

Research paper

Murder in the dark: Can parasites bring jellyfish blooms to fall?

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Jellyfish form irregular and seemingly unpredictable blooms that can be the result of redistribution/aggregation events or peaks in population growth. Such blooms can affect ecosystem structure and stability due to the role of jellyfish as top predators of fish larvae and eggs and as competitors of fish preying on the same zooplankton resources. Factors leading to jellyfish bloom formation have received a lot of attention during the past decades. However, factors causing blooms to collapse are less studied. The helmet jellyfish *Periphylla periphylla* is a bloom-forming jellyfish species that shows mass occurrences in several Norwegian fjords with substantial socioeconomic implications. The success of *P. periphylla* to form massive blooms is attributed to its longevity, the lack of natural predators and its holoplanktonic life cycle with a continuous reproduction throughout the year. In Trondheimsfjorden, central Norway, *P. periphylla* has established large populations over the last decades. However, population estimates with a high spatiotemporal resolution are scarce and the regulating mechanisms affecting *P. periphylla* dynamics remain largely unknown. Using *in-situ* imaging techniques during pelagic dives with a remotely operated vehicle (ROV), enabled insights on the potential role of parasites as bloom-controllers. ROV footage provided unique information on high levels of prevalence and intensity of parasitic amphipods in *P. periphylla*. In parallel, these parasitic associations were documented by underwater photography in the same area and season. The combination of non-invasive imaging techniques allowed estimates on the degree of parasite infestation and on how parasitism can affect the condition of jellyfish populations thus eventually causing blooms to collapse. We suggest taking investigations on parasite-host interactions and the role of parasitism as a population control mechanism into the spotlight. Future research in this field will benefit from using non-invasive imaging tools to study parasite-host interactions and animal behaviour *in-situ*.

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INTRODUCTION

Blooms of jellyfish are phenomena that occur frequently, with potential substantial impacts on the community structure, functioning, and stability of marine ecosystems. Such blooms are either the result of population growth (true bloom), physical redistribution/aggregation of jellyfish specimens (apparent bloom), or the combination of both (Graham *et al.* 2001). The development of true blooms depends on the life cycle strategies of jellyfish with either one annual sexual reproduction event for species with a metagenic life cycle, or an opportunistic, continuous reproduction throughout the year for holoplanktonic species (Schnedler-Meyer *et al.* 2018). Factors promoting the formation of true blooms e.g. in relation to environmental conditions (e.g. temperature, prey availability, predation) have received much attention in the last decades (Lucas 2001, Schnedler-Meyer *et al.* 2018), while those causing blooms to collapse are less studied so far (Pitt *et al.* 2014).

The helmet jellyfish *Periphylla periphylla* (Péron & Lesueur, 1810) (Scyphozoa, Coronatae) has been frequently reported in deep Norwegian fjords such as Trondheimsfjorden, Sognefjorden, Halsafjorden and Lurefjorden from the early 1990 onwards, although specimens are documented in museum collections from almost 100 years back (Majaneva *et al.* 2023, Bakken *et al.* 2024). This jellyfish is considered a cosmopolitan species with a main distribution in the meso- and bathypelagic zones of the oceans (Arai 1997, Morita *et al.* 2017, GBIF.org 2022). In Norwegian fjords, *P. periphylla* occurs in much higher abundances than in the open ocean (Fosså 1992, Dalpadado *et al.* 1998, Jarms *et al.* 2002, Sornes *et al.* 2007, Tiller *et al.* 2017). Similarly to other large scyphozoan jellyfish, aspects related to life-history dynamics, reproductive success, behavior, and impacts on artisanal fisheries have been the focus of *P. periphylla* studies so far (Jarms *et al.* 2002, Kaartvedt *et al.* 2015, Bozman *et al.* 2017, Tiller *et al.* 2017, Bamstedt *et al.* 2020, Aberle *et al.* 2023). However, large uncertainties remain regarding the sources and sinks of *P. periphylla* blooms and the driving forces that affect its population dynamics leading to “boom and bust” events.

