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Plankton community structure and role of Oithona similis on the western coast of Greenland during the winter-spring transition

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Abstract:

The cyclopoid copepod *Oithona similis* is one of the most abundant copepods in the oceans and has a potentially important role in pelagic food webs. However, there is a lack of knowledge on aspects of its biology and function in planktonic communities. In the present study, we aimed to assess and compare the species' trophic role in Greenlandic coastal waters during the winter-spring transition, with a focus on its winter behaviour, when large calanoids are not present in the surface layer. Two locations were studied: waters offshore from Godthåbsfjord (Nuuk) in winter, and Qeqertarsuaq (Disko Bay) in spring (bloom and post-bloom period). The potential prey of adult females of *O. similis* was quantified, and grazing experiments were conducted to determine the feeding rates of adult females on phytoplankton and protozooplankton >10 µm. The abundance, stage composition, and egg production of *O. similis* was also investigated. Ciliates were the preferred prey for *O. similis*, which confirms its importance as a link between the microbial food web and higher trophic levels. We observed high egg production rates and efficiencies of *O. similis* in winter, confirming that it is active and successfully reproductive in food-limited winter conditions. Our results stress that *O. similis* is a key component of Arctic and subarctic marine communities throughout the year.

Keywords: *Oithona similis* ; Trophic role ; Egg production ; Greenland ; Winter ; Bloom ; Arctic

1. Introduction

Most studies on copepods carried out in Arctic and subarctic seas have focused on large calanoid species, such as *Calanus*. This is mainly due to their high contribution to the copepod biomass relative to smaller species, but also conditioned by the historical undersampling of small copepods due to use of coarse (> 200 *µ*m) plankton nets (Gallienne and Robins 2001). Recent investigations, however, have shown the relevance of small copepods in the Arctic (Auel & Hagen 2002, Hopcroft et al. 2005, Svensen et al. 2011). Although smaller in size, these copepods are important in terms of abundance, biomass and production, especially in coastal waters and fjord systems of the northern hemisphere (Nielsen & Andersen 2002; Lischka & Hagen 2005; Arendt et al. 2010). From an abundance point of view, small copepods often outnumber larger species (Møller et al. 2006, Madsen et al. 2008); and in contrast to large calanoids, which spend winter in diapause (Conover et al. 1988, Conover & Siferd 1993), small copepods can be present all year-round in polar seas (Ward & Hirst 2007, Dvoretsky & Dvoretsky 2009*a*).

Among small copepods *Oithona* is the most abundant pelagic zooplankton genus on the western coast of Greenland (Head et al. 2003, Thor et al. 2005, Madsen et al. 2008), and within the genus, *Oithona similis* is a cosmopolitan species. *Oithona* spp. have been described to have year-round presence (Hansen et al. 2004) and reproductive activity (Nielsen & Sabatini 1996, Ward & Hirst 2007), and it has been argued that these copepods can exploit microbial food webs more efficiently than calanoid copepods (Nielsen & Sabatini 1996), characteristics that make *Oithona* spp. populations more stable in time and space than those of calanoid copepods (Paffenhöfer 1993). Consequently, *Oithona* spp. could be important food sources for fish larvae and larger zooplankton, especially in those periods of the year when other potential prey are not available.

In Arctic marine environments only few studies on the biology of *Oithona* spp. are available (Nielsen et al. 2002, Madsen et al. 2008, Ward & Hirst 2007, Narcy et al. 2009) and even less is known about their feeding ecology. It has been reported that *Oithona similis* prefer motile prey, especially ciliates (Nakamura & Turner 1997; Lonsdale et al. 2000; Castellani et al. 2005*a*), although many aspects of their natural diet are still unknown. Thus, our knowledge on their feeding activity in winter in high latitude environments is almost non-existent, since most of the studies have focused on more productive periods of the year (Atkinson 1996, Møller et al. 2006), and lower latitudes (Castellani et al. 2005*a*). The present study represents the first attempt to investigate the role of *Oithona similis* on the western coast of Greenland, mainly focusing on aspects of its feeding ecology. For that purpose we carried out different samplings and feeding experiments from winter to late spring to describe seasonal differences in the role of *Oithona similis* in the plankton community, with a strong interest on their feeding behaviour in winter. Additionally, other aspects of *O.similis* biology and ecology (egg production and population structure) were also investigated during the period; and the microplankton and copepod community were described.

Material and Methods

Study sites and sampling

Sampling for the present study took place in two areas located at different latitudes on the west coast of Greenland (Fig. 1), waters offshore from Godthåbsfjord (Nuuk) and Qeqertarsuaq (Disko Bay).

