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Causes for mass occurrences of the jellyfish *Periphylla periphylla*: a hypothesis that involves optically conditioned retention

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The mesopelagic coronate medusa Periphylla periphylla *has been very abundant (20–320 individuals* m^{-2}*), with as many as 2.5 individuals* m^{-3}*, for more than a decade in certain Norwegian fjords. These abundances are two to three orders of magnitude higher than reported from open ocean environments. Comparisons of the size, density and behavior of this jellyfish in three fjords (Lurefjorden, Sognefjorden and Halsafjorden) support the hypothesis that retention of* P. periphylla *is related to basin topography, light attenuation and photosensitivity. Furthermore, we hypothesize that the abundances of* P. periphylla *in Lurefjorden and Halsafjorden, but not in Sognefjorden, have been stimulated by increased light absorbance of water masses formed in the North Sea.*

INTRODUCTION

Physical processes and biological factors can initiate mass occurrences of gelatinous zooplankton. One such mass occurrence is that of the coronate scyphomedusa *Periphylla periphylla* in Lurefjorden, western Norway (Fosså, 1992). This phenomenon is of particular interest, because the persistent abundance of this species has been correlated with an almost complete absence of fish competitors (Fosså, 1992; Eiane *et al.*, 1999) that has been attributed to a higher basin water light absorbance (Aksnes *et al.*, 2004). The relatively small spatial scale (surface area of ~30 km^2), shallow sill depth (20 m) and narrow entrance (~200 m wide) make Lurefjorden resemble a marine lake. This characteristic reduces the sampling efforts relative to those for the open sea and facilitates opportunities to examine the ecological relationships. Lurefjorden is, therefore, an ideal habitat to study the population dynamics of this jellyfish and can serve as a testbed for developing models that seek to predict the potential impact of gelatinous predators in other coastal environments.

An important physical feature in Lurefjorden is the low exchange rate of water masses, which promotes the retention and proliferation of *P. periphylla* (Youngbluth and Båmstedt, 2001). Planktonic eggs and larvae were first observed in 1993, and local spawning has been observed in all seasons (Jarms *et al.*, 1999). In addition to low advective loss and continuous spawning, high longevity and low mortality are believed to maintain the high population density within the fjord (Jarms *et al.*, 1999; Youngbluth and Båmstedt, 2001). Low rates of oxygen consumption of *P. periphylla* (Thuesen and Childress, 1994; Youngbluth and Båmstedt, 2001) suggest that this species can survive on a relatively low food intake. Consistent with the impression of a low

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feeding rate is a low observed winter mortality rate of the common prey *Calanus* spp. in Lurefjorden when compared with other nearby fjords containing large stocks of mesopelagic fishes (Bagøien *et al.*, 2001).

Unlike the coastal, mostly epipelagic gelatinous zooplankton reviewed by Mills (1995, 2001), Purcell and Arai (2001) and Purcell (2005), *P. periphylla* is an oceanic, mesopelagic species well-adapted to the dark environment of the deep sea. When compared with the oceanic environment, however, Lurefjorden is not very deep (maximum depth is 438 m). This, together with the absence of visual predators in the basin water, suggested that the basin water may have higher than normal light attenuation. This was confirmed by the first light absorbance measurements in 1995 (Eiane *et al.*, 1999), and the high basin water light absorbance has persisted (Sørnes and Aksnes, 2006). Specifically, the photon flux at 300 m depth is approximately four orders of magnitude lower than that in the ocean. Thus, although Lurefjorden is a quite shallow fjord, it has a relatively large dark habitat (Aksnes *et al.*, 2004).

According to local fishermen (Fosså, 1992), Lurefjorden became a *Periphylla* fjord in the 1970s. What happened at this time, what circumstances can reverse the *Periphylla* dominance and will other fjords become *Periphylla* fjords? The answers to these questions are relevant to the analyses of mass occurrences of gelatinous predators, causal mechanisms and regime shifts in general (Mills, 1995, 2001; Purcell, 2005).

Here, we report on *P. periphylla* mass occurrences in two additional western Norwegian fjords to the north of Lurefjorden: Sognefjorden and Halsafjorden. Small *P. periphylla* have been observed in Sognefjorden for almost a century (Broch, 1913; Lid, 1979; Fosså, 1992 and references therein). In Halsafjorden, the first reports on mass occurrences of *P. periphylla* came in February 1984 when medusae clogged fishing nets (Sneli, 1984). On the basis of several cruises conducted from 2001–3, we describe the seasonal abundance, size composition and vertical distributions of *P. periphylla* in all three fjords. We discuss to what extent the observed mass occurrences in Sognefjorden and Halsafjorden are consistent with the knowledge that has been obtained for Lurefjorden. These comparisons provide the framework for a simple descriptive model of mass occurrences, which can serve as basis for future studies in other coastal habitats.

