatially. Therefore, a fjord once unsuitable to *P. periphylla* mass occurrence may shift to a suitable system as a consequence of increased water column light attenuation and vice versa (Dupont and Aksnes, 2010). Such a process may explain the variations observed in Vefsnfjorden's over a seven-year period from a system with no reported *P. periphylla*, to a mass occurrence, and again back to low population numbers (Table 1).

The response to environmental change by scyphozoans includes swimming behaviour that is ultimately advantageous for survival and growth (Hays et al., 2012, Fossette et al., 2015, Moriarty et al., 2012). *Periphylla's* own migratory response to its ambient light environment by (Bozman et al., 2017) could imply that this jellyfish also avoid locations where conditions are sub-optimal for the species. An alternative speculation includes the use of fjords and coastal areas as nursery grounds for developing jellyfish (Goldstein et al., 2018). In Norwegian fjords, the deep and dark environment below the sill depth provides highly suitable for the smaller stages of *P. periphylla*. Environmental conditions such as temperature and salinity are relatively constant below sill depth (Sørnes et al., 2007, Fosså, 1992), the initial six *P. periphylla* stages do not require food and instead utilize yolk granules (Jarms et al., 1999) and the overwintering *Calanus* spp (Bagøien et al., 2001) may provide food for the later small stages,

and the predation risk is low (Fosså, 1992). In shallow fjords, however, the role of light attenuation related mortality with increasing prevalence during periods of increasing duration and intensity of solar irradiance levels would limit the success of these systems as nursery grounds (Bozman et al., 2018).

Predictions for species diversity scenarios in a changing climate suggest that warming temperatures may result in increased biomass and distribution ranges (Proud et al., 2017). However, photoperiod will stay constant in a changing climate and so light rather than temperature may be of greater influence for the distribution of mesopelagic species is an alternative hypothesis (Kaartvedt, 2008, Kaartvedt et al., 2018). Under current conditions, the incoming light at night increases two to three orders of magnitudes along a latitudinal gradient from 63°N to 67°N in May (Norheim et al., 2016). Mesopelagic fish and invertebrates distribute at depth according to the fluctuations in incoming light (Norheim et al., 2016). It appears a similar restriction may apply to *P. periphylla* (Table 2). Future predictions of an increased supply of light absorbing DOM of terrestrial origin (to NCW) is a potential scenario associated with climate change (Larsen et al., 2011, Wolf and Heuschele, 2018) and may promote mesopelagic regime shifts through the increased availability of habitat preferential to light-sensitive mesopelagic jellies (Aksnes et al., 2009). Such an environment would be substantially dark enough to promote mass occurrence levels of mesopelagic jellyfish (Sørnes et al., 2007) while at the same time would limit the feeding success of visual predators, such as fish, thus minimize food competition pressures for jellies (Eiane et al., 1997, Eiane et al., 1999, Haraldsson et al., 2012).

An influx of jellyfish into a system can be inaccurately labelled as a real population increase when the actual event is only a localized re-distribution of a population through physical or behavioural means (Graham et al., 2001). There are no indications that the cosmopolitan *P. periphylla* has recently been introduced into Norwegian waters (Fig 1; Table 1). Its presence was noted a century ago (Broch, 1913) and it is regularly caught in low numbers throughout the northern Atlantic Ocean (Fosså, 1992, Dalpadado et al., 1998). Bloom and bust of jellyfish populations may not be an anomaly but rather reflect natural variability that occurs on decadal scales (Condon et al., 2012, Condon et al., 2013, Boero et al., 2008). A global analysis of changes in jellyfish numbers revealed a 20-year cyclic pattern, including a jump in the 1990s that led to a perceived notion of increasing populations (Condon et al., 2013). Further and more detailed studies of the mesopelagic realm at higher latitudes may reveal cyclic changes in the distribution of mesopelagic jellyfish in relation to environmental fluctuations. Monitoring of the optical conditions in the water column may reveal if a potential coastal water darkening event (Aksnes et al., 2009) might contribute to more persistent mass occurrences of jellyfish at high as well as at low latitudes.

