Size distribution pattern and abundance of Periphylla periphylla in western Norwegian fjords

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ABSTRACT

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## 1. Introduction

Periphylla Periphylla in the Norwegian fjords.

The abundance of *Periphylla periphylla* in Norwegian fjords has been the subject of several studies since the last century. Some of these fjords have been identified as "jellyfish fjords" due to the high densities of *Periphylla periphylla* compared to adjacent fjords with higher fish abundance, as in the case of Lurefjorden (Ugland, Aksnes, Klevjer, Titelman, & Kaartvedt, 2014). The population of Periphylla periphylla in some Norwegian fjords has been reported to be several orders of magnitude greater than in the open sea (Youngbluth & Bamstedt, 2001). This may be of concern as periphylla are active predators that prey on crustaceans, small mesopelagic fish species, and also the larva of large fish species (Fossa, 1992; Youngbluth & Bamstedt, 2001). These concerns have also given rise to speculations as to the real cause of its population growth in some fjords which were narrowed to some factors such as eutrophication, overfishing, and climate changes (Aksnes et al., 2009; Sornes, Aksnes, Bamstedt, & Youngbluth, 2007). The recorded increase or population bloom of periphylla was also speculated to be as a result of their ability to survive in almost hypoxic conditions, slow growth rate, the low mortality rate of the prominent individuals, and their high longevity of about 10 – 30 years (Youngbluth & Bamstedt, 2001). Increased light attenuation due to the presence of dissolved organic matter causing darkening of the water and dim light conditions, low water mixing, the shallow sill, and narrow inlet are the major factors for Periphylla periphylla bloom in the fjords (Aksnes et al., 2009; Sornes et al., 2007). Studies have suggested that jellyfish blooms, including those of *Periphylla periphylla*, are increasing globally in response to human-induced stresses (Purcell, Uye, & Lo, 2007). In addition, the occurrence of Periphylla periphylla in high Arctic fjords in Svalbard has been attributed to the low solar irradiance during the polar night and the increased inflow of relatively warm Atlantic water in the European Arctic (Geoffroy et al., 2018).

A study conducted in Lurefjorden showed that the vertical migration behavior of individual *Periphylla periphylla* was influenced by the low advective environment of the deep fjord basin (Kaartvedt, Klevjer, Torgersen, Sornes, & Rostad, 2007). Acoustic studies of vertical migration of periphylla conducted by Kaartvedt et al., (2007) and Klevjer et al., (2009) in Lurefjorden has revealed a mixture of synchronous and asynchronous migrating pattern also a population of

nonmigrating individuals of P. periphylla. This is a deviation from the conventional DVM pattern of periphylla migration to the surface at night and returning to depth at dawn.

Another factor that may favor the presence of *Periphylla periphylla* in Norwegian fjords is eutrophication. Eutrophication can increase the abundance of small-zooplankton, turbidity, and hypoxia (Breitburg et al., 2003), all of which may create favorable conditions for jellyfish over fish who are visual predators (Eiane et al., 1997, 1999). Additionally, fishing activities can remove predators of jellyfish and competitors for zooplankton, further improving conditions for jellyfish (Purcell et al., 2007).

#### Periphylla periphylla

*Periphylla periphylla* (Péron & Lesueur, 1810) belongs to the class Scyphozoa the "true jellies" of the phylum Cnidaria, They are holopelagic, having only the medusoid life stage (Jarms, Bamstedt, Tiemann, Martinussen, & Fossa, 1999; Jarms, Tiemann, & Bamstedt, 2002). They are members of the order Coronatae which are mostly deep-water jellies, they are a prominent member of the family Periphyllidae inhabiting all oceans (Rusell, 1970) including the arctic (Geoffroy et al., 2018), they are deep-water species found in low aggregations of two to three individuals and were discovered since 1970 in the Norwegian fjords (Fosså, 1992).

*Periphylla periphylla* is bioluminescence and reddish In colour, the coloration has been attributed to the presence of porphyrin pigment (Herring, 1972) which has been shown to be the reason for the avoidance of light by the medusae as porphyrin has a deadly effect when combined with daylight (Jarms et al., 2002). Jarms et al., (2002) hypothesized that undisturbed periphylla does not emit light but that the porphyrin pigment serves as a camouflage during its period of resting. Periphylla emits luminous flash pattern when touched, this serves as a warning sign to visual predators and as a defense to confuse their predators (Jarms et al., 2002). Periphylla is voracious feeders, they feed mainly on small crustaceans and small sized gelatinous zooplanktons (Sornes, Hosia, Bamstedt, & Aksnes, 2008; Youngbluth & Bamstedt, 2001).

*Periphylla periphylla* undergo diel vertical migrations mostly to avoid the light, feed, and for mating (Sornes et al., 2007; Tiemann, Sotje, Johnston, Flood, & Bamstedt, 2009; Youngbluth & Bamstedt, 2001), they are the most eurythermic of the order Coronatae occurring between 0° C and 16° C, mostly < 10° C (Fossa, 1992). Studies have shown that the nocturnal movement of

periphylla to the surface is likely related to feeding, they follow the diel vertical migration of their prey organisms (Kaartvedt, Titelman, Rostad, & Klevjer, 2011). Periphylla aggregates or cluster on surface waters at night, and this was attributed to reproduction especially in oceanic environments where the population is sparse, this allows for easy mating of individuals present in the population (Tiemann et al., 2009). Periphylla is holopelagic with a perennial life span (Bamstedt, Sotje, Tiemann, & Martinussen, 2020; Jarms et al., 1999). The medusae develop directly from eggs with no planula and ephyra stages, the eggs are released into the water as freefloating and non-mobile organisms for several months (Jarms et al., 1999; Jarms et al., 2002; Youngbluth & Bamstedt, 2001). Studies carried out in Lurefjorden suggested that periphylla spawn all year round, the mating encounters of this medusa in the fjords are strongly facilitated by surface aggregations at night (Bamstedt et al., 2020). According to simulations by Båmstedt, fertilized eggs released near the surface at twilight sink to a depth with insufficient light for visual predators and where there is low advective current (Bamstedt et al., 2020). The released eggs then go through several developmental stages before developing into a miniature medusae (Bamstedt et al., 2020; Jarms et al., 1999; Youngbluth & Bamstedt, 2001).



Figure 1. Image of Periphylla periphylla in swimming posture. Retrieved from <a href="https://www.natureplprints.com/popular-themes/creative-set-10/deep-sea-jellyfish-periphylla-periphylla-periphylla-18853271.html">https://www.natureplprints.com/popular-themes/creative-set-10/deep-sea-jellyfish-periphylla-periphylla-periphylla-18853271.html</a>.

#### The Norwegian fjord system

The fjords occur in many areas of the world and are found in cold temperate regions, they are long, narrow inlets with steep sides or cliffs often separated by shallow sills. These shallow sills are located at the mouth of the fjord and are usually old moraines (Salvanes et al. 2018).

One of the significant features of Norwegian fjords is their high productivity. The combination of nutrient-rich waters and favorable environmental conditions supports a wide range of marine life, including phytoplankton, zooplankton, fish, and seabirds. The nutrient input into these fjords is primarily derived from a combination of freshwater runoff, glacial meltwater, and upwelling of deep nutrient-rich waters (Salvanes, Aksnes, & Giske, 1992). The fjords are often subjected to seasonal variations, mostly due to mixing of the colder surface water and the warmer deeper water in winter, creating a uniform water layer (Salvanes et al. 2018). Most of the fjords have uniform salinity concentration from the sill depth almost to the surface during the winter months but receive fresh water supply during spring, summer, and autumn when the snow melts creating an apparent salinity gradient from the outer to the inner part of the fjord (Sætre.R., 2007).

