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SHORT NOTE

Increased occurrence of the jellyfish *Periphylla periphylla* in the European high Arctic

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Abstract

The jellyfish *Periphylla periphylla,* which can have strong ecological impacts on its environment, is ubiquitous in the Norwegian Sea and its range was predicted to extend northwards. The occurrence of *P. periphylla* in the northern Barents Sea increased since 2014 and, for the first time, several individuals were collected within a high Arctic fjord (> 78°N) in western Spitsbergen in January 2017. The low solar irradiance prevailing during the polar night and an increased inflow of relatively warm Atlantic water in the European Arctic since the last decade likely provide suitable conditions for the medusa to colonize Svalbard's fjords during the winter months. However, light avoidance constrains the photophobic *P. periphylla* to deeper offshore areas during the midnight sun period. The current occurrence of *P. periphylla* in high Arctic fjords during the polar night will have a limited impact on marine ecosystems in the short term, but long-term effects are more uncertain if its abundance continues to increase.

Keywords Helmet jellyfish · Polar night · Arctic Ocean · Barents Sea · Svalbard · Borealization

Introduction

The jellyfish *Periphylla periphylla* is a cosmopolitan deep-water species, generally occurring in low densities (< 0.02 individuals m^{-3}) at meso- and bathypelagic depths (Lucas and Reed 2010 and references therein). Yet, under appropriate environmental conditions *P. periphylla* can also thrive in coastal fjords. For instance, it has reached exceptionally high densities of > 2 individuals m^{-3} in some Norwegian fjords since the 1970s (e.g., Fosså 1992; Sørnes et al. 2008). High light absorption, resulting in dim light conditions, and limited water exchanges within the fjords are the main factors behind blooming populations of this tactile and photophobic predator (Sørnes et al. 2007; Aksnes et al. 2009; Dupont and Aksnes 2010).

Periphylla periphylla inhabits the Norwegian, Iceland, and Greenland Seas (Dalpadado et al. 1998), but is rarely reported in the northern Barents Sea or in high Arctic fjords (Gulliksen and Svensen 2004; Gjøsæter et al. 2017). Exhaustive reviews of marine organisms from the Barents Sea and Svalbard archipelago during the last decades documented the presence of other scyphomedusae, mainly *Cyanea capillata*, but not that of *P. periphylla* (Zelickman 1972; Palerud et al. 2004). More recently, Tiller et al. (2017) predicted a

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northward expansion of the coastal distribution of *P. periphylla* as a result of climate change (Tiller et al. 2017). In that case, the low solar irradiance prevailing during the polar night could provide ideal conditions for the jellyfish to colonize high Arctic fjords in winter.

Here, we report records of *P. periphylla* in the Barents Sea and in high Arctic fjords of the Svalbard archipelago, which indicate increased occurrence of the jellyfish in the European high Arctic in recent years. We further discuss the potential causes and ecological implications of recent occurrence of *P. periphylla* in Svalbard fjords.

Methods

Biological sampling

We conducted biological sampling in Svalbard in January, May, and August 2017, with a Harstad pelagic trawl (9 × 20-m opening and 1-cm cod end mesh) towed at a given sampling depth for 20 min at three knots by the R/V *Helmer Hanssen* (Online Resource 1). Samples were sorted and counted on board. *Periphylla periphylla* drifting at the surface of Kongsfjorden in January were also collected with a dip net (< 1-cm mesh) from the pier in Ny-Ålesund (Fig. 1a). Three of these individuals in good conditions were dissected for stomach content analyses.

In addition to the original sampling in 2017, we reviewed annual reports from the Norwegian Institute of Marine Research (IMR, www.imr.no) documenting the occurrence of marine fish and zooplankton in offshore areas of the Barents Sea from 2005 to 2016. The Institute sampled an average of 291 trawling stations year^{-1} (SD = 65) during their fall surveys (August–October; details in Prozorkevich and Sunnanå 2017). The location of the stations remained similar from year to year and covered the entire Barents Sea (Johannesen et al. 2017).