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Tables and Figures

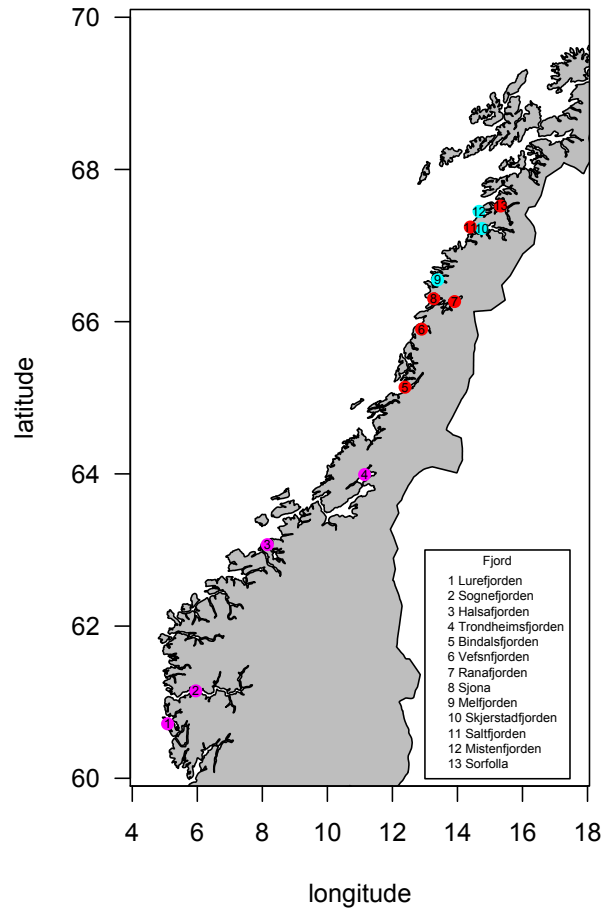


Figure 1: Study sampling locations with (red circles) *Periphylla periphylla* populations and (blue circles) no sampled individuals. See Table 1 for the abundance level classifications in each fjord. Also included are (purple circles) four locations in western Norway where mass occurrences have been studied previously by other authors (e.g. Sørnes et al 2007; Tiller et al 2015). This figure does not show the complete distribution or occurrence of *P. periphylla* in Norwegian fjords and coastal waters, and does not discount the presence of this jellyfish in other fjords not sampled in this study.