The southwestern coast of Norway is a typical structure of a fjord system consisting of major rocks and few sandy beaches. These fjords were formed by the activity of the glaciers during the ice era (Salvanes et al. 2018, Eiane et al., 1998). Due to its shallow sill, the fjord creates unique and relatively stable marine environments to study different species, which are sometimes difficult to study in the open sea (Eiane et al., 1998), this also provides a suitable habitat for *Periphylla periphylla* thereby enhancing population maintenance of the medusae due to the fjords low advective loss (Fosså, 1992).

The coast of southwestern Norway is made up of several fjords systems. In my thesis we will be looking at the presence and the abundance of *Periphylla periphylla* in two fjords. Biomass data were collected over a period of eleven (11) years in Masfjorden and length measurement from 2019 to 2022, the data that will be used for this paper were collected in autumn of 2011 to 2022, while Fensfjorden data was collected from 2020 to 2022. This data is unique and thus allows for

the monitoring and follow up of the changes in abundance and size distribution of periphylla in the two fjords in the following years. It is pertinent to also state that additional data collections also are available from other fjords a few times, from February and/or May - and that this allows comparisons between fjords.

The objective of this thesis is to describe the changes in the size distribution and abundance of *Periphylla periphylla* over the period of 11 years in Masfjorden and Fensfjorden , also to compare the size distribution and its abundance in the two fjords.

# 2. Materials and Methods

## 2.1. Data Collection

The Data for this thesis was collected on several cruises spanning over a decade (from 2012 to 2022) in Masfjoden and Fensfjorden and (Table 1). The cruises were combination of the HypOnFjordFish project and field courses for master's students at the department of Biology which were done in the months of September, October and November. The data material consists of hydrographic measurements and samples of the helmet jellyfish Periphylla periphylla.

| Table 1. An overview of the cruises | where sample data were | collected from 2012 to 2022. |
|-------------------------------------|------------------------|------------------------------|
|-------------------------------------|------------------------|------------------------------|

| Fjord       | Year | Month(s)           |
|-------------|------|--------------------|
| Masfjorden  | 2012 | October            |
| Masfjorden  | 2013 | November           |
| Masfjorden  | 2014 | October            |
| Masfjorden  | 2015 | September          |
| Masfjorden  | 2016 | September          |
| Masfjorden  | 2017 | October            |
| Masfjorden  | 2018 | August and October |
| Masfjorden  | 2019 | October            |
| Fensfjorden | 2020 | June and September |
| Masfjorden  | 2020 | June and September |

| Fensfjorden | 2021 | February and September |
|-------------|------|------------------------|
| Masfjorden  | 2021 | February and September |
| Fensfjorden | 2022 | May and September      |
| Fensfjorden | 2022 | May and September      |

### 2.1. Study Area

The study areas are Masfjorden and Fensfjorden

Masfjorden and Fensfjorden (Figure 2.) are western Norwegian fjords. Masfjorden (60<sup>0</sup>50`N, 5<sup>0</sup> 30`E) is 20 km long and 0.5 to 1.5 km wide fjord, it is separated from Fensforden by a 75 m deep shallow sill and has a maximum depth of 494 m (Salvanes et al., 1992). The surface water of this fjord is dynamic and has a link to the coastal waters via wind-driven advective currents while the deep basin water below the sill has little connection with the waters outside the fjords and this accounts for the low oxygen content that decreases towards the seabed (Syvitski et al., 1987). The deeper part of the fjord has been hypoxic since 2016 due to little renewal, but it was reoxygenated in 2021. Fensfjorden is 30 km long with a maximum water depth of 680 m in its inner part, it has a good connection with the coastal water due to its deep sill depth of 380 m, it is well oxygenated down to its seabed.



Figure 1. Map of Masfjorden and Fensfjorden (Salvanes, Anne Gro Vea & Jaru Tryti Nordeide 1993 12 30).

### 2.2. Sampling design

### 2.2.1. Hydrographical data

A Sea-Bird SME 9 CTD was used in measuring the physical properties of the water, the CTD measures conductivity, temperature, and depth, and the salinity is calculated based on the electrical conductivity measurements. An additional sensor, an oximeter (auxiliary oxygen sensor) was mounted on the CTD. The CTD was lowered vertically at a speed of 0.5ms<sup>-1</sup> and measurements were taken at every meter from the surface to ca 5 m above the seabed.

Several CTD stations were taken in the two fjords (Masfjorden and Fensfjorden) during the period (Table 2) salinity is given in PSU (Practical Salinity Unit), Temperature at degrees Celsius, and Oxygen at ml I-1.

Table 2. An overview of the CTD stations with maximal lowering depths and bottom depths

| Year | Fjord       | Season | CTD     | Latitude   | Longitude   | Bottom    |
|------|-------------|--------|---------|------------|-------------|-----------|
|      |             |        | Station |            |             | Depth (m) |
| 2011 | Masfjorden  | Autumn | 992     | 60 52.33 N | 005 24.04 E | 472       |
| 2012 | Masfjorden  | Autumn | 443     | 60 52.36 N | 005 24.84 E | 479       |
| 2013 | Masfjorden  | Autumn | 1084    | 60 52.35 N | 005 24.05 E | 477       |
| 2014 | Masfjorden  | Autumn | 387     | 60 52.35 N | 005 24.31 E | 467       |
| 2015 | Masfjorden  | Autumn | 691     | 60 52.23 N | 005 22.27 E | 469       |
| 2016 | Masfjorden  | Autumn | 950     | 60 52.14 N | 005 22.02 E | 474       |
| 2017 | Masfjorden  | Autumn | 300     | 60 52.25 N | 005 24.67 E | 489       |
| 2018 | Masfjorden  | Autumn | 411     | 60 52.31 N | 005 23.87 E | 463       |
| 2019 | Masfjorden  | Autumn | 385     | 60 52.33 N | 005 24.52 E | 487       |
| 2020 | Fensfjorden | Autumn | 309     | 60 45.89 N | 005 12.82 E | 659       |
| 2020 | Fensfjorden | Autumn | 309     | 60 45.89 N | 005 12.82 E | 659       |
| 2021 | Masfjorden  | Autumn | 370     | 60 52.12 N | 005 22.03 E | 470       |
| 2021 | Fensfjorden | Autumn | 375     | 60 45.90 N | 005 12.82 E | 655       |

### 2.2.2. Sampling gear

Sampling was conducted using two gear types: Pelagic trawls and a MultiSampler. Pelagic trawls samples throughout the water column, while a MultiSampler is used to sample pelagic zone. Pelagic hauls without a MultiSampler are referred to as "Periphylla hauls" or "Deep pelagic trawl", and this gear is used to sample the deep pelagic as close to the seafloor as possible without risk of damaging the trawl, approximately 50-150 m above the seabed. Pelagic trawls often have openings that measure tens of meters in height and width with a towing speed of 2.5 – 3knots, the trawl is usually open throughout the entire trawling period and therefore sampled on the way up and down. Periphylla hauls were done at daytime (Table 3) and at nighttime (Table 4) for 15 - 30 minutes, these timings vary from year to year and between fjords, but it was ensured that they are within the sample time range.

A MultiSampler is a metal frame with three separate codends (20 mm mesh size) which can be opened and closed sequentially at designated depth intervals, either at fixed depth intervals (300-200 m, 200-100 m, 100-0 m) or echo layers (acoustic scattering layers). Samples collected with a MultiSampler were encoded as "T1", "T2", and "T3", where T1 is the deepest codend, and T3 is the shallowest.