We also reviewed trawl and plankton datasets from marine biology field courses offered at the University Centre in Svalbard (UNIS) to document the occurrence of *P. periphylla* in the Svalbard area since 2003 (Jørgen Berge, Paul Renaud and Janne Søreide, UNIS; unpublished data). A minimum of 10 trawl stations year^{-1} were sampled by UNIS, either during fall (2003–2014) or during spring and fall (2015–2016). The stations were concentrated on the western and northern coasts of Svalbard, from Isfjorden to Rijpfjorden and to the ice-edge of the central Arctic. Both IMR and UNIS surveys were conducted with a Harstad or Åkra pelagic trawl and a Campbell 1800 bottom trawl, as well as with plankton nets (WP2, WP3, and MIK-net). It is worth noting that, in the past decades, gelatinous zooplankton were often disregarded during marine surveys in the Arctic (Raskoff et al. 2005), but IMR and UNIS documented the occurrence of gelatinous zooplankton. See Renaud et al. (2012) and Prozorkevich and Sunnanå (2017) for details about IMR and UNIS sampling, respectively.

Environmental sampling

We used moored instrumentation to measure water temperature in Kongsfjorden, a fjord with a maximum depth of 380 m, for the period 2002 until 2017 (Cottier et al. 2005; Berge et al. 2015). The mooring was located in water depths of 200–250 m in the outer part of Kongsfjorden, which provided a direct connection with the shelf waters (Cottier et al. 2007). It included 10 temperature sensors (manufactured by either Seabird or Vemco) positioned from ~ 20 m below the surface to within 15 m of the seabed. The precision of the

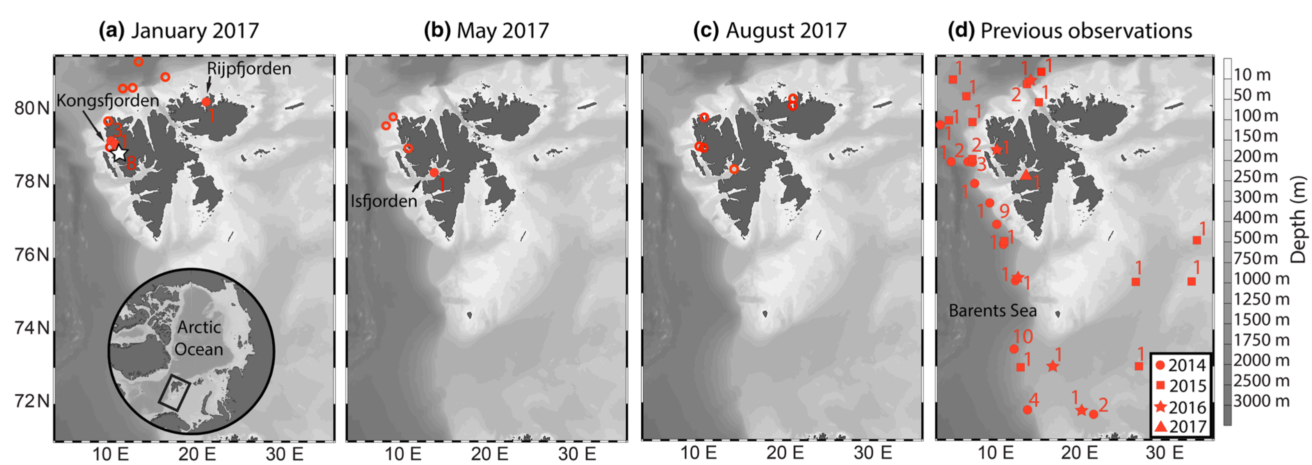

Fig. 1 **a–c** General map (inset) and survey area in Svalbard. Stations without (empty circle) and with (dot) *P. periphylla* are indicated. The white star indicates surface observations in Ny-Ålesund. **d** Previous observations by year. The numbers of *P. periphylla* sampled at each location are included

temperature sensors was > 0.1 °C after calibration. We calculated the relationship between years and temperatures and tested for autocorrelation using the R package nlme, and the best model was selected based on the Akaike information criterion corrected for small sample size (AICc; Hurvich and Tsai 1993) calculated with the R package MuMIn.

