

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

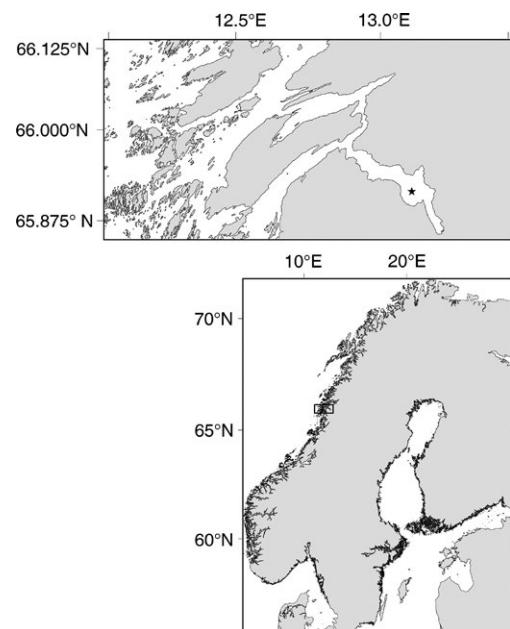


FIGURE 1 Sampling location, Vefsnfjorden, Norway. Star denotes the study site in the deepest section of the fjord basin, where the samples of *Periphylla periphylla* were collected



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*.

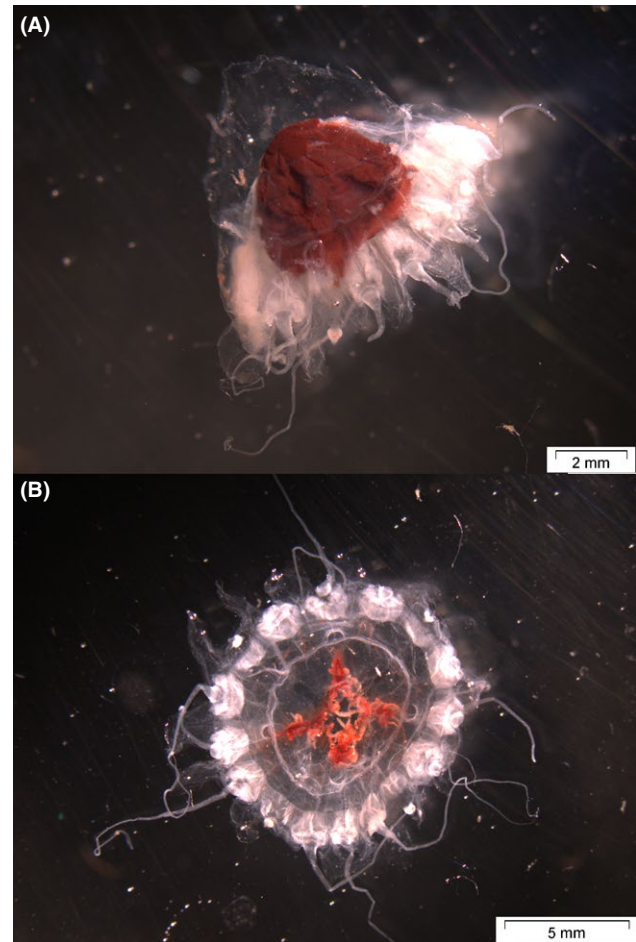


FIGURE 2 An example of young developmental stages of (A) alive *P. periphylla* versus (B) *P. periphylla* corpse collected in Vefsnfjorden during sample dates in the 2010–2011 (see Table 1). The live *P. periphylla* has full stomach pigmentation, whereas the *P. periphylla* corpse not only lacks stomach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