METHODS

Sampling protocol

The three study sites, Lurefjorden, Sognefjorden and Halsafjorden, are located on the Norwegian west coast (Fig. 1). The abundance, size and vertical distribution of *P. periphylla* were assessed at several stations within each fjord (Table I). In Lurefjorden and Halsafjorden, five predetermined stations along the fjords' entire longitudinal axes were selected for intensive sampling. The station depths ranged from 135 to 435 and 240 to 530 m, respectively. The considerable length of Sognefjorden (178 km) prevented a similar sampling strategy. For logistic reasons, sampling was confined to two to three stations along each of two neighboring transect lines [05.18 to 05.30°E and 05.30 to 05.48°E in the outer deep basin (1120–1260 m)]. Each station was sampled 1–6 (Lurefjorden), 1–5 (Halsafjorden) and 1–2 (Sognefjorden) times per cruise. Stratification of temperature, salinity and dissolved oxygen in the water column were defined from vertical profiles with a Seabird SBE 911 CTD.

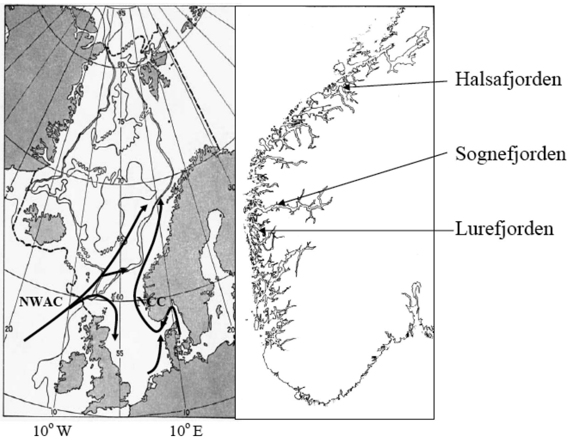

Fig. 1. The location of the three investigated western Norwegian fjords. Schematic representation of currents and water masses affecting the water properties of Norwegian fjord basins. The Norwegian Atlantic Current (NWAC) transports saline AW northwards along the Norwegian coast, whereas the Norwegian Coastal Current (NCC) transports less saline NCW from the North Sea northwards along the coast. AW is denser than NCW and underlies this water mass and can intrude into fjord basins with deep sills. The NTW (not shown) is also denser than NCC and found below this water mass.

Table I: Sampling overview for Lurefjorden, Sognefjorden and Halsafjorden, western Norway, October 2001 to October 2003

	October 2001	April 2002	June 2002	April 2003	October 2003
Lurefjorden	X O	X O	X O	X O	X O
Sognefjorden	X	O	X O	X O	X
Halsafjorden			X O	X O	X

X and O indicate that plankton net hauls and ROV dives were performed, respectively. ROV dives were not performed in Sognefjorden in October 2001 and October 2003 and Halsafjorden in October 2003 due to technical problems.

Abundance and size distribution

A large plankton net (2 m in mouth diameter, 12.5 m long and 1−3 mm graded mesh size) was hauled vertically through the water column, at a rate of 6 m min^{-1}, to gently collect *P. periphylla*. A large plastic bag was attached at the cod end to mitigate damage to the medusae. Each medusa was counted and sized [coronal diameter (CD), ± 1 mm]. Medusae <1 cm in CD were only enumerated. When estimating the mean size in a population (see Results), the <1 cm medusae were assigned a mean CD of 0.5 cm. To enable population size comparisons between seasons and years, we calculated a mean abundance per cruise and fjord. Each station was represented by the mean number of medusae m^{-2} sampled at that location and thus contributed equally to the overall estimate (per fjord and cruise).

Vertical distribution

The vertical distributions of *P. periphylla* were determined using the Remotely Operated Vehicle (ROV) *Aglantha*. Vertical excursions were performed from surface to bottom, both at day and at night. The depth of occurrence of each medusa observed in the field of view of a Sony Hi-8 video camera, set at minimum focal length, was noted. Four 500 W halogen lights and four 150 W high intensity discharge gas-arc lights illuminated the field of view. The descent rate of the vehicle was $<0.5\ \text{m s}^{-1}$ and constant for any given dive. Each video profile ($n = 40$) was assigned to the category day or night (i.e. between sunset and sunrise). To characterize the vertical distributions for a particular season and fjord, we calculated the mean depth (Z_m) and the standard deviation (Z_s) of the frequency distribution along the depth axis. Generally, these statistics are obtained by estimating the second and the square root of the third moment of a frequency distribution, and we applied the trapezoidal method (Manly, 1977):

$$Z_{\text{m}} = \frac{1}{2}\sum_{j=1}^{n}\frac{(h_j + h_{j+1})f_j z_j}{O} \tag{1}$$

$$Z_{\text{s}} = \sqrt{\frac{1}{2}\sum_{j=1}^{n}(h_j + h_{j+1})f_j z_j^2/O - Z_{\text{m}}^2} \tag{2}$$

where O corresponds to the area under the frequency curve (i.e. the surface-integrated abundance):

$$O = \frac{1}{2}\sum_{j=1}^{n}(h_j + h_{j+1}) \times f_j \tag{3}$$

Here, n is the number of depth intervals, z_j the depth, $h_j = z_j - z_{j-1}$ and f_j the number of medusae observed in depth interval h_j.