A custom-made light sensor deployed at 77.00°N and 16.35°E on January 14, 2018 measured ambient irradiance at 1 m depth (50 m from the research vessel with external lights off) in the 400–700 nm wavelength range. Measurements were conducted during daytime (15h30–16h30 UTC). To obtain absolute irradiance, we calibrated the light sensor by comparing raw data from the light sensor (digital counts) with absolute values from a QEPro spectrometer attached to a 2-m long optical fiber (model QP1000-2-vis-bx) and equipped with a 2pi light collector (model CC-3-UV-S; all from Ocean Optics, USA) when exposed to a projector at different light intensities in a darkroom (range $0.24–42.8 \times 10^{-5}$ W m^{-2}). The QEPro spectrometer was calibrated for absolute irradiance using an HL-3-cal calibration lamp connected to a cosine corrector through an optical fiber (Ocean Optics).

Results

Occurrence of *Periphylla periphylla* in Svalbard fjords in 2017

In January 2017, *P. periphylla* was present in at least two Svalbard fjords (Fig. 1a). In Kongsfjorden, four were sampled at 336–349 m depth and eight were observed drifting at the surface (Online Resource 1). Five of the latter, all with a bell diameter > 6.5 cm, were collected from the pier in Ny-Ålesund (Fig. 1a). In Rijpfjorden, one *P. periphylla* was caught at 223 m. In May 2017, a single specimen was captured at 236 m depth in Isfjorden (Fig. 1b). No *P. periphylla* were caught in August 2017 (Fig. 1c). The specimens captured at the surface had a low number of prey in their stomach (average of five prey individual^{-1}) and a varied diet consisting of copepods (27% of prey abundance), pteropods (23%), amphipods (20%), euphausiids (17%), and chaetognaths (13%).

Review of existing datasets

The IMR collected scyphomedusae, identified as *Cyanea capillata* and *Aurelia aurita*, in 2006 and 2008–2013. Yet, no *P. periphylla* were reported from 2005 to 2013. In 2014, 29 specimens of *P. periphylla* were captured and, since then, the jellyfish has been caught annually during IMR's surveys (Fig. 1d, Online Resource 2). No *P. periphylla* were collected by UNIS between 2003 and 2015, but one was caught in 2016 (Online Resource 2).

Environmental conditions in western Svalbard

Mean water temperature during polar night (November–February) in Kongsfjorden increased significantly from 0.3 °C (2004) to 4 °C (2017) (Fig. 2). The significance of the regression did not vary when tested for autocorrelation (i.e., *p* value remained 0.001) and the linear non-correlated regression model provided the best fit of the data (AICc of 37.2 vs. 47.1 for the autocorrelated model). Mean fall (August–October) temperatures in 2017 were the highest recorded during any year, but did not significantly increase between 2002 and 2017 despite a variation between 1.7 °C and 4.6 °C ($p = 0.14$; Fig. 2). Ambient irradiance at 77°N during the polar night (January) remained $< 3.6 \times 10^{-6}$ W m^{-2} ($< 1.66 \times 10^{-5}$ μmol quanta m^{-2} s^{-1}) at 1 m depth.

Discussion

The occurrence of *Periphylla periphylla* increased in the European high Arctic since 2014. Apart from a non-georeferenced mention of *Periphylla periphylla* in Svalbard (Gulliksen and Svensen 2004) based on occasional encounters during scientific diving expeditions (Bjørn Gulliksen; personal communication), the jellyfish was not reported in the northern Barents Sea prior to 2014. Fosså (1992) documented occasional occurrence in the southern Barents Sea (< 76.5°N), but not in Svalbard. From 2014 to 2016, however, it was annually sampled offshore, west and north of Svalbard (Fig. 1d). In high Arctic fjords, the first specimen was collected in Kongsfjorden in January 2016 (Online Resource 2), and we observed high numbers at the same location for the first time in January 2017. The West Spitsbergen Current (WSC) can transport organisms from the Norwegian Sea to the European high Arctic in < 1 year (Berge et al. 2005; Gjøsæter et al. 2017). Similarly to other