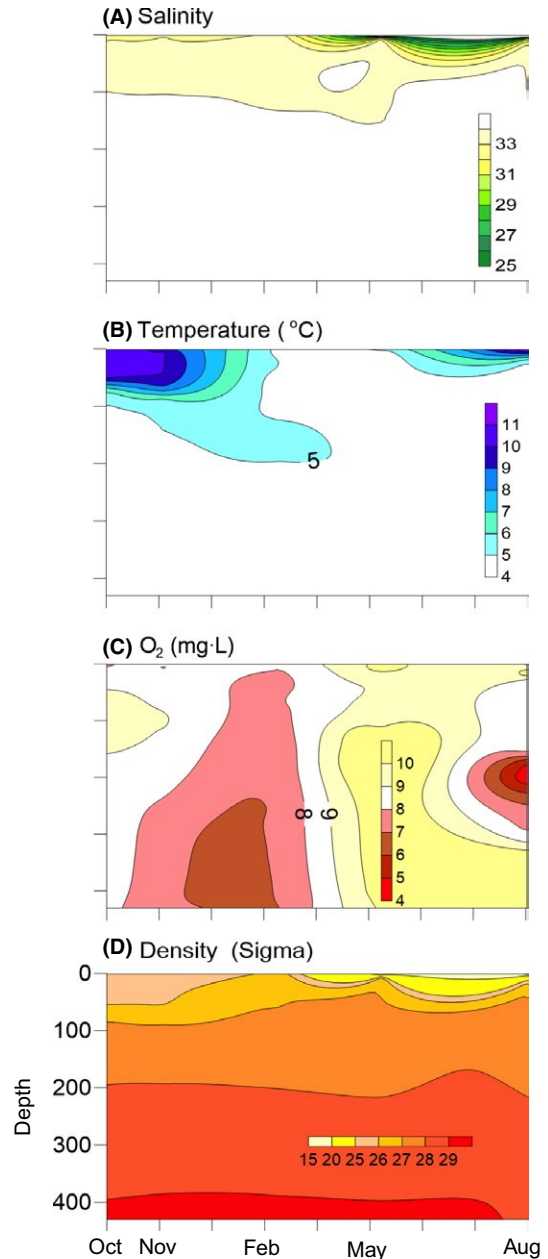


FIGURE 3 (A) Salinity, (B) temperature, (C) oxygen and (D) density depth profiles in Vefsnfjorden on 6 October and 18 November 2010, and 15 February, 3 May and 23 August 2011

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

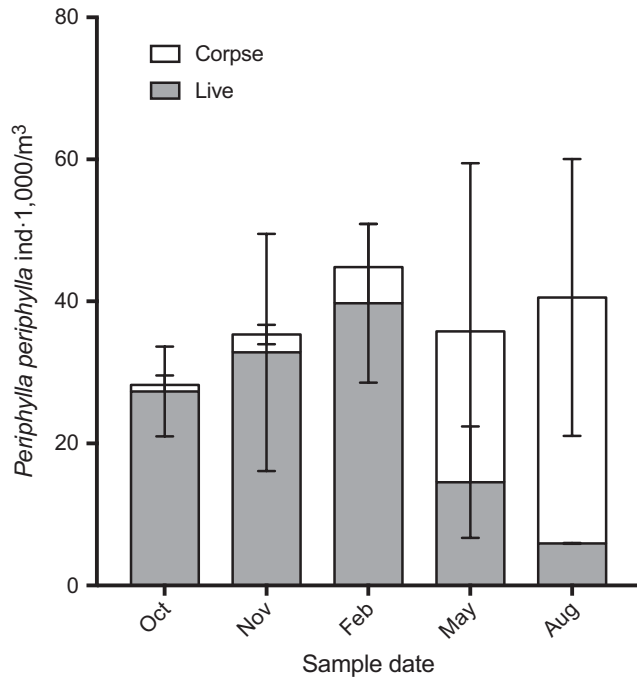


FIGURE 4 Mean abundance and SD for live (grey bars) and dead (white bars) *P. periphylla* collected in Vefsnfjorden on 6 October and 18 November 2010, and 15 February, 3 May and 28 August 2011

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).