### Table 3. overview of fishing time of daytime trawls

| Fjord      | Year | Month | Day.Or.Night | Starttime. | Endtime. | Fishing.Time.Min |
|------------|------|-------|--------------|------------|----------|------------------|
|            |      |       |              | Local      | Local    |                  |
| Masfjord   | 2012 | 10    | day          | 11:48:00   | 12:03:00 | 15               |
| Masfjord   | 2012 | 10    | day          | 13:09:00   | 13:24:00 | 15               |
| Masfjord   | 2012 | 10    | day          | 14:20:00   | 14:35:00 | 15               |
| Masfjord   | 2012 | 10    | day          | 15:26:00   | 15:41:00 | 15               |
| Masfjord   | 2012 | 10    | day          | 16:41:00   | 16:56:00 | 15               |
| Masfjord   | 2012 | 10    | day          | 17:31:00   | 17:46:00 | 15               |
| Masfjord   | 2014 | 10    | day          | 9:21:00    | 9:45:00  | 15               |
| Masfjord   | 2014 | 10    | day          | 10:47:00   | 11:19:00 | 15               |
| Masfjord   | 2014 | 10    | day          | 14:24:00   | 14:45:00 | 15               |
| Masfjord   | 2015 | 9     | day          | 10:35:00   | 11:05:00 | 30               |
| Masfjord   | 2015 | 9     | day          | 11:52:00   | 12:22:00 | 30               |
| Masfjord   | 2015 | 9     | day          | 12:21:00   | 12:58:00 | 37               |
| Masfjord   | 2016 | 9     | day          | 9:57:00    | 10:27:00 | 30               |
| Masfjord   | 2016 | 9     | day          | 11:31:00   | 12:01:00 | 30               |
| Masfjord   | 2017 | 10    | day          | 9:47:00    | 10:15:00 | 28               |
| Masfjord   | 2017 | 10    | day          | 11:21:00   | 11:48:00 | 27               |
| Masfjord   | 2019 | 10    | day          | 12:32:00   | 12:54:00 | 22               |
| Masfjord   | 2019 | 10    | day          | 15:15:00   | 15:35:00 | 20               |
| Masfjord   | 2019 | 10    | day          | 17:31:00   | 17:51:00 | 20               |
| Osterfjord | 2019 | 9     | day          | 10:01:00   | 10:15:00 | 14               |
| Osterfjord | 2019 | 9     | day          | 11:25:00   | 11:37:00 | 12               |
| Osterfjord | 2019 | 9     | day          | 12:43:00   | 12:54:00 | 11               |
| Fensfjord  | 2020 | 9     | day          | 8:51:00    | 9:11:00  | 20               |
| Fensfjord  | 2020 | 9     | day          | 10:20:00   | 10:30:00 | 10               |
| Fensfjord  | 2020 | 9     | day          | 15:03:00   | 15:13:00 | 10               |
| Masfjord   | 2020 | 9     | day          | 9:57:00    | 10:17:00 | 20               |
| Masfjord   | 2020 | 9     | day          | 11:25:00   | 11:45:00 | 20               |
| Masfjord   | 2020 | 9     | day          | 15:07:00   | 15:27:00 | 20               |
| Fensfjord  | 2021 | 9     | day          | 8:54:00    | 9:04:00  | 10               |
| Fensfjord  | 2021 | 9     | day          | 11:07:00   | 11:18:00 | 11               |
| Fensfjord  | 2021 | 9     | day          | 14:52:00   | 15:02:00 | 10               |
| Fensfjord  | 2021 | 9     | day          | 17:59:00   | 18:10:00 | 11               |
| Fensfjord  | 2021 | 2     | day          | 8:58:00    | 9:59:00  | 10               |
| Masfjord   | 2021 | 9     | day          | 9:20:00    | 9:31:00  | 11               |
| Masfjord   | 2021 | 9     | day          | 11:09:00   | 11:29:00 | 20               |
| Masfjord   | 2021 | 9     | day          | 12:26:00   | 12:37:00 | 11               |
| Masfjord   | 2021 | 2     | day          | 14:10:00   | 15:05:00 | 10               |
| Fensfjord  | 2022 | 9     | day          | 0:00:01    | 0:00:01  | 10               |
| Fensfjord  | 2022 | 9     | day          | 0:00:00    | 0:00:00  | 10               |
| Fensfjord  | 2022 | 5     | day          | 0:00:00    | 0:00:00  | 10               |
| Fensfjord  | 2022 | 5     | day          | 0:00:01    | 0:00:01  | 10               |
| Masfjord   | 2022 | 9     | day          | 0:00:01    | 0:00:01  | 10               |

| Masfjord   | 2022 | 9 | day | 0:00:01 | 0:00:01 | 10 |
|------------|------|---|-----|---------|---------|----|
| Masfjord   | 2022 | 9 | day | 0:00:00 | 0:00:00 | 10 |
| Masfjord   | 2022 | 9 | day | 0:00:00 | 0:00:00 | 10 |
| Masfjord   | 2022 | 5 | day | 0:00:01 | 0:00:01 | 10 |
| Masfjord   | 2022 | 5 | day | 0:00:01 | 0:00:01 | 10 |
| Masfjord   | 2022 | 5 | day | 0:00:01 | 0:00:01 | 10 |
| Masfjord   | 2022 | 5 | day | 0:00:00 | 0:00:00 | 11 |
| Osterfjord | 2022 | 5 | day | 0:00:01 | 0:00:01 | 10 |

Table 4. overview of fishing time of nighttime trawls

| Fjord      | Year | Month | Day.Or.Night | Starttime.<br>Local | Endtime.<br>Local | Fishing.Time.Min |
|------------|------|-------|--------------|---------------------|-------------------|------------------|
| Masfjord   | 2012 | 10    | night        | 21:41:00            | 21:56:00          | 15               |
| Masfjord   | 2012 | 10    | night        | 23:04:00            | 23:20:00          | 16               |
| Masfjord   | 2012 | 10    | night        | 0:38:00             | 0:53:00           | 15               |
| Masfjord   | 2012 | 10    | night        | 1:56:00             | 2:10:00           | 14               |
| Masfjord   | 2012 | 10    | night        | 3:13:00             | 3:27:00           | 14               |
| Masfjord   | 2012 | 10    | night        | 4:19:00             | 4:35:00           | 16               |
| Masfjord   | 2012 | 10    | night        | 19:48:00            | 20:03:00          | 15               |
| Masfjord   | 2012 | 10    | night        | 21:06:00            | 21:22:00          | 16               |
| Masfjord   | 2012 | 10    | night        | 22:13:00            | 22:28:00          | 15               |
| Masfjord   | 2014 | 10    | night        | 4:36:00             | 5:00:00           | 15               |
| Masfjord   | 2014 | 10    | night        | 20:10:00            | 20:29:00          | 15               |
| Masfjord   | 2014 | 10    | night        | 0:19:00             | 0:29:00           | 15               |
| Masfjord   | 2015 | 9     | night        | 20:50:00            | 21:22:00          | 32               |
| Masfjord   | 2015 | 9     | night        | 0:33:00             | 0:52:00           | 19               |
| Masfjord   | 2015 | 9     | night        | 1:58:00             | 2:22:00           | 24               |
| Masfjord   | 2016 | 9     | night        | 21:09:00            | 21:39:00          | 30               |
| Masfjord   | 2016 | 9     | night        | 22:35:00            | 23:05:00          | 30               |
| Masfjord   | 2017 | 10    | night        | 22:50:00            | 23:15:00          | 25               |
| Masfjord   | 2017 | 10    | night        | 0:34:00             | 1:02:00           | 28               |
| Masfjord   | 2018 | 10    | night        | 21:01:00            | 21:18:00          | 17               |
| Masfjord   | 2019 | 10    | night        | 21:06:00            | 21:27:00          | 21               |
| Masfjord   | 2019 | 10    | night        | 22:40:00            | 23:00:00          | 20               |
| Masfjord   | 2019 | 10    | night        | 1:08:00             | 1:28:00           | 20               |
| Osterfjord | 2019 | 9     | night        | 23:27:00            | 23:38:00          | 11               |
| Osterfjord | 2019 | 9     | night        | 1:02:00             | 1:16:00           | 14               |
| Osterfjord | 2019 | 9     | night        | 3:18:00             | 3:58:00           | 40               |
| Fensfjord  | 2020 | 9     | night        | 20:49:00            | 21:09:00          | 20               |
| Fensfjord  | 2020 | 9     | night        | 22:16:00            | 22:36:00          | 20               |
| Fensfjord  | 2020 | 9     | night        | 0:19:00             | 0:29:00           | 10               |
| Masfjord   | 2020 | 9     | night        | 21:52:00            | 22:12:00          | 20               |
| Masfjord   | 2020 | 9     | night        | 23:20:00            | 23:40:00          | 20               |