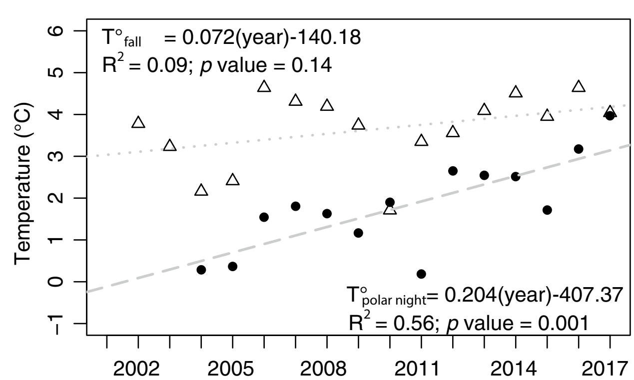

Fig. 2 Mean fjord temperatures measured from 20 m to bottom in Kongsfjorden during fall (August-October; triangles; dotted line indicates the regression) and the polar night (November-February; dots; dashed line indicates the regression)

boreal species, it is highly probable that *P. periphylla*, a species ubiquitous to the Greenland and Norwegian seas (Dalpadado et al. 1998), was advected with the more persistent inflow of Atlantic water entering western Svalbard fjords since 2006 (e.g., Willis et al. 2008).

During the polar night, we measured that irradiance in western Svalbard fjords remains $< 1.66 \times 10^{-5}$ µmol quanta m^{-2} s^{-1} at 1 m depth. Such values fall exactly within the range of light preferences of *P. periphylla* (i.e., 10^{-7}–5×10^{-3} µmol quanta m^{-2} s^{-1}; Bozman et al. 2017).

Despite northwards advection within the WSC and favorable ambient irradiance conditions, most *P. periphylla* avoided western Svalbard fjords until winter 2017. Until then, winter temperatures remained below their known temperature tolerance range of 4–19.8 °C (Arai 1997 and references therein). Although low temperature has never been proven to limit the occurrence of *P. periphylla* and the species inhabits cold waters near 0 °C in Antarctica (Larson 1986), in the northern hemisphere, high abundances occur in fjords where water temperature remains > 4 °C (e.g., Jarms et al. 2002; Sørnes et al. 2007, 2008; Bozman et al. 2017). We thus suggest that the unique combination of low irradiance and higher temperature which prevailed in January 2017 (for the first time, mean water temperature reached 4 °C during the polar night; Fig. 2) allowed *P. periphylla* to temporarily colonize Kongsfjorden.

The phototoxic porphyrin pigments of *P. periphylla* cause them potentially lethal lesions when they are exposed to light (Jarms et al. 2002), and they generally avoid surface waters with higher irradiance during daytime (Kaartvedt et al. 2007; Bozman et al. 2017). Hence, surface aggregations of *P. periphylla* are only possible during the polar night in the high Arctic. During the midnight sun period, *P. periphylla* needs to descend to depth and likely prefers deeper aphotic offshore regions to coastal areas, which would explain why only one specimen was collected in May and none in August (Fig. 1b, c). Scyphozoan jellyfish conduct vertical migrations, but also exhibit horizontal active swimming behavior (Moriarty et al. 2012; Kaartvedt et al. 2015). *Periphylla periphylla* could thus descend to depth and/or actively avoid Kongsfjorden from March onwards, prior to the midnight sun period.

Potential ecological impacts of *P. periphylla* occurrence in high Arctic fjords

Despite an increasing number of *P. periphylla* in the European high Arctic, its current abundance remains low compared to blooming populations further south. Acoustic surveys conducted in Kongsfjorden in January 2017 suggested that the abundance of *P. periphylla* in the top 100 m was < 0.07 individuals m^{-2} (Online Resource 3). Moreover, *P. periphylla* has a varied diet and a low predation rate (i.e., 1–34 prey day^{-1}; Youngbluth and Båmstedt 2001). Hence, the occurrence of *P. periphylla* in high Arctic fjords during polar night will likely have a limited impact on marine ecosystems in the short term. If low temperature limits the presence of *P. periphylla* in the high Arctic, the ongoing increase in water temperatures could result in higher abundance, and higher impact, in the long term.

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Compliance with ethical standards

Conflict of interests The authors declare that they have no conflict of interests.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. This study was carried out with permission from the Governor on Svalbard and followed the strict regulations regarding health, environment and safety enforced at UNIS and UiT.

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