Among the factors that are likely to affect jellyfish population growth negatively is parasite infestation. In particular, parasitic arthropods have long been known to associate with bloom-forming jellyfish (Harbison *et al.* 1977, Laval 1980), but only few studies have discussed their role in bloom decline (Dittrich 1988, Mills 1993). Several crustacean taxa are known to associate with *P. periphylla* in the North Atlantic, including the pycnogonid *Bathypallenopsis scoparia* (Fage, 1956) (Child and Harbison 1986) and the hyperiid amphipods *Hyperoche medusarum* (Krøyer, 1838), *Hyperia spinigera*, Bovallius, 1889, and *Hyperia medusarum* (Müller, 1776) (Thurston 1977, Youngbluth and Bamstedt 2001, Borgersen 2013). Elsewhere in the world, the hyperiids *Cylopus magellanicus* Dana, 1853 and *Themisto quadrichaudii* Guérin, 1825 have also been recorded as *Periphylla* symbionts (Pages *et al.* 1996). While the exact nature and dynamics of these associations is still unclear, the relationship is considered detrimental to the host (Pages *et al.* 1996, Youngbluth and Bamstedt 2001, Borgersen 2013).

Whether parasite infestation could cause *P. periphylla* populations to collapse remains unknown. The uncertainty derives partly from methodological limitations that hinder the characterization of the ecological interactions of this species and its parasites. Today, most of our knowledge about trophic and symbiotic associations of jellyfish is based on observations from specimens collected with nets and trawls (Phillips and Levin 1973, Mauchline 1984, Pages *et al.* 1996, Youngbluth and Bamstedt 2001). However, predation and parasitism

are easily disrupted by trawling since predators and symbionts, particularly ectosymbionts, are prone to detaching and being lost or damaged during the sampling process. Submersible technologies and image-based surveys are suggested to improve our understanding of different interactions in the mesopelagic (Quattrini and Demopoulos 2016, Stenvers *et al.* 2022), but parasites and symbionts are yet not commonly included in studies on ecologically relevant gelatinous species. Thus, *in situ* documentation of intensity and prevalence of these associations is needed to critically evaluate the role of symbionts in the population dynamics of *P. periphylla* and other blooming jellyfish species.

Here, we provide a glimpse into the interactions between hyperiid amphipods and *P. periphylla* *in situ* thus demonstrating how parasites can affect jellyfish performance (e.g. swimming performance, tissue damage) with potential consequences on jellyfish mortality and bloom dynamics.

MATERIAL AND METHODS

Study area

The study sites were located in Trondheimsfjorden, Mid-Norway, in the relatively shallow sounds Verrasundet and Verrabotten that are connected to Beistadfjorden in the innermost part of Trondheimsfjorden (Figure 1). A list of deployments with the respectively geographic positions, date, depths, sampling gear and duration of deployment are given in Table 1.

Remotely operated vehicle (ROV) operations

Three deployments with the ROV MINERVA (Sperre, Akva Group) were conducted on 28–29 September 2021 (ROV Dive I–III). The ROV was equipped with a Sony FCB-SE600 full-HD camera system and a hydraulic Schilling Orion manipulator arm. Vertical transects from the uppermost surface layer to the bottom of the seafloor (101.5 m and 55.6 m in Verrasundet and Verrabotten, respectively) were performed with the ROV (Table 1) and each *P. periphylla* encounter was registered. In addition, size measurements of the medusae were performed with aid of the manipulator arm and a ruler.

Analyses of parasite infestations based on video footage

During ROV deployments, individual specimens were observed and videoed for several minutes to allow inspection for parasites from several perspectives. The number of parasitic amphipods on the tentacles and umbrella of individual *P. periphylla* specimens were estimated based on ROV video footage saved in MPG format. To obtain parasite estimates on the umbrella of individual *P. periphylla* specimens, screenshots from video footage of the same specimen were taken from different perspectives and saved as Bitmap (BMP) files (Microsoft Windows) to enable the counting of parasites.

Bottom trawling operations

Bottom trawling with a shrimp trawl (inner lining of fine mesh net, stretched 36 mm mesh size) in Verrabotten on 29 September 2021 provided abundance and biomass data for *P. periphylla*, and allowed physical inspection of individuals to account for damage caused by amphipods. For each specimen, the coronal diameter (CD, in cm) was measured, and the total biomass was quantified using volumetric measures (L) as an estimate for jellyfish biomass caught during trawling. The ‘catch-per-unit effort’ (CPUE) was calculated based on the volume of *P. periphylla* (L) caught during the entire trawl time