| Masfjord  | 2020 | 9 | night | 4:54:00  | 5:14:00  | 20 |
|-----------|------|---|-------|----------|----------|----|
| Masfjord  | 2020 | 6 | night | 23:52:00 | 0:12:00  | 20 |
| Fensfjord | 2021 | 2 | night | 19:05:00 | 20:06:00 | 10 |
| Masfjord  | 2021 | 9 | night | 1:52:00  | 2:13:00  | 21 |
| Masfjord  | 2021 | 9 | night | 4:20:00  | 4:32:00  | 12 |
| Masfjord  | 2021 | 2 | night | 19:05:00 | 20:04:00 | 10 |
| Fensfjord | 2022 | 9 | night | 0:00:01  | 0:00:01  | 10 |
| Fensfjord | 2022 | 9 | night | 0:00:01  | 0:00:01  | 10 |
| Fensfjord | 2022 | 9 | night | 0:00:01  | 0:00:01  | 10 |
| Fensfjord | 2022 | 5 | night | 0:00:01  | 0:00:01  | 8  |
| Masfjord  | 2022 | 9 | night | 0:00:01  | 0:00:00  | 10 |
| Masfjord  | 2022 | 5 | night | 0:00:00  | 0:00:00  | 10 |
| Masfjord  | 2022 | 5 | night | 0:00:00  | 0:00:00  | 11 |

### 2.2.3. Sorting of samples and subsampling

### Pelagic trawl sampling

After the pelagic trawl was hauled onto the deck, the samples were sorted by; (1) selecting the big fishes, big periphylla medusae and other big jellies. (2) The contents of each bucket were weighed, and the figures written on the catch recording form. The total sum of all the buckets is the "total catch weight". (3) The remaining small species samples were collected in a single bucket named "mixed catch". This is the total catch weight minus the weight of the big fish and jellyfish (i.e., Mixed catch (g) = Total catch weight (g) – weight of big fish and jellies (g)). For mixed catch that weighs more than 1 kilogram, a random subsample of about 1000 grams from the well mixed organisms was taken. (4) The subsample was weighed and recorded as "subsample weight", the subsamples were sorted into different species/organism. Individual periphylla in the subsample portion was weighed, and the size of and the coronal width of each specimen measured to the nearest millimeters.

The periphylla were counted to 100 hundred individuals, weighed and length measured but instances where the individuals present in the subsamples were less than 100 all the individuals were weighed, and length measured.

The coronal width of *Periphylla periphylla* was measured on board by measuring the diameter of the medusae bell from one side of the bell to the other (figure 3), this measurement was done to the nearest millimeter.



Figure 3. Diagram showing the defining of measurement of Periphylla periphylla (Fossa, 1992).

### Depth Stratified sampling

This is the sample collected using a MultiSampler gear at a fixed depth range. The procedures are the same as the sorting of samples in the pelagic trawl, but each depth stratum was processed separately.

### 2.3. Data analysis

### 2.3.1. Distribution

To standardize the abundance indices, Catch Per Unit Effort (CPUE) was calculated for each haul in the various sampling methods.

$$CPUE = \frac{C(g)}{t(min)} \tag{1}$$

CPUE was calculated using trawling time in minutes (t) and total number of individuals caught in the respective haul (C) (Gremillet 1997). C was divided by the trawling time (min) to get the catch per minute (Equation 1).

### 2.3.2. Statistical analysis

All statistical analyses were performed using R statistical software version 4.2.1 (2022-06-23 ucrt), using the packages tidyverse (Wickham et al. 2019), ggplot2 (Wickham 2016).

# 3. Result

## 3.1. Hydrographic data

## 3.1.1. Oxygen level

Time series of the dissolved oxygen recorded in Masfjorden between 2011 - 2021 (Figure 4) revealed decline in dissolved oxygen concentration from 2014 - 2018. The dissolved oxygen level recorded in the fjord varied between 3 - 6 ml l<sup>-1</sup> throughout the water column, between 2017 - 2018 the dissolved oxygen level dropped to hypoxic level of < 2 ml l<sup>-1</sup> between 300 m - 500 m depth (Pitcher et al., 2021). The fjord however experienced a reoxygenation, and the dissolved oxygen level was 4 ml l<sup>-1</sup> between 100 m - 400 m depth (Figure 4).



Figure 4. Contour plot showing the depth profile in Masfjorden showing oxygen levels (ml  $l^1$ ), between 2011 – 2021 (Autumn).

Dissolved oxygen records from Fensfjorden in 2020 – 2021 shows that the fjord was well oxygenated from surface to seabed in both years, the oxygen level was  $\sim 6$  ml l<sup>-1</sup> (Figure 5).



Figure 5. Depth profile in Masfjorden and Fensfjorden showing oxygen levels (ml  $l^1$ ), in 2020 and 2021 (Autumn). Fensfjorden is red while Masfjorden is blue.

## 3.1.2. Temperature

The time series of Temperature of Masfjorden from 2011 to 2021 reveals a uniform trend, the temperature varied from  $13^{\circ}$ C to  $9^{\circ}$ C in the first 70 m depth (Figure 6). The temperature then dropped to  $8^{\circ}$ C at ~75 m – 500 m depth (Figure 6).



Figure 6. Contour plot showing temperature ( $^{\circ}C$ ) of depth in Masfjorden from 2011 to 2022 (Autumn).

In Fensfjorden, the temperature ( $^{0}$ C) recorded for Masfjorden and Fensfjorden in 2021 and 2021 are similar, the temperate varied from  $15^{0}$ C –  $8^{0}$ C from the surface water to about 75 m depth in Masfjorden in both years and ~ $15^{0}$ C - ~ $7^{0}$ C between surface to ~70 m depth in Fensfjorden (Figure 7). The basin water (water below the sill depth) ~75 m – 500 m depth is a little warmer in Masfjorden than in Fensfjorden (Figure 7).





Figure 7. Depth profile in Masfjorden and Fensfjorden showing Temperature measurement (<sup>0</sup>C), in 2020 and 2021 (Autumn). Fensfjorden is red while Masfjorden is blue.