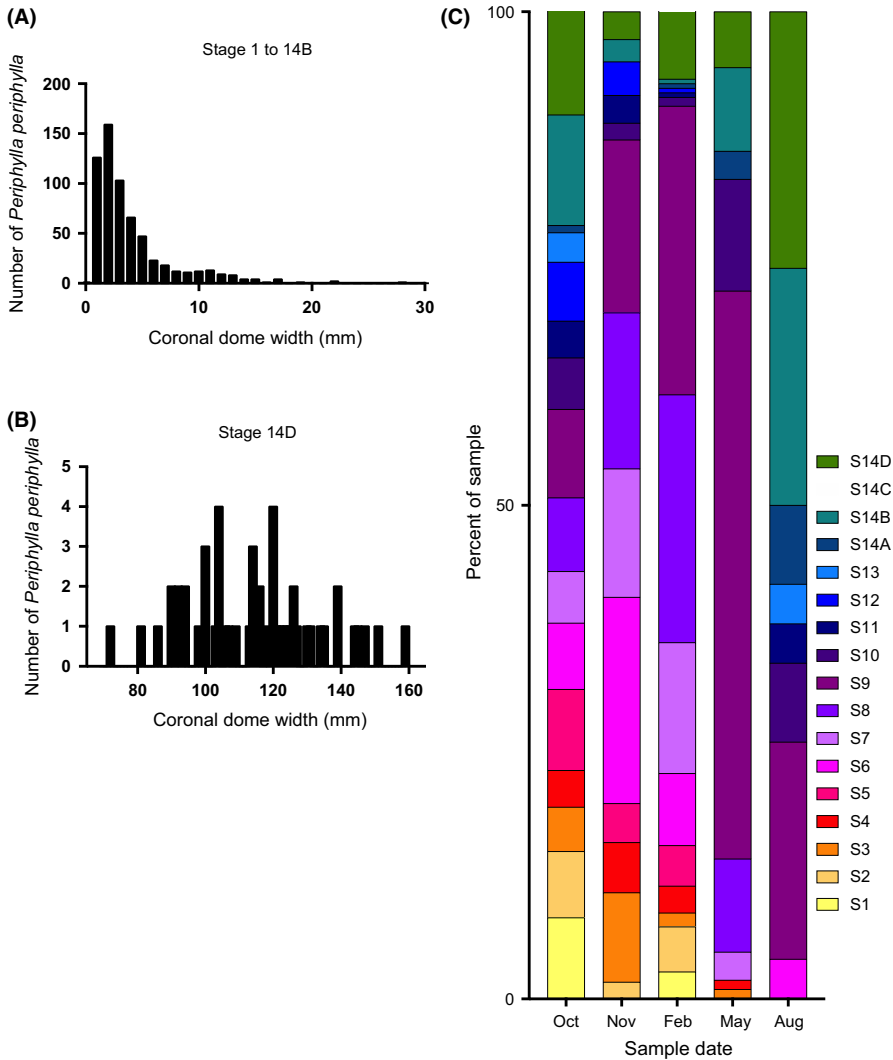


FIGURE 5 (A) Size class distribution for developmental stages 1–14B, (B) stage 14D and (C) the developmental stage composition of the total catch of *P. periphylla* collected in Vefsnfjorden. Stage 14C is left intentionally blank in the legend as no individuals in this developmental stage were recorded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

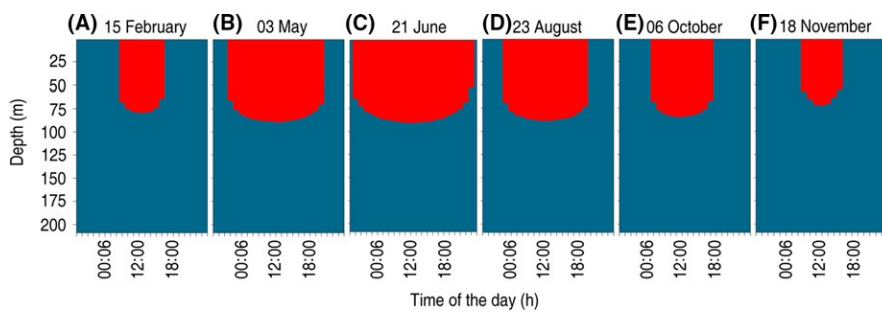


FIGURE 6 Estimated total irradiance ($\mu\text{mol quanta m}^{-2} \text{s}^{-1}$) levels on the sampling dates and midsummer (21 June) in Vefsnfjorden. The red area represents the upper limit of *P. periphylla*'s light comfort zone with total irradiance levels greater or equal to $5 \times 10^{-3} \mu\text{mol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

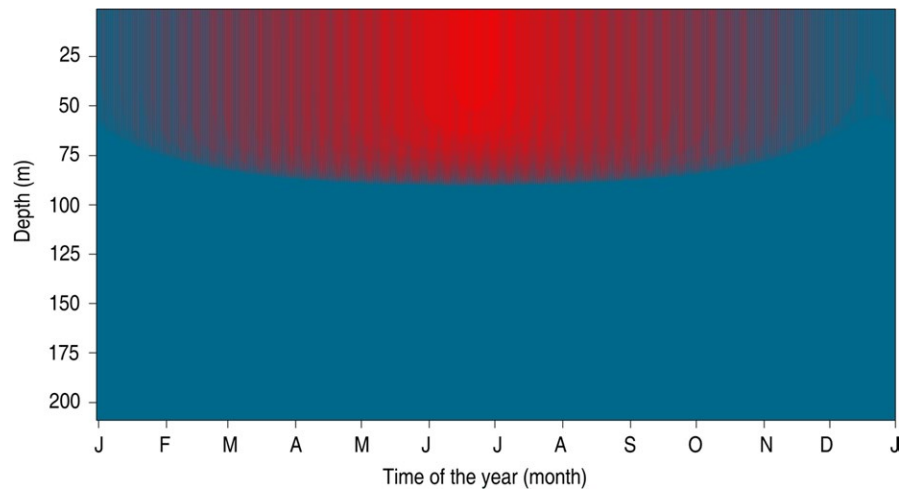
4.1 | Solar irradiance and *Periphylla periphylla* mass mortality

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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