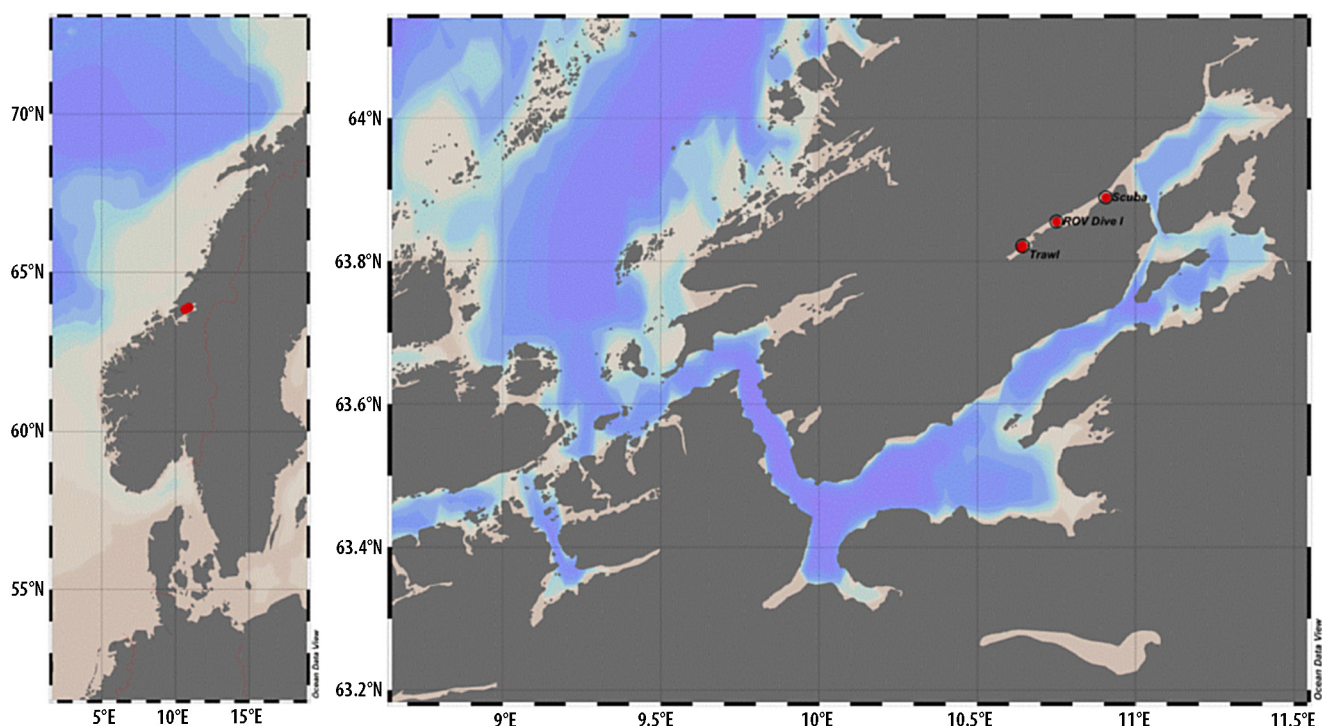


Figure 1. Map of Norway (left) with the sampling position in Trondheimsfjorden at 63°N (red dot), mid-Norway (left) and the deployment stations in Verrasundet and Verrabotten (red dots) in the innermost part of Trondheimsfjorden (right). The station marked as ‘Trawl’ overlaps with the positions of ROV Dive II and ROV Dive III.

Table 1. Location, gear type, date, geographic positions, depth and time of deployments in Verrasundet and Verrabotten, Trondheimsfjorden, Norway.

Location	Gear type	Date	Geographic positions		Max. depth (m)	Time of deployment (min.)
Verrasundet	Scuba	16.09.2021	N63°53.32'	E10°54.37'	35	-
	ROV Dive I	28.09.2021	N63°51.326'	E10°45.065'	107	63
Verrabotten	ROV Dive II	28.09.2021	N63°49.101'	E10°38.287'	63	67
	ROV Dive III	29.09.2021	N63°49.159'	E10°38.439'	57	59
	Trawl (start)	29.09.2021	N63°49.163'	E10°38.414'	60	-
	Trawl (end)	29.09.2021	N63°49.264'	E10°38.632'	60	7