Index of advective impact

Water exchange between fjords and adjacent coastal regions can be substantial and is related to fjord topography, regional wind patterns and the strength of the Norwegian Coastal Current (Sætre *et al.*, 1988; Aksnes *et al.*, 1989; Aure *et al.*, 1996; Asplin *et al.*, 1999). For convenience, the water masses within fjords were divided into four layers (Fig. 2): surface, intermediate (with upper and lower layers) and deep layers. Currents within the surface layer and the intermediate layer, which extends down to sill depth, strongly influence the abundance and diversity of plankton present in these layers (Lindahl and Hernroth, 1988; Aksnes *et al.*, 1989; Basedow *et al.*, 2004). Local winds and freshwater runoff affect the surface layer, but generally, the most influential advective processes occur in the intermediate layer. Winds moving northwards induce downwelling along

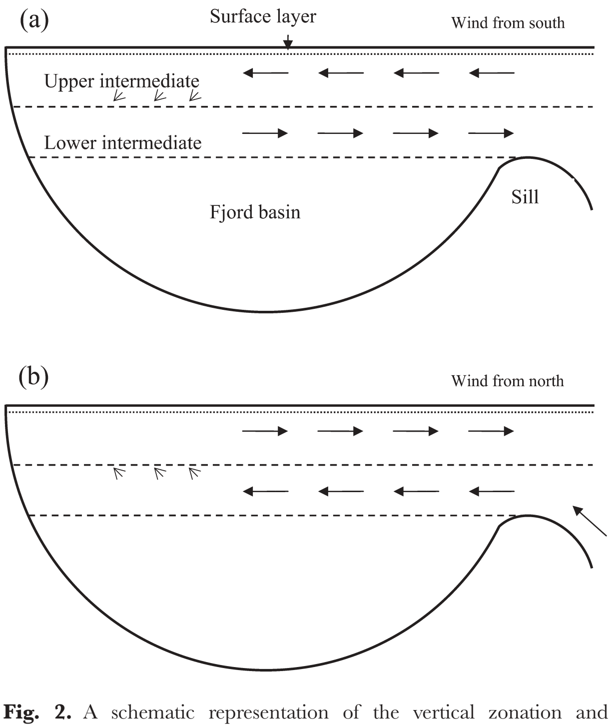

Fig. 2. A schematic representation of the vertical zonation and generalized circulation patterns in fjords (after Aksnes *et al.*, 1989). (a) In fjords with deep (>50 m) sills, the estuarine circulation is small when compared with water transport in the intermediate layer. Winds directed northwards induce downwelling along the western Norwegian coast, leading to inward transport of coastal water in the upper region of the intermediate layer and outward transport in the lower region of the fjord. (b) Winds directed southwards induce upwelling along the coast and cause currents in the intermediate layer opposite to those with downwelling.

Table II: Topographical features of Lurefjorden, Sognefjorden and Halsafjorden, western Norway, and concentrations of dissolved oxygen

	Length (km)	Maximum depth (m)	Sill depth, D_s (m)	Area above D_s (A, m^2)	Fjord volume (V, m^3)	DO (mL L^{-1})
Lurefjorden	22	439	20	3.81×10^3	5.73×10^9	2.18–6.85
Sognefjorden	178	1304	165	8.81×10^5	5.25×10^{11}	4.48–5.59
Halsafjorden	45	534	135	4.42×10^5	4.22×10^{10}	4.72–5.73

Values of dissolved oxygen (DO) are minima to maxima, October 2001–October 2003, from 100 m downwards to the bottom. The area, *A*, represents the cross-sectional area above the sill at the fjord entrance, as defined in Aksnes *et al.* (1989).

the western Norwegian coast, leading to an inward transport of coastal water in the upper region of the intermediate layer and an outward transport in the lower region (Fig. 2a). Winds flowing southwards cause upwelling along the coast, which reverses the current pattern in the intermediate layer (Fig. 2b). In this case, both the surface and intermediate layers are regarded as the advective layers of a fjord.

We devised an advective index (α) that expresses to what extent the observed depth range of *P. periphylla* overlapped with the advective layers of the fjord, because the time spent here decreases the probability of local retention. By subtracting and adding 2 SDs of the *P. periphylla* depth distribution [Z_s, equation (3)] to the mean depth [Z_m, equation (2)], we obtained a depth range ($Z_m - 2Z_s$, $Z_m + 2Z_s$). We assume that this depth range is representative for the vertical habitat of *P. periphylla* and that the individuals migrate vertically within this habitat. If this habitat was located deeper than the sill depth [i.e. if $(Z_m - 2Z_s) > Z_{sill}$, where depth is a positive quantity], there was no overlap with the advective layers and $\alpha = 0$. If the habitat was shallower than the sill depth [$(Z_m + 2Z_s) < Z_{sill}$], $\alpha = 1$. This area corresponds to the highest advective exposure. Finally, in cases where this habitat encompassed the sill depth:

$$\alpha = \frac{Z_{Sill} - (Z_m - 2Z_s)}{4Z_s} \qquad (4)$$

From this expression, $\alpha = 0.5$ was obtained when the mean depth was equal to the sill depth ($Z_{sill} = Z_m$). Thus, the higher the α, the higher the exposure to the advective layers of the fjord.