### 3.1.3. Salinity

The lowest salinity reading was recorded on the surface water of about 20 PSU which then rapidly increased to 32 PSU in the first 20 m, then about 34 PSU from approximately 70 m 400 depth (Figure 8). The basin water below the sill recorded a uniform temperature as well as salinity, which is an indication that the water below the sill is filled with Norwegian coastal waters.



*Figure 8. Contour plot showing salinity (PSU) as a function of depth in Masfjorden from 2011 to 2022 (Autumn).* 

The salinity concentration in Masfjorden and Fensfjorden between 2020 - 2021 is almost the same. The salinity varied from ~25 PSU t0 ~35 PSU from about 50 m - 500 m depth in both fjords (Figure 9).



*Figure 9. Salinity (PSU) as a function of depth in two different fjords, Masfjorden and Fensfjorden from 2020 – 2021 (Autumn). Fensfjorden is red while Masfjorden is blue.* 

The vertical profile of the Masfjorden and Fensjorden in 2020 and 2021(Autumn) revealed the same trend in the Temperature and salinity readings indicating that both fjords' basins contain coastal waters in depth below their sill depth and are both stratified.

## 3.2. Distribution

## 3.2.1. Changes in biomass of Periphylla periphylla in Masfjorden

The abundance of *Periphylla periphylla* in Masfjorden was calculated based on the catch per unit effort measured in g/min of periphylla caught over a period of 11 years (Figures 10 & 11). The time series revealed an increase trend in biomass over the years. The boxplot showed a statistical illustration of the mean, median, and level of dispersal of periphylla caught per minute.



Figure 10. Catch per unit effort/biomass of Periphylla periphylla caught in Masfjorden from 2012 to 2022 at a fixed depth range, (a) fixed depth range (T1 = 300-200 m, T2 = 200-100 m, T3 = 100-0 m). The black dot in the plot is the mean biomass of periphylla, the red is night trawl sample while blue is the day trawl sample.



Figure 11. Catch per unit effort/biomass of Periphylla periphylla caught in Masfjorden from 2012 to 2022 using periphyla haul. The biomass was measured in g/min on the y-axis and the years on the x-axis. The black dot in the plot is the mean biomass of periphylla, the red is night trawl sample while blue is the day trawl sample.

The periphylla haul samples and the fixed depth range samples show the same trend, there was an increase in periphylla biomass from 2018 to 2022(Figures 10 & 11). A glance at the plot

revealed that the presence of *Periphylla periphylla* in Masfjorden has increased over the years going by the increase in biomass (Figure 10 & 11).

## 3.2.2. Changes in biomass of Periphylla periphylla in Fensfjorden

Samples collected at Fesfjorden using a pelagic haul and a MultiSample between 2020 – 2022 revealed an increase trend in the biomass of Periphylla over the years, with no significant difference in the day and night hauls (Figures 12 & 13).



Figure 12. Catch per unit effort/biomass of periphylla periphylla caught in Fensfjorden from 2020 to 2022 from the fixed depth stratum data (T1 = 300-200 m, T2 = 200-100 m, T3 = 100-0 m). The black dot in the plot is the mean biomass of periphylla, the red is night trawl sample while blue is the day trawl sample.

Surprisingly, in 2022 we observed unusual trend were the biomass of periphylla recorded for the day trawls for pelagic haul and the multiSampler showed biomass higher than the night trawls.



Figure 13. Catch per unit effort/biomass of Periphylla periphylla caught in Fensfjorden from 2020 to 2022 using periphylla haul. The black dot in the plot is the mean biomass of periphylla, the red is night trawl sample while blue is the day trawl sample.



Figure 14. Catch per unit effort / biomass(g/min) of Periphylla periphylla caught in Masfjorden with a priphylla haul from 2012 to 2022. This represents the biomass over the years using a linear model.

The regression plot above further revealed the change in the biomass of periphylla over the years. The fjord experiences an increasing trend between 2018 – 2022 (Figure 14).

## 3.2.3. Size Distribution of Periphylla periphylla Masfjorden

The Size distribution (Figure 15) of *Periphylla periphylla* is based on the subsample of periphylla caught and measured during cruises between 2020 – 2022 in Masfjorden using a periphylla haul, the organisms were sampled throughout the water column in the fjord.

The plot revealed more than one cohort in the population, the smallest individual in the smallest cohort has a coronal diameter of  $\sim$ 10 mm while the largest individual in bigger cohort measured  $\sim$ 300 mm in coronal diameter (Figure 15).





Figure 15. Length distribution of individuals caught at night versus individuals caught during the day at Masfjorden from 2020 – 2022 with a periphylla haul. The coronal diameter is measured in mm (Length mm) on the x-axis and the number of individuals by count on the y-axis, in both day and night trawls.

The plot revealed three size peaks which represent cohorts of periphylla present in the fjord, the cohort grow as the number of larger individuals in the population increases from year to year (Figure 15).

3.2.4. Size Distribution of Periphylla periphylla Fensfjorden



Figure 16. Length distribution of individuals caught at night versus individuals caught at daytime in Fensfjorden from 2020 – 2022 with a periphylla haul. The coronal diameter length is measured in mm on the x-axis and the number of individuals by count on the y-axis, the count represents the number of individuals in a subsample measured.

The length distribution (Figure 16) of *Periphylla periphylla* is based on the periphylla that were caught and measured during cruises from 2020 - 2022 in Fensfjorden (not all periphylla caught were length measured), this revealed that there are different cohort in the population of periphylla in Fensfjorden. In 2020, data revealed that the population has several size classes varying from <50 mm – 200 mm, both the night and day trawl data showed a similar trend. Only day trawl data was recorded for 2021, this data also follows the same trend as 2020 data with a high number of individuals recorded for 0 mm-50 mm cohort and the lowest number of individuals recorded for 150 mm - >200 mm cohort. 2022 data has individuals from all the cohorts with fewer number of individuals in the cohort as compared to the previous year in both the night and day trawl data.





Figure 17. Length distribution of individuals caught at night versus individuals caught during the day at Masfjorden from 2020 - 2022 using multiSample with three codends((T1 = 300-200 m, T2 = 200-100 m, T3 = 100-0 m),). The coronal diameter length is measured in mm on the x-axis and the number of individuals by count on the y-axis.

The length distribution (Figure 17) of *Periphylla periphylla* is based on the periphylla that were caught and measured during cruises from 2020 - 2022 in Masfjorden using multisampler trawl. The data revealed different size classes, 2020 trawl data showed three different cohorts. The data shows three cohorts between depth range 300 - 200 m between 2020 - 2022, while depth range 200 - 100 shows sparse population in 2020, a cohort in 2021 and more population in 2022 with two distinct cohorts. There is an increase in the number of larger individuals present in the population thereby causing the cohort to grow (Figure 17).



Figure 18. Length distribution of individuals caught at night versus individuals caught during the day at Fensfjorden from 2020 - 2022 using multisample with three codends (T1 = 300-200 m, T2 = 200-100 m, T3 = 100-0 m). The coronal diameter length is measured in mm on the x-axis and the number of individuals by count on the y-axis.

The length distribution of periphylla in Fensfjord were measured from multisampler trawl samples from year consecutive years (Figure 18). 2020 data revealed several cohorts were

represented in all the samples taken from the three codends, majority of the individuals measured were from periphylla samples from the night trawl, and the distribution shows high populations of young periphylla with a coronal diameter range of 0 mm - < 50mm with the lowest population in the size class 80 mm - 100 mm and >200 mm. 2021 showed more varied distribution with the highest population of younger individuals recorded in the depth range 100 - 0 m and a scanty population recorded between 50 mm - 160 mm in the 300 - 200 m depth range.