(min). Sampling of amphipods from retrieved jellyfish specimens failed since the parasites were leaving their hosts during trawling procedure. This escape behaviour limited the taxonomic identification to species level of the amphipods and only assumptions can be made. Underwater photography observations and amphipod identification Since amphipods were not encountered on individuals of *P. periphylla* caught with the trawl, high quality underwater photography provided more detailed insights on the identity of the parasites and the damage caused by them during the same time of the year. Close-up images of *P. periphylla*, associated amphipods on the umbrella, and umbrella ruptures with released gastric filaments from the inside and attached parasites were taken during a scuba dive in Verrasundet (Trondheimsfjord, Norway) on 16 September 2021. Based on taxonomic criteria for amphipods (Zeidler 2004, Vinogradov *et al.* 1996), the following morphological characters were evaluated in the photographed specimens to identify them to the lowest possible taxonomic level: the shape and size of the head and eyes relative to the first pereon somite; the point of attachment and morphology of the antennae; the relative size and shape of the pereopods, including the presence of distinct chelae and carpal processes; and the presence of free rami on the uropods.

RESULTS

In total, 17 specimens of *P. periphylla* with an average CD of 11 cm (size range: 5–19 cm) were encountered in the water column of Verrasundet and Verrabotten during the three ROV deployments while additional specimens were observed decaying at the seafloor. Fourteen out of these specimens were observed in the water column were parasitized by amphipods (prevalence = 77%). The parasitized specimens were colonized by in mean nine amphipods located on the umbrella and tentacles (ranging between a minimum of 2 and a maximum of 34 amphipods per host) (Figure 2). All specimens encountered in the water column showed reduced performance in terms of swimming behaviour due to heavy damage of umbrella and tentacle tissue. Some specimens were damaged to such a high degree that gastric filaments were visible from outside and holes with several centimetres in diameter were observed in the umbrella (Figure 3).

A total of 1125 specimens of *P. periphylla* were caught with the trawl, with a CD ranging between 1.5 and 19.5 cm, an average wet weight of 251 g, a total wet weight of 282 kg, and a total volume of 498 L. A catch-per-unit effort of 71 L min⁻¹ was calculated. The trawling activity was part of a long-term sampling campaign of *P. periphylla* conducted at several stations in Trondheimsfjorden during the period

from 2006–2021 (Aberle *et al.* 2023).

The amphipods on the mesoglea and tentacles of *P. periphylla* were identified as *Hyperia* sp. based on the high-quality underwater pictures taken in Verrabotten/Verrasundet at the same time of the year (Figure 4). In all cases in which identification was possible, the specimens were unambiguously assigned to family Hyperiidae (Dana, 1852) based on the observed combination of large heads (longer than somite I of the pereon), large eyes occupying most of the head, free rami in the uropods, a simple structure of the fifth pereopod pair, and the presence of antennae 1 attached to the anterior surface of the head and lacking both a conspicuous basal special socket and an

enlarged first article followed by few rudimentary subsequent articles. Identification to genus level was possible in several photographed specimens because their images show non-prehensile pereopods 3 and 4 (no dilated carpus was observed) that are longer than pereopods 5 and 6, as well as pereopods 1 and 2 that lacked a long carpus projection (i.e. lacking the well-defined ‘claw’ that is commonly observed in *Hyperoche* spp. in Norwegian waters). While these characters suggest that the parasites belonged to genus *Hyperia*, a more detailed taxonomic identification to species level could not be achieved since species-specific characters were not visible on the images.



Figure 2. Screenshots from remote operated vehicle (ROV) video footage showing specimens of *Periphylla periphylla* with amphipods on umbrella and tentacles (white patterns) filmed during Dive I with ROV MINERVA in Verrasundet (Trondheimsfjorden, Norway) on 28 September 2021.



Figure 3. A, B) Two specimens of *Periphylla periphylla* with holes in umbrella, C) Close-up of gastric filaments on the inner side of a *P. periphylla* specimen. Pictures photo-documented from a trawl catch in Verrabotten (Trondheimsfjorden, Norway) on 29 September 2021. (Photos: Nicole Aberle-Malzahn).