RESULTS

Water masses in the three fjords

The shallow sill (20 m) of Lurefjorden ensures communication with Norwegian Coastal Water (NCW, with salinities <34.50), and this water mass filled the entire fjord basin. Observed oxygen levels were always >2.18 mL L^{-1} (Table II) and temperatures 6–7°C (Fig. 3).

The deep sill (165 m, Table II) of Sognefjorden allows direct communication with dense Atlantic Water (AW), which is characterized by salinities >34.95 and temperatures slightly >7°C (Fig. 3). This dense water mass filled the large basin of the fjord. Here, observed oxygen levels were never <4.48 mL L^{-1} (Table II).

The basin water in Halsafjorden was less saline (34.50–34.95) than that in Sognefjorden and corresponds to Norwegian Trench Water (NTW). But, because Halsafjorden is located north of the Norwegian Trench, the basin water is most likely a mixture of NCW and AW (J. Aure, personal communication). Below sill depth (135 m, Table II), observed oxygen levels were always >4.72 mL L^{-1} (Table II) and temperatures 7–8°C (Fig. 3).

Abundance

There were no significant differences in overall mean abundance between cruises (Fig. 4), either in Lurefjorden (ANOVA, $F_{4,20} = 0.3$, $P > 0.05$), Sognefjorden

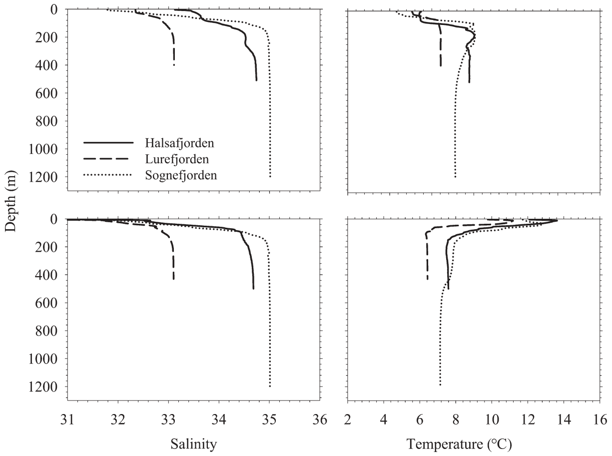

Fig. 3. Representative vertical profiles of salinity and temperature in spring (April 2003, upper panels) and autumn (October 2003, lower panels) for Lurefjorden, Sognefjorden and Halsafjorden, western Norway.

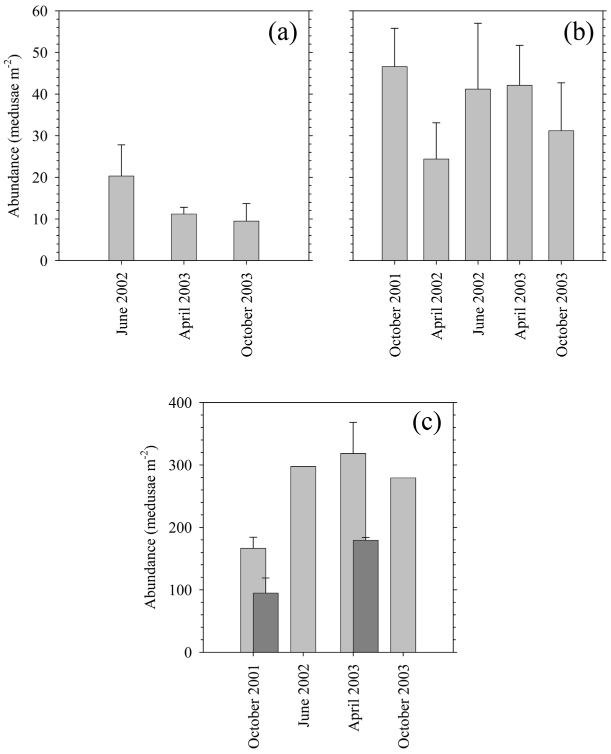

Fig. 4. The abundance (means ± standard errors) of *P. periphylla* in (a) Halsafjorden, (b) Lurefjorden and (c) Sognefjorden, western Norway. The density estimates are based on plankton net hauls. For Sognefjorden, light grey: the westernmost transect line and dark grey: the easternmost transect line. See Methods for further details. In June 2002 and October 2003, no standard error is indicated because data from only one transect line were available.

(westernmost transect line; ANOVA, $F_{3,4} = 3.6$, $P > 0.05$) or in Halsafjorden (ANOVA, $F_{2,12} = 1.3$, $P > 0.05$). In Sognefjorden, the mean abundance was significantly higher on the westernmost than on the easternmost transect line (Fig. 4c) in April 2003 (*t*-test, $P < 0.05$, df = 3), but not in October 2001 (*t*-test, $P > 0.05$, df = 3). Hence, the three sites contained persistent and extraordinary abundant populations of *P. periphylla* throughout the study period.

Size distribution

In Lurefjorden (Fig. 5b), the decrease in the mean size (CD ± std) from 3.53 ± 0.11 cm ($n = 587$) in October 2001 to 2.58 ± 0.09 cm ($n = 665$) in April 2002 was statistically significant (*t*-test, $P < 0.0001$, df = 1250). Further, there was no significant difference in the mean size (*t*-tests, $P > 0.05$) between April 2002, June 2002 (2.67 ± 0.09 cm, $n = 646$) and April 2003 (2.82 ± 0.06 cm, $n = 1900$), before the statistically significant increase (*t*-test, $P < 0.0001$, df = 2388) from April 2003 to October 2003 (4.12 ± 0.13 cm, $n = 490$).