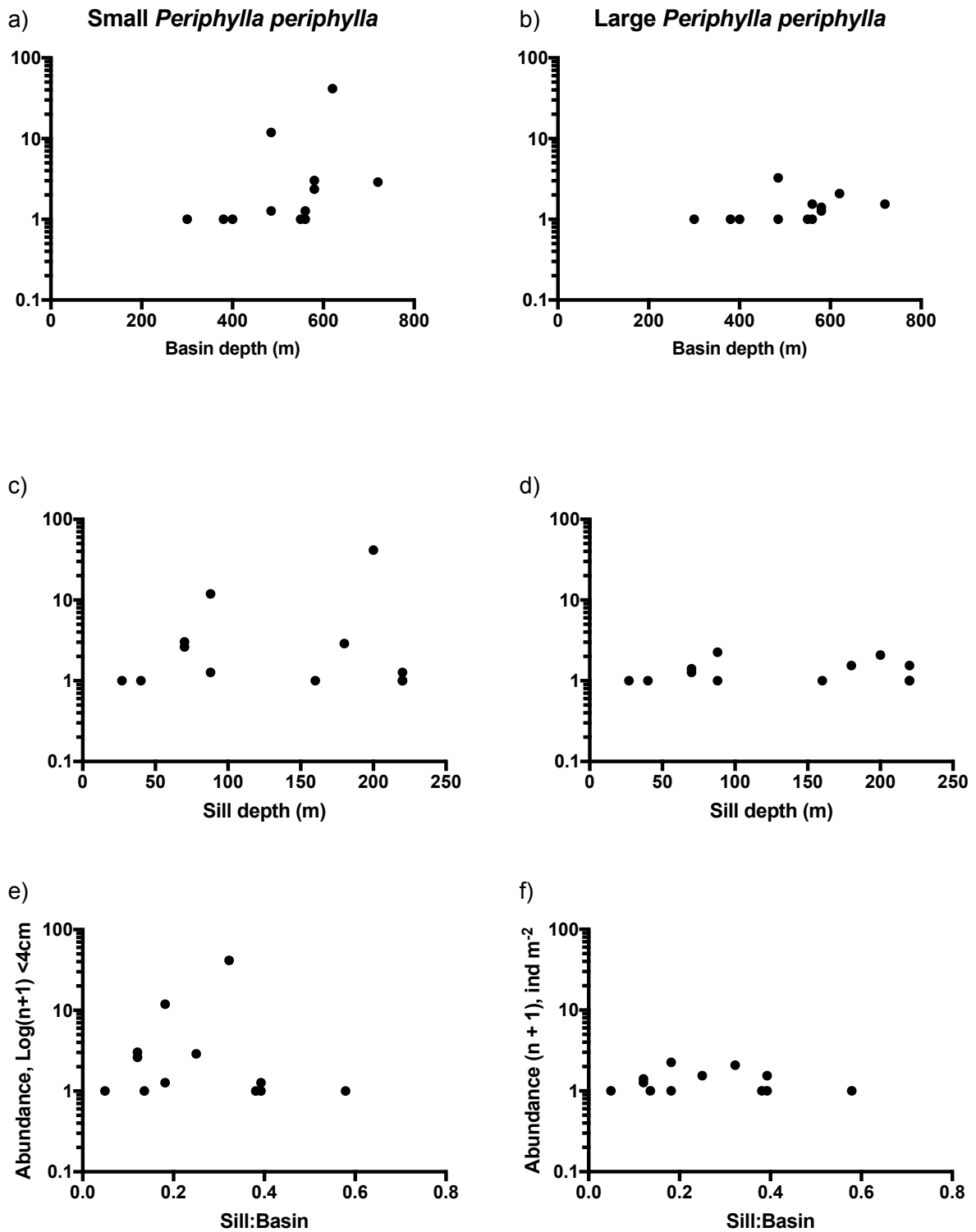


Figure 2: (a) Abundance of small *Periphylla periphylla* (coronal dome width < 4 cm) and (b) for large *P. periphylla* (coronal dome width > 4 cm) versus fjord basin depth (m); (c) small and (d) large *Periphylla periphylla* versus sill depth (m); and (e) small and (f) large *Periphylla periphylla* versus ratio of sill to basin depth.

Table 1: Overview of sampling locations and associated criteria, bathymetry, sampling depth, hydrography, characteristic water masses (Norwegian Coastal Water (NCW), Atlantic Water (AW)), *Periphylla periphylla* abundance, and population size classification in nine fjords above 65°N studied between 2007-2015.