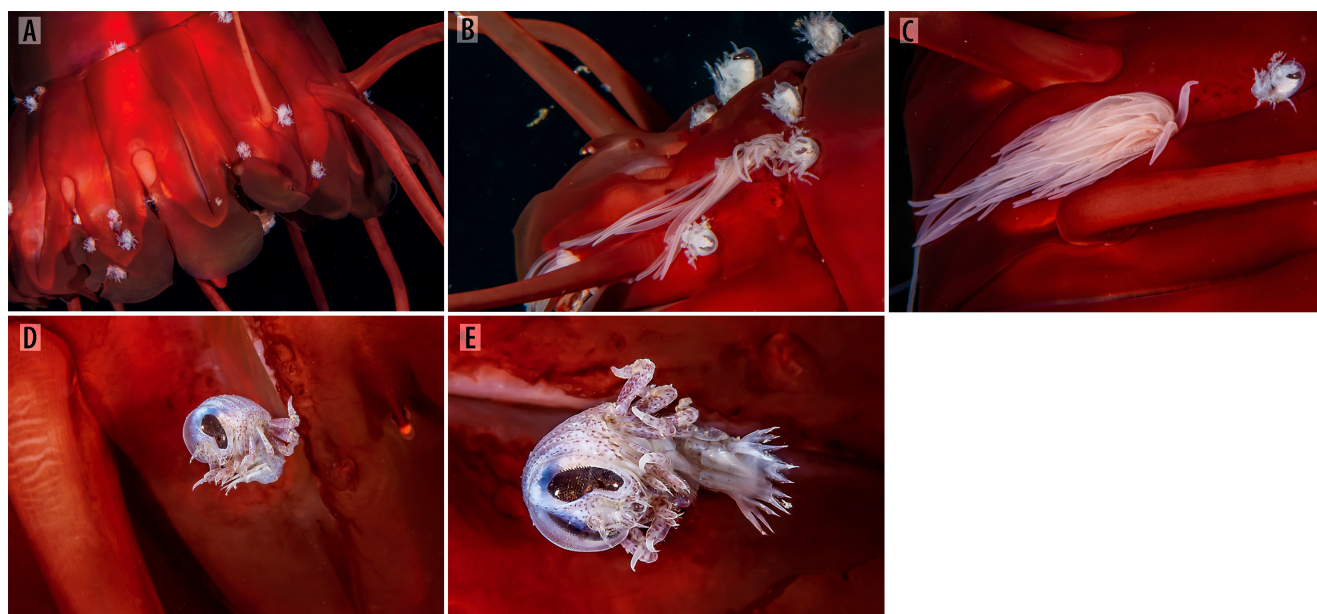


Figure 4. A) Several specimens of amphipods on the umbrella of *Periphylla periphylla* B) Several specimens of amphipods on the umbrella in the proximities of ruptures in the umbrella tissue visibly releasing gastric filaments from the inside and C) Close-up of ruptures and gastric filaments on the outer umbrella of *P. periphylla* together with a single *Hyperia* specimen. D, E) Close-ups of a single *Hyperia* specimen on the outer umbrella of *P. periphylla*. Pictures photo-documented in Verrasundet (Trondheimsfjorden, Norway) on 16 September 2021. (Photos: Erling Svensen).

DISCUSSION

Jellyfish bloom dynamics: Drivers & challenges

To understand the causes and consequences of jellyfish blooms and to allow for more reliable predictions on jellyfish population dynamics, it is crucial to identify the factors that drive bloom dynamics and lead to jellyfish bloom formation and subsequently to the collapse and decay of jellyfish blooms. The formation of jellyfish blooms is a natural phenomenon characterized by temporary and sudden population increases that usually last for shorter periods and collapse after days or weeks as a result from unfavourable environmental conditions and reduced health of the population due to e.g. food shortage or predation (Lucas and Dawson 2014). However, assessing jellyfish bloom dynamics *in situ* is challenging due to the sudden and regional nature of bloom onset and decay. So far, most studies assessing jellyfish bloom dynamics are based on snapshot observations documenting the occurrence of jellyfish at a certain location at a given time thus hindering more detailed analyses on the drivers of bloom dynamics. To overcome these challenges, more comprehensive datasets providing details on environmental parameters, the timing of species occurrence and the duration of blooms are needed (e.g. in the framework of monitoring programs, time-series data or citizen science observations) to allow more detailed analyses on jellyfish bloom dynamics with a

high spatiotemporal resolution.

When analysing jellyfish bloom dynamics, the focus is traditionally more on the drivers of bloom formation (Lucas *et al.* 2012, Duarte *et al.* 2013) rather than on the factors that cause blooms to collapse (Schneider-Meyer *et al.* 2018). So far, top-down control by apex predators (e.g., fish and sea turtles), food shortage, senescence after reproduction, and strandings caused by physical forcing have mainly been discussed as potential regulating factors of jellyfish populations (Pitt *et al.* 2014). However, the role of parasite infestation as a controlling factor of jellyfish blooms has received little attention.