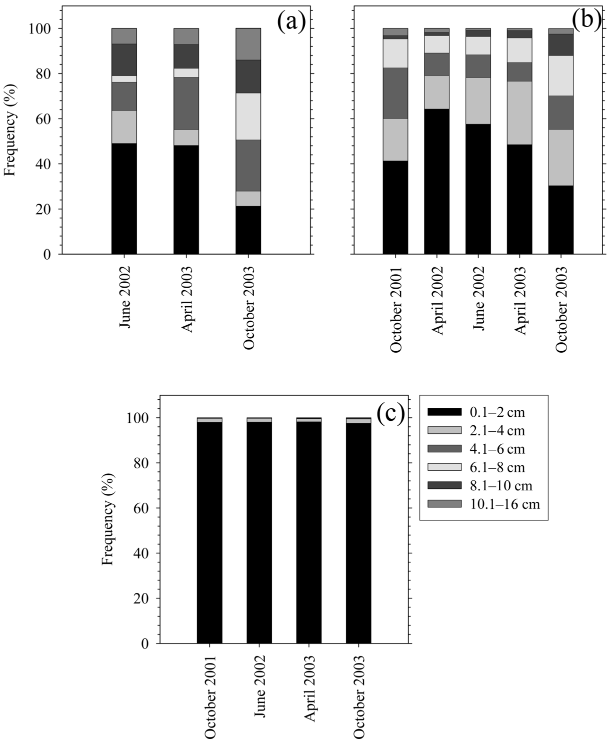

Fig. 5. The size (CD, cm) distribution of *P. periphylla*, based on medusae captured in plankton net hauls, for (a) Halsafjorden, (b) Lurefjorden and (c) Sognefjorden, western Norway. See Results for number of medusae per cruise and fjord.

In Sognefjorden (Fig. 5c), the numerical dominance (>97%) of small *P. periphylla* was consistent throughout the study period. Large medusae were rarely observed or collected. The increase in the mean size from 0.60 ± 0.02 cm ($n = 1046$) in October 2001 to 0.67 ± 0.02 cm ($n = 935$) in June 2002 was statistically significant (*t*-test, $P < 0.05$, df = 1979). Further, there was no significant difference in the mean size (*t*-tests, $P > 0.05$) between June 2002, April 2003 (0.65 ± 0.01 cm, $n = 3157$) and October 2003 (0.63 ± 0.02 cm, $n = 877$).

In Halsafjorden, small medusae (0.1–2 cm CD) dominated in both June 2002 and April 2003 (Fig. 5a). The small increase in the mean size from 3.60 ± 0.12 cm ($n = 925$) to 3.77 ± 0.26 cm ($n = 199$) was not statistically significant (*t*-test, $P > 0.05$, df = 1122). In October 2003, the distribution was skewed toward higher size classes, significantly increasing the mean size to 5.92 ± 0.29 cm ($n = 150$) (*t*-test, $P < 0.0001$, df = 347).

Vertical distribution

In accordance with Youngbluth and Båmstedt (Youngbluth and Båmstedt, 2001), *P. periphylla* from the

Table III: Vertical distributions of P. periphylla *in Lurefjorden, Sognefjorden and Halsafjorden, western Norway, represented by the mean depth [Z_m, equation (1)] and the SD [Z_s, equation (2)] of the depth distributions.*

	Daytime			Nighttime		
	Z_m (m)	Z_s (m)	n (individuals)	Z_m(m)	Z_s(m)	n (individuals)
Small medusae (<4 cm)						
Lurefjorden						
Oct 2001	204.8	30.8	125	129.4	50.1	311
Apr 2002	224.6	32.0	1509	181.2	14.6	304
Jun 2002	222.4	28.7	644			
Apr 2003	172.2	17.3	208	112.2	44.1	800
Oct 2003	214.0	46.3	150	166.3	50.7	540
Sognefjorden						
Apr 2002	839.5	290.6	595	735.0	278.9	270
Jun 2002				908.7	264.5	677
Apr 2003	946.6	263.2	446			
Halsafjorden						
Jun 2002	364.9	53.5	700			
Apr 2003	275.9	43.1	27	213.3	37.5	26
Large medusae (>4 cm)						
Lurefjorden						
Oct 2001	345.0	72.1	30	144.3	73.1	228
Apr 2002	186.4	86.7	644	141.0	49.0	87
Jun 2002	167.1	68.9	254			
Apr 2003	139.7	38.7	135	100.3	80.1	330
Oct 2003	234.9	87.8	73	157.6	66.8	428
Sognefjorden						
Apr 2002	507.5	59.3	8	511.7	247.8	6
Jun 2002				459.1	365.4	11
Apr 2003	584.3	270.5	7			
Halsafjorden						
Jun 2002	378.7	75.2	2082			
Apr 2003	279.5	81.7	154	203.9	57.4	46

These were calculated from the individual depth observations made with an ROV (see Methods). *n*, number of observations.

