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

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Published in:
Polar Biology

Publication date:
2018

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 abundance 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 colonise 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 can reach 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 et al. 1972; Palerud et al. 2004). More recently, Tiller et al. (2017) predicted a 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 colonise 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 3 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 conducted 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 one year to another 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 Prozorkevich and Sunnanå (2017) and Renaud et al. (2012) 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 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 0.24–42.8×10^{-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 dissected specimens captured at the surface had a low number of prey in their stomach (average of 5 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 and 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 $<3.6\times10^{-6}$ W m^{-2} ($<1.66\times10^{-5}$ 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, a 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 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 $<1.66\times10^{-5}$ µmol quanta m^{-2} s^{-1} at 1 m depth, which is 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 to 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 et al. 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 colonise 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.

Acknowledgements. Pedro de la Torre and Daniel Vogedes provided logistic supports. Elena Eriksen provided valuable information regarding IMR samples. Bodil Bluhm, Marine Cusa, Néstor Santana Hernandez, Janne Søreide, and Malin Daase contributed to sampling in 2017. Calum Bachell, Dora Marie Alvsvåg, Øystein Sture, Kertu Liis Krigul, Jonathan Björklund contributed to fieldwork in January 2017 through the University Center in Svalbard course AB334/834. A particular thanks to Colin Griffiths for overseeing the collection of mooring data in Kongsfjorden since 2002.

Funding. The study was co-funded by two projects supported by the Research Council of Norway (NFR): Arctic ABC (#244319) and AMOS (#223254), and by the Norwegian Biodiversity Information Centre project GooseAlien (#47-15-70184235). The mooring work was supported by the UK Natural Environment Research Council Oceans 2025 and Northern Sea Program with further support from NFR projects Circa (#214271), Cleopatra (#178766), Cleopatra II (#216537), and Marine Night (#226471). TJL acknowledges funding through the MARmaED project, that received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No 675997. This study is a contribution towards the ARCTOS research network (www.arctos.uit.no), the Arctic Science Partnership (ww.asp.org) and the Ocean Frontier Institute funded through Canada's First Research Excellence Fund. The results of this publication reflect only the authors' view and funding agencies are not responsible for any use that may be made of the information it contains.

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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Figure captions

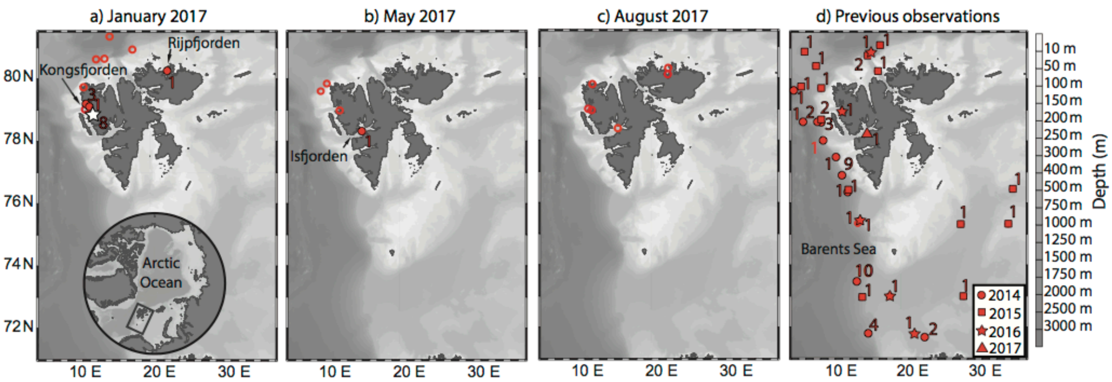

Fig. 1 (a-c) General map (insert) and survey area in Svalbard. Stations without (empty circle) and with (black dot) *P. periphylla* are indicated. The white star indicates surface observations in Ny-Ålesund. (d) Previous observations by year. The numbers of *P. periphylla* sampled at each location are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

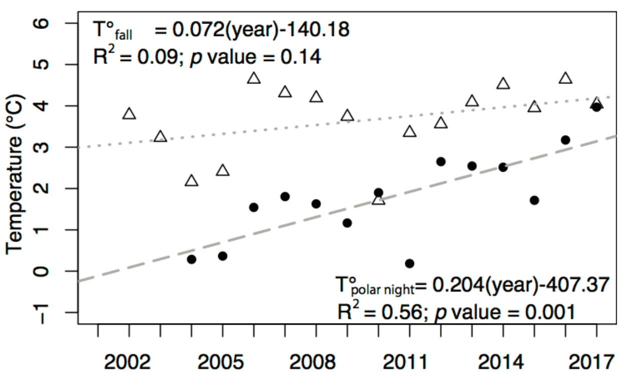

Fig. 2 Mean fjord temperatures measured from 20 m to bottom in Kongsfjorden during fall (August-October; triangles) and the polar night (November-February; dots)

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Electronic Supplementary Material 1

Supplementary Table ESM1. Details of sampling conducted in Svalbard in January, May and August 2017.