Population dynamics of *P. periphylla* in Trondheimsfjorden

Specimens of *P. periphylla* are regularly observed in several deep Norwegian fjord ecosystems since the early 1990 where populations have established throughout the year showing usually higher abundances compared to open ocean populations (Fosså 1992, Dalpadado *et al.* 1998, Jarms *et al.* 2002, Sornes *et al.* 2007, Tiller *et al.* 2017). Based on long-term data, the density of *P. periphylla* shows considerable spatiotemporal and inter-annual variation in Trondheimsfjorden with a mean catch-per-unit effort (CPUE) of 149 *P. periphylla* L min⁻¹ in Verrabotten during the period from 2006–2021 and CPUEs ranging between a minimum of 2 (October 2006) and a maximum of 350 (June 2014) (Aberle *et al.* 2023). With a CPUE of

71 *P. periphylla* L min⁻¹ in Verrabotten on 29 September 2021, the population density assessed in this study was rather at a moderate level. Since this dataset is a compilation of snapshot observations from few sampling events at certain stations, this limits a proper analysis of the boom and bust dynamics of *P. periphylla* in Trondheimsfjorden over large spatiotemporal scales and hampers a detailed interpretation of the bloom status based on trawl data only. In this study, we performed underwater photography and ROV-deployments in concert with trawling activities thus providing additional underwater images and video footage that allowed detailed insights on bloom condition and jellyfish performance e.g. in relation to parasite infestation. To enhance our understanding, it is thus beneficial to combine field sampling with non-invasive imaging tools to obtain a more comprehensive picture on the factors affecting bloom dynamics.

Effects of parasite infestation on the seasonal dynamics of *P. periphylla*

Hyperiid amphipods are considered as particularly relevant jellyfish parasites since they are known to target a variety of gelatinous hosts including medusae, siphonophores, salps, and ctenophores (Gasca et al. 2007). The amphipods on the mesoglea and tentacles of *P. periphylla* were identified as *Hyperia* sp. Based on previous observations, *Hyperia galba* is considered one of the most common hyperiid amphipods on a variety of gelatinous zooplankton species (Dittrich 1988), while (Thurston 1977) stated that both *Hyperia spinigera* and *Hyperia medusarum* are found in association with *P. periphylla* in the Atlantic Ocean, and Youngbluth and Bamstedt (2001) recorded *Hyperoche medusarum* as an associate of *P. periphylla* in Lurefjorden.

In our study, a high prevalence of amphipods was recorded on the mesoglea and tentacles of *P. periphylla* during field observations in the innermost parts of Trondheimsfjorden in autumn. Any of the above-mentioned hyperiid species (or a combination of several) have most likely induced the high degree of parasite infestation of *P. periphylla* populations in Trondheimsfjorden with subsequent mass mortalities and the termination of the bloom in September 2021.

Our observations are in line with earlier studies where entire or large proportions of jellyfish populations were infected by parasites later in the season when jellyfish had reached the adult medusa life-stage (Dittrich 1988, Mills 1993). In contrast to young spring medusae that usually show good physical condition, the proportion of damage (due to i.e. grazing and parasite infestation) is known to accumulate throughout the season (Mills 1993) leading to a weakening of the fitness, a progressive breakdown and subsequently a full collapse of jellyfish populations (Dittrich 1988, Mills 1993). Especially adult medusae of long-lived species are prone to damage late in the season (Mills 1993). Thus, the reduced physical condition of *P. periphylla* populations observed in Trondheimsfjorden in autumn reflect a common pattern.