vertical video profiles was assigned to two size categories: small (less than ~4 cm CD) and large (larger than ~4 cm CD). Vertical distribution patterns were significantly different between day and night (Kolmogorov–Smirnov tests, Smirnov's chi-square approximation $P < 0.0001$), irrespective of fjord, season, station and size class. As determined from the mean depths (Z_m) of the populations (Table III), small and large medusae resided 40–105 and 35–205 m deeper at day than at night, respectively, regardless of fjord and season. The large medusae, however, had a broader depth span, as indicated by the SD of the depth distribution (Z_s). Sognefjorden is a possible exception, but the number of observations of large medusae was limited in this fjord. However, without doubt, the medusae observed in Sognefjorden resided much deeper and were more vertically dispersed than in the other two fjords (Table III). The average daytime depths of small medusae, over all sampling occasions, were 208, 893 and 320 m for Lurefjorden, Sognefjorden and Halsafjorden, respectively.

Advective impact

Small medusae did not occur within the advective layers ($\alpha = 0$), which consist of the surface and the intermediate layers, regardless of fjord, year, season and time of day. Within each fjord, the α-estimates for large medusae were not significantly different between day and night samplings or between cruises (*t*-tests, $P > 0.05$). We therefore pooled the observations. For large medusae, the mean α-values were intermediate for Lurefjorden (0.05 ± 0.02, $n = 2209$), highest for Sognefjorden (0.14 ± 0.06, $n = 32$ medusae) and lowest for Halsafjorden (0.02 ± 0.01, $n = 2282$).

DISCUSSION

Our results demonstrate that large populations of *P. periphylla* were present in Lurefjorden, Sognefjorden and Halsafjorden throughout the study period. Records of persistent year-round mass occurrences of gelatinous zooplankton are rare. Among the few examples are the scyphomedusa *Mastigias* sp. in the marine lakes in Palau (Hamner and Hamner, 1998; Dawson *et al.*, 2001) and the ctenophore *Mnemiopsis leidyi* in the Black Sea (Kideys, 2002; reviewed by Bilio and Niermann, 2004).

Recent investigations in Lurefjorden have indicated that the initial surveys (Fosså, 1992) of *P. periphylla* underestimated their abundance and population structure. For 1998 and 1999, Youngbluth and Båmstedt (Youngbluth and Båmstedt, 2001) reported densities two to three orders of magnitude higher than those noted in 1991 (Fosså, 1992). This disparity was not surprising, since Fosså (Fosså, 1992) based his density estimates on sampling with a coarse-mesh (30–100 mm) Harstad trawl towed at 1.5 m s^{-1}. Both Fosså (Fosså, 1992) and Youngbluth and Båmstedt (Youngbluth and Båmstedt, 2001) restricted their sampling to a single station in the fjord's deep basin. Because our abundance estimates are based on more extensive spatial sampling, our numbers are not directly comparable with their numbers. However, the mean densities we observed in Lurefjorden (25–50 individuals m^{-2}, Fig. 3) were greater than those reported by Youngbluth and Båmstedt (Youngbluth and Båmstedt, 2001). The concentration of *P. periphylla* varies according to the vertical migration patterns and might approach 2.5 individuals m^{-3} (Youngbluth and Båmstedt, 2001). Although the abundance of *P. periphylla* in Lurefjorden has remained high throughout a 12-year period (Fosså, 1992; Jarms *et al.*, 1999, 2002; Youngbluth and Båmstedt, 2001; Båmstedt *et al.*, 2003), the high occurrences probably began in the 1970s according to the information provided by local fishermen (Fosså, 1992).

In Sognefjorden, the abundances (100–300 individuals m^{-2}, Fig. 4c) were much higher than those observed in Lurefjorden and Halsafjorden, but the population consisted almost exclusively of small individuals (mean size = 0.60–0.65 cm). The abundance decreased from the westernmost to the easternmost transect (Fig. 4c), which supports our current impression of decreasing densities toward the fjord head (U. Båmstedt, unpublished results).

P. periphylla has been a nuisance in Halsafjorden for the last 2–3 decades (Sneli, 1984). In 1999 and 2000, Aksnes *et al.* (Aksnes *et al.*, 2004) learned that the biomass of *P. periphylla* in Halsafjorden was similar to that in Lurefjorden (~3 g WW m^{-3}). The abundances (10–20 individuals m^{-2}, Fig. 4a) in Halsafjorden were somewhat lower than those in Lurefjorden. The population size structure was skewed toward a higher mean size in Halsafjorden (3.60–5.92 cm) than in Lurefjorden (2.58–4.12 cm, Fig. 5).

For all three fjords, the observed densities of *P. periphylla* were several orders of magnitude higher than those known from the open oceans (Pagès *et al.*, 1996; Dalpadado *et al.*, 1998). The mass occurrences of the three fjords have two peculiar differences. The most prominent one is the absence of large medusae in Sognefjorden and the other is the pronounced differences in the vertical distributions of *P. periphylla* in the three fjords (Table III). As discussed below, optically conditioned retention of *P. periphylla* can explain these different patterns in abundances and distributions.