In 2022, ILength measurement was taken from only night trawls (Figure 18), the coronal diameter measured in the trawl sample of 2022 indicated scanty distribution in the 300 – 200 m depth range, with few individuals represented in all the size classes, 200 – 100 m depth range showed more even distribution, and all size classes represented the younger population with the highest number of individuals, samples were recorded from only night trawl in 2022. The length distribution data for Fensfjorden revealed that there was more than one cohort in the periphylla population in the fjord.

# 4. Discussion

This study aims to investigate the change in size distribution and abundance of *Peripylla periphylla* in Masfjorden and Fensfjorden. Masfjorden and Fensfjorden are adjacent fjords with a shallow sill and stagnant basin, masfjorden has low oxygen concentration that lasted several years because of its shallow sill and low mixing of water below the sill (Aksnes, Aure, Johansen, Johnsen, & Salvanes, 2019). This study is based on a time series data collected over a decade to investigate the change in the abundance and size distribution of Periphylla in the last decade and to look at the hydrographic trend of the fjord.

Dense population of *Periphylla periphylla* have been reported in the Norwegian fjords during the last century (Fossa, 1992; Youngbluth & Bamstedt, 2001). Although several studies were done in Lurefjorden, 50km north of Bergen since 1992 to investigate its life cycle (Bamstedt et al., 2020;

Jarms et al., 1999) and its behavioral pattern in relation to light (Sornes et al., 2007). Our data revealed an increase trend in the biomass and size distribution of Periphylla in Masfjorden and Fensjorden which may suggest that these two fjords provide suitable habitat for this tactile organism as suggested by Fossa (1992) that periphylla are most successful in some fjords because of its stable ocean-like environment, shallow sill depth, deep basin water and very low food competition, contribute to the success of periphylla.

#### Biomass:

In Masfjorden, our data revealed increasing trend in the biomass of periphylla over the years, the increase was from 2018 to 2022 with no significant difference in the day and night data. We however observed in our stratified depth data i.e fixed depth range that periphylla seems to be distributed throughout the water column during the day and at night. We however suggest that it may be as a result of the fact that samples were collected between depth ranges (i.e. 300-200 m, 200-100m, 100-0m depth).

In Fensfjorden, the data obtained from the sampling method showed a positive trend in the periphylla biomass from 2020 to 2022. The biomass recorded follows the same trend as that of Masfjorden with higher night catches. However, a negative trend was observed in 2022 where the day trawl data was much higher than the night trawl data, this observation is strange and we are uncertain about this unusual trend as periphylla is negatively phototactic and tend to move into deep waters at the onset of daylight (Youngbluth & Bamstedt, 2001). Fensfjorden is an adjacent fjord to Masfjorden and both are influenced by the influx of the Norwegian coastal water, the NCW has high dissolved organic matter which is one of the factors influencing the darkening of the fjord water thereby enhancing light attenuation (Sornes & Aksnes, 2006; Sornes et al., 2007). We cannot say that this is the situation in this case as our study is not focused on investigating the rate of light absorbance in both fjords to corroborate the possibility of the darkening of the water of Fensfjorden at the time of the survey, more data is required to further confirm the reason for the negative trend noted in Fensfjorden in 2022.

#### Length distribution:

The actual population biomass reflects the overall effect of recruitment and growth over a period. Our result showed the presence of different size classes in both Masfjorden and Fensfjorden during the review period (2020 – 2022). Our length size measurement was based on subsamples of periphylla caught using the two-sampling gear (MultiSampler and the periphylla haul), this is not a total representation of all periphylla caught during the survey.

In Masfjorden, our result revealed that more than two size classes were represented from 10mm to 300mm for individuals caught with periphylla haul. There was a trend in the size classes from year to year, there were new cohorts every year and the population size increased from year to year. The MultiSampler data also shows the same trend at all fixed depth ranges but with sparse population when compared with the periphylla haul data.

In Fensfjorden, our results show that more than one size class was present in the fjord just like in Masfjorden. Individuals caught with periphylla haul in 2020 have more population than the ones recorded for subsequent years, no night trawl data for periphylla haul in 2021. The same trend was observed for the length measurement result for the Multisampler haul but with very sparse population, there was however no data for night trawl in 2021.

Our result on the length distribution in both Masfjorden and Fensfjorden suggest that periphylla has a continuous population in both fjords, and it also indicates that there is a continuous recruitment as there are representation of almost all size classes between 10mm to about 300mm. A study by Jarms et. al., (1999); Youngbluth and Bamstedt, (2001) confirms that the maintenance and abundance of periphylla in the Norwegian fjords is because of its continuous spawning, high longevity, and it very low mortality rate.

#### Low oxygen tolerance:

Low catches of periphylla were observed in Masfjorden until 2017, an increase in catches from 2018 to 2022. Deoxygenation is one of the factors that affect mesopelagic and benthic habitats in the fjords, these are dysphotic zones in most fjord that has light only sufficient for some visual predators (Aksnes et al., 2019). Masfjorden experienced deoxygenation between 2014-2016 where the dissolved oxygen concentration was declined from 3ml l<sup>-1</sup> to 2ml l<sup>-1</sup> between 300m depth to the seabed, and it became hypoxic between 2017 and 2018 when the dissolved oxygen concentration between 2017 and 2018 when the dissolved oxygen the following years. According to our data, deoxygenated water at these depths could explain the

increased presence of periphylla in Masfjorden from 2018 to 2022, since some studies have shown that mesopelagic hypoxic waters have high rate of light attenuation (Aksnes et al., 2019; Kaartvedt, Langbehn, & Aksnes, 2019). Periphylla is negatively phototactic, it prefers deep dark waters of the fjords, which are typically low in oxygen, the low oxygen consumption of periphylla is an indication that it can survive on relatively low energy intake (Youngbluth & Bamstedt, 2001). We can thus hypothesize that hypoxia has no impact on the distribution or abundance of *Periphylla periphylla* in Masfjorden in accordance with what is presented in our result.

Comparing the oxygen concentration in relation to depth in Masfjorden and Fensfjorden shows that both fjords have a similar trend of increasing biomass of periphylla from 2020 to 2022. Fensfjorden is well oxygenated during the period of review (we are looking at data from 2020 to 2022) despite the two fjords been adjacent fjords. Our result further corroborate the fact that hypoxic condition has no effect or impact on the abundance and distribution of periphylla in the fjord basin because they are tactile organisms that are adapted to life in the dark and can survive under low oxygen levels (Youngbluth & Bamstedt, 2001).

# 5. Limitations

Pelagic trawls (MultiSampler) Samples of *Periphylla periphylla* was conducted in Masfjorden between 2011 – 2022, but only length measurement from 2020 – 2022 were available for analysis. In Fensfjorden, sampled data available was from 2018 to 2022 while only 2020 – 2022 length measurement data were available.

Our biomass, and hydrographical result for Masfjorden were analyzed from 2011 – 2022, while Fensfjorden biomass result was analyzed from 2018 to 2022, CTD data from 2020 – 202` and the length distribution result was from 2020 – 2022. This created a limitation for us as we are unbale to compare results from Masfjorden and Fensfjorden over the same period to give a clear understanding of the distribution and abundance of Periphylla periphylla in both fjords.