Fjord	Fjord criteria	Sample date	Bottom depth (m)	Sill depth (m)	Tow depth (m)	Net opening (m)	Basin waters				<i>Periphylla</i> abundance ± stdev (ind m ⁻²)		Classification
							Salinity PSU	Oxygen ml/L	Temp °C	Water mass	CD < 4 cm	CD < 4 cm	
Bindalsfjorden 65°11'N:12°18'E	<i>Periphylla</i> reports	11-Nov-11	720	180	490	1.25	34.60	6.60	6.60	NCW/AW	1.90 ± 3.29	0.54 ± 0.94	low
Vefsnfjorden 65°55'N:13°5'E	<i>Periphylla</i> reports	15-Apr-08	485	88	410	1.5	34.10	5.16	5.97	NCW	10.92 ± 0.33	2.26 ± 0.98	mass
		6-Jul-15				1.25	33.76	5.01	5.49	NCW	0.27 ± 0.47	0.00	low
Ranafjorden 66°12'N:13°14'E	<i>Periphylla</i> reports	26-Oct-09	580	70	400	1.25	34.17	5.72	6.1	NCW	2.03 ± 1.69	0.41 ± 0.47	low
		19-Nov-13	580	70	485	1.25	33.99	4.03	5.82	NCW	1.36 ± 0.47	0.27 ± 0.47	low
Sjøna 66°17'N:13°16'E	similar bathymetry, no reports	20-Nov-13	620	200	450	1.25	34.79	3.96	6.83	NCW/AW	40.65 ± 3.25	1.08 ± 0.47	mass
Melfjorden 66°33'N:13°24'E	different bathymetry, no reports	20-Nov-13	400	160		1.25	34.66	7.04	7.04	NCW/AW	0.00	0.00	no sampled individuals
Saltfjorden 67°15'N:14°33'E	different bathymetry, no reports	08-Nov-13	380	220	360	1.25	35.14	4.62	7.08	AW	0.00	0.00	no sampled individuals
Skjerstadjorden 67°15'N:15°08'E	similar bathymetry, no reports	20-Apr-12	550	27		1.25	33.50	6.43	5.31	NCW	0.00	0.00	no sampled individuals
Mistenfjorden 67°26'N:14°52'E	different bathymetry, no reports	07-Nov-13	300	40	285	1.25	33.87	3.51	5.05	NCW	0.00	0.00	no sampled individuals
Sørfolla 67°31'N:15°18'E	<i>Periphylla</i> reports	26-Apr-12	565	220	540	1.25	34.92	4.82	7.00	NCW/AW	0.00	0.00	no sampled individuals
		27-Apr-12			500	1.25	34.61	4.98	7.00	NCW/AW	0.27 ± 0.47	0.54 ± 0.94	low

Table 2: Estimated depth of the upper limit of suitable light level habitat for *Periphylla periphylla* during the periods of highest (noon) and lowest (midnight) solar irradiance levels during midsummer and the amount of time in a 24-hour period during which the upper waters are too illuminated for this jellyfish in selected sampled locations. *Data used for Lurefjorden and Sognefjorden estimations are from previous studies (Bozman et al 2017 and Aksnes 2015, respectively).

Fjord	Location	Basin depth (m)	Estimated unsuitable habitat for <i>Periphylla periphylla</i>		Amount of time upper waters are unsuitable
			Depth, noon (m)	Depth, midnight (m)	
Lurefjorden*	60°42'N 5°5'E	440	73	0	5 h
Sognefjorden*	61°8'N 5°46'E	1308	110	0	4 h
Bindalsfjorden	65°11'N 12°18'E	720	99	0	3 h
Vefsnfjorden	65°55'N 13°5'E	485	90	0	2 h
Ranafjorden	66°12'N 13°14'E	580	90	0	1 h
Islands outside Melfjord	66°38'N 13°6'E	400	87	41	0 h
Skjerstadvfjorden	67°15'N 15°08'E	550	85	55	0 h
Sørfolla	67°31'N:15°18'E	565	90	57	0 h

Table 3: Statistical results for Spearman’s rank correlation test between abundance of *Periphylla periphylla* and environmental parameters. (*results with correlation)

Small <i>Periphylla periphylla</i>		
	ρ	P
Salinity	-0.312	0.319
Temperature	-0.096	0.762
Oxygen	-0.011	0.978
Sill depth	-0.002	0.997
Basin depth	0.657	0.024*
Sill:basin	-0.237	0.451
Large <i>Periphylla periphylla</i>		
Salinity	-0.127	0.693
Temperature	0.064	0.843
Oxygen	0.015	0.968
Sill depth	0.168	0.595
Basin depth	0.600	0.043*
Sill:basin	-0.062	0.848

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