Retention of *P. periphylla*

Advection and retention of planktonic organisms are important features of fjord ecology (Kaartvedt, 1993; Skei *et al.*, 2003). As mentioned by Fosså (1992), Broch (Broch, 1913) refers to a discussion between himself and Hjort concerning the mechanisms behind the abundance of *P. periphylla* in Sognefjorden. Hjort pointed out that the sill may cause retention of medusae brought into the fjord, whereas Broch emphasized the biophysical factors that could enhance population growth. In general, the local residence time of a zooplankter is determined by its vertical behavior and, in particular, by the fraction of time spent in the basin water versus the advective layers (Aksnes *et al.*, 1989; Eiane *et al.*, 1998). The time scale for renewal of passively advected constituents in the layers above sill depth is of the order of days to weeks (Sætre *et al.*, 1988; Aksnes *et al.*, 1989). Although such residence times might be sufficient for local blooms of phytoplankton, long-lived pelagic animals such as *P. periphylla* cannot reside in this layer within a particular fjord, unless their presence is governed by a specific retention behavior. In contrast, the fjord basin, which extends from sill depth down to the bottom, acts as a retention habitat for planktonic organisms. The advective index (α) provides an estimate for the exposure of *P. periphylla* to the advective layers. For the small medusae, this index was zero, irrespective of fjord and season. This means that for all 3 years, small medusae were essentially not observed in the advective layers of the fjords, but apparently retained within the fjord basins. Thus, the sill-mediated retention argument of Hjort seems valid for the small *P. periphylla* in all three fjords. The vertical range of the large medusae, however, clearly extended into the advective layers, and the α-index suggests that the large *P. periphylla* in Sognefjorden were most prone to advection. Thus, the low number of large medusae in this fjord, compared with the two other fjords, can be attributed to high advective impact.

Possible impact of the light regime on the vertical distribution of *P. periphylla*

Extensive diel vertical migrations have previously been described for *P. periphylla* (Fosså, 1992; Youngbluth and Båmstedt, 2001; Båmstedt *et al.*, 2003), and such migrations were also reflected in our calculated day and nighttime depths (Table III). These medusae possess complex sense organs (= rhopalia) that act as photo and gravity receptors (Tiemann *et al.*, 2002; Becker *et al.*, 2005). Hence, the medusae are capable of sensing directional environmental information. Light is normally considered to be the zeitgeber that triggers diel movements of animals, including gelatinous fauna (Graham *et al.*, 2001). Whether and how this applies to the populations of *P. periphylla* remains uncertain, as does their motivation for undertaking vertical displacements. However, the very existence of extensive diel migrations and the observation that light has lethal effects on *P. periphylla* (Jarms *et al.*, 2002) suggest that light influences their life history.

For a period of almost 10 years (1996−2004), a much higher light absorbance has been observed in the basin water of Lurefjorden than in Sognefjorden (Sørnes and Aksnes, 2006). If we hypothesize that *P. periphylla* has a preference for a certain range of ambient irradiance levels, we would expect *P. periphylla* to distribute according to a specific optical depth range, rather than to a range of absolute depths. For a given surface radiance, a diffuse optical depth is characterized by a certain photon flux density (Preisendorfer, 1986). The diffuse optical depth is calculated as the dimensionless product of the light attenuation for downwelling radiance and the depth that corresponds to the preferred light intensity (this depth is more likely to be in the range of preferred light intensities that allow for phenotypic plasticity).

Unfortunately, we do not have simultaneous measurements of light attenuation and the vertical distribution of *P. periphylla*. However, in Table IV, we have approximated optical depth ranges for *P. periphylla* by applying measurements of basin water light absorbance obtained in 2004 in Lurefjorden and Sognefjorden (Sørnes and Aksnes, 2006). Although the observed depth range of the small *P. periphylla* in Lurefjorden (155−190 m) was much shallower than that in Sognefjorden (683−1210 m), the calculated optical depth ranges were similar; 11.9−14.6 for Lurefjorden and 13.7−24.2 for Sognefjorden (Table IV). Such overlapping optical depth ranges also apply to the large size category of *P. periphylla* in the two fjords. Furthermore, the vertical distributions in Halsafjorden (Table IV) also fit into the optical depth ranges if absorbance measurements from 1999 to 2000 are applied (Aksnes *et al.*, 2004, additional measurements were not conducted in Halsafjorden). Thus, if *P. periphylla* has a preference for the ambient light regime, the optical depths calculated here (Table IV) suggest that the observed differences in the vertical distributions can be explained by a light-mediated behavior of *P. periphylla*, which is common to all three fjords.