Date	Latitude (°N)	Longitude (°E)	Sampling Depth (m)	Type	# of *P. periphylla*
2017-01-09	79.016	11.177	322	Pelagic trawl	0
2017-01-10	79.085	11.434	336	Pelagic trawl	3
2017-01-10	79.091	11.442	349	Pelagic trawl	1
2017-01-11	80.390	13.533	206	Pelagic trawl	0
2017-01-11	80.378	12.472	1041	Pelagic trawl	0
2017-01-13	81.218	14.364	2194	Pelagic trawl	0
2017-01-14	80.570	17.397	354	Pelagic trawl	0
2017-01-14	80.202	22.117	223	Pelagic trawl	1
2017-01-16	79.444	11.061	211	Pelagic trawl	0
2017-01-19	78.936	11.915	0	Dip net	1
2017-01-21	78.936	11.915	0	Dip net	4
2017-01-21	78.936	11.915	0	Visual obs.	3
2017-05-08	78.177	15.063	236	Pelagic trawl	1
2017-05-09	78.583	11.551	266	Pelagic trawl	0
2017-05-11	79.502	10.046	401	Pelagic trawl	0
2017-05-12	79.387	9.338	302	Pelagic trawl	0
2017-08-08	79.003	11.370	215	Pelagic trawl	0
2017-08-08	79.006	11.279	380	Pelagic trawl	0
2017-08-09	78.577	11.567	335	Pelagic trawl	0
2017-08-11	79.480	12.010	215	Pelagic trawl	0
2017-08-12	80.192	22.140	230	Pelagic trawl	0
2017-08-13	80.067	22.109	164	Pelagic trawl	0
2017-08-17	78.231	15.281	226	Pelagic trawl	0

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Electronic Supplementary Material 2

Table ESM2. Details of *P. periphylla* previously sampled in the European high Arctic. NA indicates information that is not available.

Date	Latitude (°N)	Longitude (°E)	Area	Sampling device	Sampling depth (m)	Sampling duration (min.)	# of *P. periphylla*	Reference
2017-04-12	78.250	15.45	Adventfjorden	Visual obs.	0	-	1	a
2016-09	71.783	21.783	South of Svalbard	Pelagic trawl	NA	NA	1	b
2016-09	73.000	18.417	South of Svalbard	Pelagic trawl	NA	NA	1	b
2016-09	75.400	14.367	South of Svalbard	Pelagic trawl	NA	NA	1	b
2016-08-28	80.828	15.880	North slope	Pelagic trawl	550	NA	1	c
2016-02	78.936	11.915	Kongsfjorden	Visual obs.	0	-	1	d
2015-09-24	72.970	14.680	South of Svalbard	Pelagic trawl	NA	71	1	b
2015-09-16	73.000	28.470	South of Svalbard	Pelagic trawl	NA	31	1	b