There was not enough length distribution data to thoroughly investigate the year class and distribution of periphylla in both fjords as some data were reported missing. There was no night

length distribution data for both haul types in Masfjorden 2021, also no night data the Multisampler trawl in Fensfjorden 2021. Despite all these limitations we are still able to conclude that there is an increase trend in the abundance and population of Periphylla periphylla in both Masfjorden and Fensfjorden during the study period. Also, we are able to observe that low oxygen levels or hypoxic condition has no significant effect on the abundance and distribution of periphylla in Masfjorden

# 6. Conclusion

The overall conclusion is that *Periphylla periphylla* has a growing population in both Masfjorden and Fensfjorden with a well-established population. The environment condition in the two fjords is conducive for its recruitment and growth as this is the same for most western Norwegian fjords, because it provides stable habitat which is crucial for growth and development and there is no severe competition for food, predation, or parasitism. Lastly, this study pointed out the fact that deoxygenation or hypoxic conditions do not have any significant effects on the abundance or distribution of periphylla in Masfjorden

# 7. References

Aksnes, D. L., Aure, J., Johansen, P. O., Johnsen, G. H., & Salvanes, A. G. V. (2019). Multi-decadal warming of Atlantic water and associated decline of dissolved oxygen in a deep fjord. Estuarine Coastal and Shelf Science, 228. doi:10.1016/j.ecss.2019.106392

Aksnes, D. L., Dupont, N., Staby, A., Fiksen, O., Kaartvedt, S., & Aure, J. (2009). Coastal water darkening and implications for mesopelagic regime shifts in Norwegian fjords. Marine Ecology Progress Series, 387, 39-49. doi:10.3354/meps08120

Aksnes, D. L., et al. (2009). "Coastal water darkening and implications for mesopelagic regime shifts in Norwegian fjords." Marine Ecology Progress Series 387: 39-49.

Bamstedt, U., et al. (2020). "Fecundity and early life of the deep-water jellyfish Periphylla periphylla." Journal of Plankton Research 42(1): 87-101.

Bamstedt, U., Sotje, I., Tiemann, H., & Martinussen, M. B. (2020). Fecundity and early life of the deep-water jellyfish Periphylla periphylla. Journal of Plankton Research, 42(1), 87-101. doi:10.1093/plankt/fbz076

Fossa, J. H. (1992). MASS OCCURRENCE OF PERIPHYLLA-PERIPHYLLA (SCYPHOZOA, CORONATAE) IN A NORWEGIAN FJORD. Sarsia, 77(3-4), 237-251. Retrieved from <Go to ISI>://WOS:A1992KG43200007

Geoffroy, M., Berge, J., Majaneva, S., Johnsen, G., Langbehn, T. J., Cottier, F., . . . Last, K. (2018). Increased occurrence of the jellyfish Periphylla periphylla in the European high Arctic. Polar Biology, 41(12), 2615-2619. doi:10.1007/s00300-018-2368-4

ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. Wickham, H., M. Averick, J. Bryan, W. Chang, L. McGowan, R. François, G. Grolemund, A. Hayes, L. Henry, J. Hester, M. Kuhn, T. Pedersen, E. Miller, S. Bache, E. Muller, J. Ooms, D. Robinson, D. Seidel, V. Spinu, K. Takahashi, D. Vaughan, C. Wilke, K. Woo, and H. Yutani. 2019. Welcome to the tidyverse. Journal of Open Source Software.

Gremillet, D. 1997. Catch per unit effort, foraging efficiency, and parental investment in breeding great cormorants (Phalacrocorax carbo carbo). ICES Journal of Marine Science 54:635-644.

Herring, P. J. (1972). "porphyrin pigmentation in deep-sea medusae." Nature 238(5362): 276-&. doi:10.1038/238276a0

Jarms, G., Bamstedt, U., Tiemann, H., Martinussen, M. B., & Fossa, J. H. (1999). The holopelagic life cycle of the deep-sea medusa Periphylla periphylla (Scyphozoa, Coronatae). Sarsia, 84(1), 55-65. doi:10.1080/00364827.1999.10420451

Jarms, G., Tiemann, H., & Bamstedt, U. (2002). Development and biology of Periphylla periphylla (Scyphozoa : Coronatae) in a Norwegian fjord. Marine Biology, 141(4), 647-657. doi:10.1007/s00227-002-0858-x

Kaartvedt, S., et al. (2011). "Beyond the average: Diverse individual migration patterns in a population of mesopelagic jellyfish." Limnology and Oceanography 56(6): 2189-2199.

Kaartvedt, S., Klevjer, T. A., Torgersen, T., Sornes, T. A., & Rostad, A. (2007). Diel vertical migration of individual jellyfish (Periphylla periphylla). Limnology and Oceanography, 52(3), 975-983. doi:10.4319/lo.2007.52.3.0975

Kaartvedt, S., Titelman, J., Rostad, A., & Klevjer, T. A. (2011). Beyond the average: Diverse individual migration patterns in a population of mesopelagic jellyfish. Limnology and Oceanography, 56(6), 2189-2199. doi:10.4319/lo.2011.56.6.2189

Péron F. & Lesueur C.A. (1810). Tableau des caractères génériques et spécifiques de toutes les espèces de méduses connues jusqu'à ce jour. Annales du Muséum national d'histoire naturelle de Paris. 14: 325-366., available online at https://www.biodiversitylibrary.org/page/3498981

Pitcher, G. C., Aguirre-Velarde, A., Breitburg, D., Cardich, J., Carstensen, J., Conley, D. J., . . . Zhu, Z. Y. (2021). System controls of coastal and open ocean oxygen depletion. Progress in Oceanography, 197. doi:10.1016/j.pocean.2021.102613

Purcell, J. E., Uye, S., & Lo, W. T. (2007). Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. Marine Ecology Progress Series, 350, 153-174. doi:10.3354/meps07093

Purcell JE, Arai MN (2001) Interactions of pelagic cnidarians and ctenophores with fish: a review. Hydrobiol 451:27–44.

R Development Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Russell, F.S. 1970. The medusae of the British Isles. II. Pelagic Scyphozoa with a supplement to the firstvolume on Hydromedusae. - Cambridge University Press, London. 284 pp.

Salvanes, A. G. V., Aksnes, D. L., & Giske, J. (1992). ECOSYSTEM MODEL FOR EVALUATING POTENTIAL COD PRODUCTION IN A WEST NORWEGIAN FJORD. Marine Ecology Progress Series, 90(1), 9-22. doi:10.3354/meps090009

Salvanes, A. G. V., et al. (1992). "Ecosystem model for evaluating potential cod production in a west norwegian fjord." Marine Ecology Progress Series 90(1): 9-22.

Salvanes, Anne Gro Vea & Jaru Tryti Nordeide 1993 12 30. Dominating sublittoral fish species in a west Norwegian fjord and their trophic links to cod (Gadus morhua L.) - Sarsia 78:221-234. Bergen. ISSN. 0036-4827.

Sornes, T. A., & Aksnes, D. L. (2006). Concurrent temporal patterns in light absorbance and fish abundance. Marine Ecology Progress Series, 325, 181-186. doi:10.3354/meps325181

Sornes, T. A., Aksnes, D. L., Bamstedt, U., & Youngbluth, M. J. (2007). Causes for mass occurrences of the jellyfish Periphylla periphylla: a hypothesis that involves optically conditioned retention. Journal of Plankton Research, 29(2), 157-167. doi:10.1093/plankt/fbm003

Sornes, T. A., et al. (2007). "Causes for mass occurrences of the jellyfish Periphylla periphylla: a hypothesis that involves optically conditioned retention." Journal of Plankton Research 29(2): 157-167.