The elevated light absorbance of Lurefjorden and Halsafjorden correlates with the presence of NCW, whereas the low absorbance of Sognefjorden correlates with Atlantic Water (Fig. 3). Thus, we cannot exclude the possibility that the different vertical distributions were governed by water mass characteristics, rather than light absorbance. From a general physiological perspective, however, we are unable to explain why

Table IV: Optical depth ranges for P. periphylla *in Lurefjorden, Sognefjorden and Halsafjorden, western Norway*

	Depth range (m)			Optical depth range (d.l.)	
	$Z_m - Z_s$	$Z_m + Z_s$	Absorbance (m^{-1}) a	$a \cdot (Z_m - Z_s)$	$a \cdot (Z_m + Z_s)$
Small medusae (<4 cm)					
Lurefjorden	154.9	189.5	0.077 ± 0.001	11.9	14.6
Sognefjorden	683.4	1209.8	0.020 ± 0.003	13.7	24.2
Halsafjorden	232.8	319.0	0.061 ± 0.004	14.2	19.5
Large medusae (>4 cm)					
Lurefjorden	101.0	178.4	0.077 ± 0.001	7.8	13.7
Sognefjorden	313.0	855.0	0.020 ± 0.003	6.3	17.1
Halsafjorden	197.5	361.5	0.061 ± 0.004	12.0	22.1

The optical depth is here the dimensionless (d.l.) product of depth and light absorbance. The observed mean depth [Z_m, equation (1) and the SD [Z_s, equation (2)] represent the vertical distributions of *P. periphylla* in April 2003 (Table III). The light absorbance (a) represents measurements made in 2004 that has been reported by Sørnes and Aksnes (2006) (Lurefjorden and Sognefjorden) and measurements made in 1999–2000 (Halsafjorden, Aksnes *et al.*, 2004). In both these studies, light absorbances were averaged for 100–300 m depth and 400–550 nm wavelength. Uncertainties represent ± s.e. for the light absorbance values.

and how the relatively slight differences in temperature (≈1°C) and salinity (≈1 U) should give the observed differences in the vertical distributions of *P. periphylla*. Nor can the small differences in oxygen concentration provide us with a plausible explanation. We will return to the question whether the light absorbances of Lurefjorden and Halsafjorden have changed over time.

A hypothesis for the existence of the mass occurrences: optically conditioned retention

We hypothesize that the mass occurrences of *P. periphylla* are governed by adequate local retention. This hypothesis implies that *P. periphylla* must spend a considerable part of its life within the basin water of a particular fjord, in order not to be advected from the fjord in the shallower layers. On the basis of the data in Table IV, we further hypothesize that *P. periphylla* has a preference for low ambient light and that its vertical position is largely determined by this preference. This means that the actual retention of *P. periphylla* in a particular fjord is determined by the combination of sill depth, basin depth and light attenuation. Sill depth determines the vertical extension of the advective layers (Fig. 2), whereas maximum depth and light attenuation determine the darkness of the fjord basin.

Predictions based on the hypothesis of optically conditioned retention

The hypothesis implies that the mass occurrences of *P. periphylla* in Lurefjorden and Halsafjorden are facilitated by the elevated light absorbance of the fjord basins. If these absorbances were replaced with the lower absorbance characterizing the basin water of Sognefjorden, we predict that these two fjords would not provide large enough optical depths for *P. periphylla* (i.e. the basins would not be sufficiently dark). This comparison might further imply that the mass occurrences in Halsafjorden and Lurefjorden have developed as a result of increased light attenuation.

Direct experimental tests of the suggested optical causality for the mass occurrences in Lurefjorden and Halsafjorden are obviously not achievable, unless nature provides them (i.e. by future changes in the light absorbance). The basic assumption of the hypothesis, however, that *P. periphylla* has a preference for ambient light can be tested. This experiment would require simultaneous measurements of temporal and spatial alterations in irradiance together with diel changes in the vertical distribution of *P. periphylla*. Direct observations of light-mediated behavior, e.g. horizontal sun-compass migration (Hamner *et al.*, 1994), should also be considered.

Possible anthropogenic and climatic impact on the mass occurrences

Western Norwegian fjords are influenced by the properties of the NCW that flows northwards with the Norwegian Coastal Current (NCC) (Fig. 1). This water mass is formed in the North Sea and characterized by a lower salinity than the AW because of an extensive drainage from Russia and Europe into the Baltic and North Sea. As discussed by Sørnes and Aksnes (Sørnes and Aksnes, 2006), this current supplies coastal waters with substantial amounts of dissolved organic matter (yellow substance), which enhances the light attenuation of NCW relative to AW. According to IPCC (2001), there have been marked increases in precipitation over northern Europe in the last part of the 20th century, linked to strong positive values of the North Atlantic Oscillation. This suggests that the amount of NCW, as well as its light transmission properties, is influenced by climate. Because the entire basin of Lurefjorden contains NCW, a link to climate through light absorbance is plausible. Also, the NCW component of Halsafjorden suggests such a link, although the light absorbance of the AW in the basin of Sognefjorden is unaffected by processes taking place in the North Sea.

Eutrophication in the Baltic and North Sea may also influence the light absorbance of fjord basins. Degradation of organic material results in colored dissolved organic matter (CDOM), which absorbs light (Hasset, 2006). Sanden and Håkansson (1996) have described a long-term shallowing of Secchi depths in the Baltic Sea that most likely reflects increased algae concentrations. CDOM originating from the Baltic and North Sea will be transported with the NCC and influence fjord basins containing NCW.

We conclude that the recent mass occurences of *P. periphylla* in Lurefjorden and Halsafjorden may have developed because of increased light attenuation mediated by eutrophication and climatic changes, whereas the occurrence of small medusae in Sognefjorden is governed by a natural deep and dark habitat.

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