2015-09-14	76.450	35.150	West of Svalbard	Bottom trawl	242	15	1	b
2015-09-13	75.320	34.570	South of Svalbard	Pelagic trawl	NA	92	1	b
2015-09-05	78.650	9.070	West of Svalbard	Pelagic trawl	NA	36	1	b
2015-09-04	79.700	9.070	West of Svalbard	Bottom trawl	404	33	1	b
2015-09-03	75.320	28.120	South of Svalbard	Bottom trawl	285	16	1	b
2015-09-03	79.759	6.350	West of Svalbard	Pelagic trawl	350-450	29	0.348 kg nmi^{-2}	e
2015-09-02	79.750	6.350	West of Svalbard	Bottom trawl	1014	70	1	b
2015-08-30	80.880	6.870	North slope	Bottom trawl	917	55	1	b
2015-08-29	80.420	8.400	North slope	Bottom trawl	861	45	1	b
2015-08-26	81.080	17.100	North slope	Bottom trawl	806	53	2	b
2015-08-23	76.350	12.700	West of Svalbard	Pelagic trawl	450	68	1	b
2015-08-23	81.561	15.294	North slope	Pelagic trawl	258-400	30	0.492 kg nmi^{-2}	e
2015-08-22	80.750	15.520	North slope	Bottom trawl	1632	155	1	b
2015-08-20	80.250	16.780	North slope	Bottom trawl	297	15	1	b
2015-08-18	78.020	9.380	West of Svalbard	Bottom trawl	577	127	1	b
2014-09-12	77.482	11.133	West of Svalbard	Pelagic trawl	NA	30	1	b
2014-09-11	76.898	11.933	West of Svalbard	Pelagic trawl	NA	15	1	b
2014-09-10	75.352	14.071	South of Svalbard	Pelagic trawl	NA	30	1	b
2014-09-10	76.406	12.785	West of Svalbard	Pelagic trawl	NA	30	2	b
2014-09-08	73.477	13.943	South of Svalbard	Pelagic trawl	NA	30	1	b
2014-09-07	71.799	15.518	South of Svalbard	Pelagic trawl	NA	30	1	b
2014-09-03	78.617	6.615	West of Svalbard	Bottom trawl	NA	141	1	b
2014-09-02	78.602	9.123	West of Svalbard	Bottom trawl	NA	65	9	b
2014-09-02	78.616	8.610	West of Svalbard	Bottom trawl	NA	63	1	b
2014-08-23	79.644	5.344	West of Svalbard	Bottom trawl	NA	120	1	b
2014-08-20	71.677	23.167	South of Svalbard	Bottom trawl	NA	16	10	b

References: a) Larissa Beumer, UNIS; Personnal communication; b) Elena Eriksen, IMR; Personnal communication c) Paul Renaud, Akvaplan-niva; Personnal communication; d) Leif Arne Håhjem, Norwegian Polar Institute; Personnal communication; e) Gjøsæter et al. (2017)

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

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Electronic Supplementary Material 3. Details of acoustic analyses conducted in Kongsfjorden in January 2017.

Sampling and analysis

To estimate the density of *Periphylla periphylla* in Kongsfjorden, acoustic transects were conducted with a Wideband Autonomous Transceiver® (WBAT; 70 kHz producing a chirp from 55 to 90 kHz) and a multifrequency (125, 200, 455, 769 kHz) Acoustic Zooplankton and Fish Profiler® (AZFP). The AZFP was mounted in two different configurations, either on an autonomous surface vehicle (January 19) or on the side of a small boat (January 21), both cruising at 2 knots. The WBAT was mounted on the side of a small boat on January 19. Both instruments were calibrated by the manufacturer.

Acoustic data were processed using Echoview® 8. The Target Strength frequency distribution (TS in dB re 1 m^2; Fig. ESM3) was calculated from the WBAT data using the single target detection and fish track algorithms (Tables ESM3a,b). The analysis was limited to the top 100 m because a lower signal-to-noise ratio prevented single detections at a farther range. Volume backscattering strength echograms (Sv in dB re 1 m^{-1}) of the WBAT and AZFP (125 kHz only) were then divided in 1-min cells before being echo integrated over the top 100 m. To compensate for noise amplification at depth by the time-varied gain, a time-varied threshold of -125 dB at 1 m was added to the WBAT data and Echoview's Background Noise Removal algorithm (DeRobertis and Higginbottom 2007) was applied to the AZFP data. The Nautical Area Backscattering Coefficient (NASC in m^{-2} nmi^{-2}) within each 1-min cell was divided by the average cross-section ($4\pi\sigma_{bs}$, in m^{-2}) estimated from the TS analysis, and multiplied by the relative abundance of signals between -64 and -59 dB (9.8%; Fig. ESM3) to estimate the average density of *P. periphylla* in the top 100 m during each transect. Single beam transducers as that of the AZFP do not allow accurate TS measurements. Hence, the TS frequency distribution from the WBAT data was used to estimate the abundance of *P. periphylla* from both the WBAT and AZFP transects.

Results and interpretation

Distinct Gaussian distributions of acoustic TS are known to indicate the occurrence of distinct species and/or size classes (Simmons and MacLennan 2005). Here, a distinct TS distribution between -64 and -59 dB (mean of -61.3 dB) was detected with the WBAT and represented 9.8% of the targets tracked in the top 100 m of Kongsfjorden on January 19 (Fig. ESM3). This TS distribution was assumed to mainly originate from *P. periphylla* individuals similar to those observed at the surface because a mean TS of -60 dB (SD 3.6 dB; n= 598) (Kaartved et al. 2007) and a peak TS of -62 dB (Klevjer et al. 2009) were previously measured at 38 kHz for *P. periphylla* detected at similar distances. Applying the 9.8% ratio to NASC values, we estimated that mean densities of *P. periphylla* could have reached 0.07 ind. m^{-2} on January 19, and 0.02 ind. m^{-2} on January 21.