On the other hand, our data contrasts with previous records of amphipod symbionts in *P. periphylla* from elsewhere in the Northern hemisphere: e.g. only 1.1% of *P. periphylla* were associated with *Hyperia* amphipods during a NE Atlantic survey in 1971 (Thurston 1977), and only 5% of the blooming *P. periphylla* were associated with the amphipod *Hyperoche medusarum* in a 1998–1999 study conducted in the Western Norwegian fjord of Lurefjorden (Youngbluth and Bamstedt 2001). Interestingly, while the former work relied only on net-caught specimens (Thurston 1977), which in turn may explain the low prevalence observed, low values of prevalence were recorded in Lurefjorden despite efforts to enumerate and capture *P. periphylla* with the help of ROVs (Youngbluth and Bamstedt 2001). Previous

surveys in Trondheimsfjorden showed a prevalence of up to ca. 33% of *Hyperia medusarum* in *P. periphylla* collected in bottom trawls in February 2013 (Borgersen 2013) but these values are less than half of the prevalence levels observed in the present study. As we can clearly see, studying jellyfish-parasite systems and their interactions is hampered by methodological constraints since traditional sampling techniques using net-techniques seem to cause biases thus often underestimating parasite loads. This is especially the case for ectoparasites and micropredators that are clearly disturbed by nets. In contrast, high-resolution imaging systems can serve as efficient tools to study host-parasite interactions in marine ecosystems *in situ*. While there are clear benefits of using ROV technology to study species interactions and behaviour *in situ*, observations are limited in spatiotemporal resolution and provide only snapshot information. Thus, ROV surveys at a higher spatiotemporal resolution are crucial to enable a more detailed understanding on the overall role of parasitism as a major bloom-control mechanism for jellyfish populations. However, such deployments are cost- and labour-intensive thus limiting the extent of such operations on larger spatiotemporal scales.

Usually, a correlation between parasitism and the density and population size of hosts is reported (Arneberg et al. 1998, Bagge et al. 2004), thus pointing at the regulatory role of parasites in bloom termination when high population sizes are reached. In the present study, population densities were at a moderate level based on comparisons with long-term data of *P. periphylla* populations in Verrabotten, Trondheimsfjorden (Aberle et al. 2023). The fact that the present population estimate is based on one single snapshot observation in September 2021 hampers a proper assessment of the population status. It can be speculated that *P. periphylla* densities in Verrabotten had reached peak densities earlier in the season and that the population was already at an advanced decaying stage at the time of sampling. Some support for this assumption is provided by earlier studies in Vefsnfjorden (Norway) where mass mortalities of *P. periphylla* were observed in late spring and summer (Bozman et al. 2018). So far, life cycle and population dynamics of *P. periphylla* in Norwegian fjords are not entirely clear, thus making it difficult to assess whether the high infestation prevalence in autumn is part of a common, yearly cycle or whether this parasite-host association has permanently established throughout the year showing varying degrees of parasite infestation in different seasons. The latter is supported by a moderate parasite prevalence reported for adult *P. periphylla* medusae in Trondheimsfjorden early in the season (Borgersen 2013) and the occurrence of two different generations of hyperiids per year, a rapid growing generation in summer and a slow growing in winter (Dittrich 1988). In contrast to other scyphozoan jellyfish, *P. periphylla* is considered to reproduce continuously (Tiemann and Jarms 2010, Bamstedt et al. 2020) thus providing ideal food and substrate for all life stages of hyperiids in Norwegian fjords throughout the year.

Further, a relationship between food shortage and the degree of parasite infestation seems likely, especially in temperate regions (Dittrich 1988, Towanda and Thuesen 2006). *Periphylla periphylla* is an efficient consumer of zooplankton standing stocks (Sornes et al. 2008). At high *P. periphylla* densities, feeding competition in adult medusae might occur which could negatively affect its performance further. Although a high longevity of *P. periphylla* is assumed (Jarms et al. 1999), this scyphomedusa might be prone to parasite infestations especially during periods when population density is high and the tissue regeneration ability reduced so that grazing losses induced by high densities of ectoparasites on their gelatinous hosts can no longer be compensated. At the same time, hyperiids have been shown to reach 100% prevalence in other large jellyfish species shortly before

these medusae disappear from the water column in temperate coastal systems (Fleming *et al.* 2014). Thus, a seasonal decay of *P. periphylla* blooms in autumn/winter and high mortalities associated with intense parasite infestation seems likely.

To date, substantial knowledge gaps exist about the life cycles, the infestation potential, and the role of amphipod parasites in controlling gelatinous zooplankton populations. While a strong negative impact of amphipod parasites on the fitness, condition, and survival of medusae is likely, it remains unclear whether high rates of parasite infestations occur only sporadically or rather at regular intervals. To allow more reliable predictions of jellyfish bloom dynamics and on the factors that cause jellyfish blooms to collapse, it is crucial to take parasite-jellyfish interactions based on *in-situ* observations into the spotlight of future research in jellyfish ecology.

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