Sornes, T. A., et al. (2008). "Swimming and feeding in Periphylla periphylla (Scyphozoa, Coronatae)." Marine Biology 153(4): 653-659.

Sornes, T. A., Hosia, A., Bamstedt, U., & Aksnes, D. L. (2008). Swimming and feeding in Periphylla periphylla (Scyphozoa, Coronatae). Marine Biology, 153(4), 653-659. doi:10.1007/s00227-007-0839-1

Sotje, I., Tiemann, H., & Bamstedt, U. (2007). Trophic ecology and the related functional morphology of the deepwater medusa Periphylla periphylla (Scyphozoa, Coronata). Marine Biology, 150(3), 329-343. doi:10.1007/s00227-006-0369-2

Syvitski, J.P., Burrell, D.C., Skei, J.M., 1987. Fjords: Processes and Products. Springer, New York, pp. 377pp

Tiemann, H., et al. (2009). "Documentation of potential courtship-behaviour in Periphylla periphylla (Cnidaria: Scyphozoa)." Journal of the Marine Biological Association of the United Kingdom 89(1): 63-66.

Tiemann, H., Sotje, I., Johnston, B. D., Flood, P. R., & Bamstedt, U. (2009). Documentation of potential courtship-behaviour in Periphylla periphylla (Cnidaria: Scyphozoa). Journal of the Marine Biological Association of the United Kingdom, 89(1), 63-66. doi:10.1017/s0025315408001264

Ugland, K. I., Aksnes, D. L., Klevjer, T. A., Titelman, J., & Kaartvedt, S. (2014). Levy night flights by the jellyfish Periphylla periphylla. Marine Ecology Progress Series, 513, 121-130. doi:10.3354/meps10942

Ugland, K. I., et al. (2014). "Levy night flights by the jellyfish Periphylla periphylla." Marine Ecology Progress Series 513: 121-130.

Youngbluth, M. J. and U. Bamstedt (2001). "Distribution, abundance, behavior and metabolism of Periphylla periphylla, a mesopelagic coronate medusa in a Norwegian fjord." Hydrobiologia 451(1-3): 321-333.

- Aksnes, D. L., Aure, J., Johansen, P. O., Johnsen, G. H., & Salvanes, A. G. V. (2019). Multi-decadal warming of Atlantic water and associated decline of dissolved oxygen in a deep fjord. *Estuarine Coastal and Shelf Science, 228*. doi:10.1016/j.ecss.2019.106392
- Aksnes, D. L., Dupont, N., Staby, A., Fiksen, O., Kaartvedt, S., & Aure, J. (2009). Coastal water darkening and implications for mesopelagic regime shifts in Norwegian fjords. *Marine Ecology Progress Series, 387*, 39-49. doi:10.3354/meps08120
- Bamstedt, U., Sotje, I., Tiemann, H., & Martinussen, M. B. (2020). Fecundity and early life of the deep-water jellyfish Periphylla periphylla. *Journal of Plankton Research*, *42*(1), 87-101. doi:10.1093/plankt/fbz076
- Fossa, J. H. (1992). MASS OCCURRENCE OF PERIPHYLLA-PERIPHYLLA (SCYPHOZOA, CORONATAE) IN A NORWEGIAN FJORD. *Sarsia*, *77*(3-4), 237-251. Retrieved from <Go to ISI>://WOS:A1992KG43200007
- Geoffroy, M., Berge, J., Majaneva, S., Johnsen, G., Langbehn, T. J., Cottier, F., . . . Last, K. (2018). Increased occurrence of the jellyfish Periphylla periphylla in the European high Arctic. *Polar Biology*, *41*(12), 2615-2619. doi:10.1007/s00300-018-2368-4
- Herring, P. J. (1972). PORPHYRIN PIGMENTATION IN DEEP-SEA MEDUSAE. *Nature, 238*(5362), 276-&. doi:10.1038/238276a0
- Jarms, G., Bamstedt, U., Tiemann, H., Martinussen, M. B., & Fossa, J. H. (1999). The holopelagic life cycle of the deep-sea medusa Periphylla periphylla (Scyphozoa, Coronatae). *Sarsia, 84*(1), 55-65. doi:10.1080/00364827.1999.10420451
- Jarms, G., Tiemann, H., & Bamstedt, U. (2002). Development and biology of Periphylla periphylla (Scyphozoa : Coronatae) in a Norwegian fjord. *Marine Biology*, 141(4), 647-657. doi:10.1007/s00227-002-0858-x
- Kaartvedt, S., Klevjer, T. A., Torgersen, T., Sornes, T. A., & Rostad, A. (2007). Diel vertical migration of individual jellyfish (Periphylla periphylla). *Limnology and Oceanography*, 52(3), 975-983. doi:10.4319/lo.2007.52.3.0975
- Kaartvedt, S., Titelman, J., Rostad, A., & Klevjer, T. A. (2011). Beyond the average: Diverse individual migration patterns in a population of mesopelagic jellyfish. *Limnology and Oceanography, 56*(6), 2189-2199. doi:10.4319/lo.2011.56.6.2189
- Pitcher, G. C., Aguirre-Velarde, A., Breitburg, D., Cardich, J., Carstensen, J., Conley, D. J., . . . Zhu, Z. Y. (2021). System controls of coastal and open ocean oxygen depletion. *Progress in Oceanography*, 197. doi:10.1016/j.pocean.2021.102613
- Purcell, J. E., Uye, S., & Lo, W. T. (2007). Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Marine Ecology Progress Series*, *350*, 153-174. doi:10.3354/meps07093
- Salvanes, A. G. V., Aksnes, D. L., & Giske, J. (1992). ECOSYSTEM MODEL FOR EVALUATING POTENTIAL COD PRODUCTION IN A WEST NORWEGIAN FJORD. *Marine Ecology Progress Series*, 90(1), 9-22. doi:10.3354/meps090009
- Sornes, T. A., & Aksnes, D. L. (2006). Concurrent temporal patterns in light absorbance and fish abundance. *Marine Ecology Progress Series, 325*, 181-186. doi:10.3354/meps325181
- Sornes, T. A., Aksnes, D. L., Bamstedt, U., & Youngbluth, M. J. (2007). Causes for mass occurrences of the jellyfish Periphylla periphylla: a hypothesis that involves optically conditioned retention. *Journal of Plankton Research*, 29(2), 157-167. doi:10.1093/plankt/fbm003
- Sornes, T. A., Hosia, A., Bamstedt, U., & Aksnes, D. L. (2008). Swimming and feeding in Periphylla periphylla (Scyphozoa, Coronatae). *Marine Biology*, 153(4), 653-659. doi:10.1007/s00227-007-0839-1
- Tiemann, H., Sotje, I., Johnston, B. D., Flood, P. R., & Bamstedt, U. (2009). Documentation of potential courtshipbehaviour in Periphylla periphylla (Cnidaria: Scyphozoa). *Journal of the Marine Biological Association of the United Kingdom, 89*(1), 63-66. doi:10.1017/s0025315408001264

Ugland, K. I., Aksnes, D. L., Klevjer, T. A., Titelman, J., & Kaartvedt, S. (2014). Levy night flights by the jellyfish Periphylla periphylla. *Marine Ecology Progress Series, 513*, 121-130. doi:10.3354/meps10942 Youngbluth, M. J., & Bamstedt, U. (2001). Distribution, abundance, behavior and metabolism of Periphylla periphylla, a mesopelagic coronate medusa in a Norwegian fjord. *Hydrobiologia, 451*(1-3), 321-333.

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