Other abundant targets in Kongsfjorden either have lower (zooplankton) or higher (fish) TS. Zooplankton in Kongsfjorden have a TS between -109 and -74 dB (Berge et al. 2014), which corresponds to the distributions to the left of *P. periphylla* targets in the TS frequency histograms (Fig. ESM3). The main pelagic fish species in Kongsfjorden comprise polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) (Hop et al. 2002). Recently, juvenile Atlantic redfish (*Sebastes* spp.) have also colonised the fjord. All these fish have a mean TS > -58 dB, corresponding to the distributions to the right of that attributed to *P. periphylla* (Fig. ESM3). Other occasional targets as *Cyanea capillata* or myctophidae could have partly contributed to the acoustic signal attributed to *P. periphylla*. Fish with a pronounced tilt angle could also have contributed to that signal. Hence, our abundance estimates of *P. periphylla* represent maximum values and were likely biased positively.

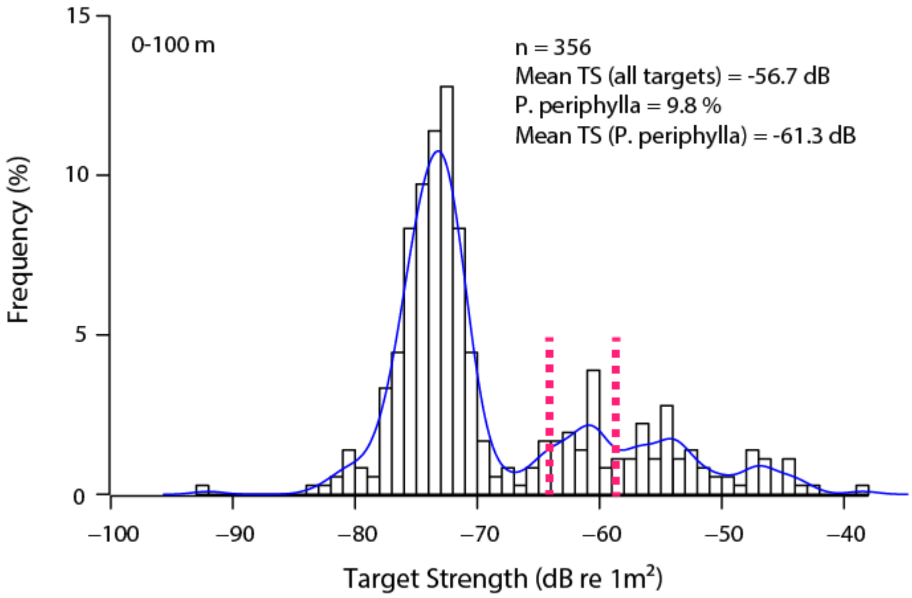
Supplementary Table ESM3a. Parameters used for the single target detection algorithm in Echoview®.

Parameters	Values
Compensated TS threshold	-120 dB
Pulse length determination level	6 dB
Minimum normalize pulse length	0.001
Maximum normalized pulse length	1.5
Beam compensation model	Simrad LOBE
Maximum beam compensation	6 dB
Maximum standard deviation of minor and major axis angles	0.6°

Supplementary Table ESM3b. Parameters used for the fish-tracking algorithm in Echoview®.

	Major axis	Minor axis	Range
Alpha	0.7	0.7	0.7
Beta	0.5	0.5	0.5
Exclusion distance (m)	4.0	4.0	0.3
Missed ping expansion %	0	0	100
Weight (%)	30	30	40

Minimum number of single targets and pings in a track were set to 3, and minimum gap between single targets was set to 5 pings. Note that for wideband systems, the value of compensated TS indicates the peak of the TS-frequency curve.



Supplementary Figure ESM3. TS frequency histogram presenting the upper 100 m of the WBAT data collected on January 19. The blue line is the kernel density estimates with a bandwidth of 0.5 (i.e. normal distribution approximations). The dashed red lines indicate the limits of the TS frequency distribution attributed to *P. periphylla* (-64 to -59 dB), and the percentage and mean TS of targets within this distribution are indicated.

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