1. Waters offshore from Godthåbsfjord

In Godthåbsfjord, the study was conducted in a 350 m deep station located at the entrance of the fjord (64 °07’N, 51 °53’W) (Fig. 1), a dynamic area (Mortensen et al. 2011) that represents the transition zone between the fjord and the marine system at Fyllas Banke, which is never covered by sea ice. Samples were collected from the small boat ‘Erisaalik’ (Greenland Institute of Natural Resources) in the daytime (09.00 to 15.00) from 16th February to 29th March. Vertical profiles of water temperature, fluorescence, salinity, and density were measured down to 340 m using a CTD (SBE19plus, SeaCat) equipped with a Seapoint chlorophyll *a* fluorometer and a Biospherical/Licor sensor. Water samples for chlorophyll *a* analyses and for estimation of vertical profile of microplankton were taken from 4 depths (1, 15, 50 and 100 m depth) using a 10 litre Niskin water sampler.

2. Disko Bay

The sampling in Disko Bay took place in a 250 m deep station (69° 15’N, 53°33’W) (Fig. 1) from 16th April to

24th May, once the sea ice was broken. The samples were collected from RV 'Porsild' (Arctic Station, University of Copenhagen) from 09.00 to 14.00. Vertical profiles of salinity, temperature, and fluorescence were taken at each sampling occasion using a Seabird SBE25-01 CTD probe, equipped with a fluorometer. Fluorescence was calibrated against chlorophyll *a* concentrations determined spectrophotometrically in water samples taken at 8 depths (1, 20, 50, 75, 100, 150, 200 and 250 m) with a 10 l Niskin water sampler. In addition, samples for determining the vertical profile of microplankton were taken from 4 depths (1, 15, 50 and 100 m).

Phyto- and protozooplankton

Samples taken for chlorophyll *a* determination (1000 ml in Godthåbsfjord and 250 ml in Disko) were filtered onto GF/F filters and kept frozen (-18ºC). Later, they were extracted in 96% ethanol for 18 hours, and fluorescence was then measured using a fluorometer (TD-700, Turner Designs) calibrated against a pure chlorophyll *a* standard.

Microplankton samples were fixed with acid Lugol's solution (2% final concentration), settled (from 50 to 1500 ml depending on the *in situ* concentration), and counted under an inverted microscope. Diatoms, dinoflagellates, and ciliates (>10μm) were identified and classified into 10-μm size classes. Microplankton biovolumes were determined from their linear dimensions and volume equations for appropriate geometric shapes (Hillebrand et al. 1999, Olenina et al. 2006), and finally converted into carbon biomass according to the equations provided by Menden-Deuer & Lessard (2000).

Zooplankton

Zooplankton samples for taxonomic and quantitative purposes were collected by vertical hauls using a 45-μm WP-2 closing net (56 cm diameter) equipped with a flowmeter, in Godthåbsfjord; and with a 50-μm Hydrobios type midi (net opening 50 cm x 50 cm) equipped with a flowmeter, in Disko. In Godthåbsfjord the samples were collected above 300 m (0-50, 50-100, 100-200, 200-300 m), whereas sampling was slightly shallower in Disko (0-50, 50-150, 150-200, 200-250 m). The samples collected for zooplankton analysis were preserved in 4% buffered formaldehyde (final concentration).

All copepods were identified, with a special focus on *Oithona* spp. naupliar and copepodite composition. The abundance of females with and without eggs sacs was quantified for *Oithona similis,* and the average number of eggs per sac was determined (n = 10). The carbon content of *Oithona* spp. nauplii and copepodites was calculated by using the length-weight regression given by Sabatini & Kiørboe (1994).

Feeding experiments

Copepods for feeding experiments were collected from the upper 50-100 m using a 50-μm WP-2 net fitted with a large non-filtering cod end. Water for incubation was collected from the depth of maximum fluorescence using a Niskin bottle. A nutrient mixture (15μM NH_4Cl and 1μM Na_2HPO_4) was added to the seawater used in the experiments to compensate for nutrient enrichment due to copepods excretion (Saiz et al. 2013). Adult females of *Oithona similis* were sorted in ice-chilled petri dishes under a stereomicroscope, washed out in filtered seawater, and transferred to polycarbonate bottles previously filled up with the collected seawater (Godthåbsfjord: 2000 ml bottles, 28-35 females per bottle; Disko: 600 ml bottles, 9-15 females per bottle). The bottles were completely filled, plastic film was put over the mouth, and bottles were then placed on a plankton wheel and incubated in a temperature-controlled cold room at light and temperature conditions close to *in situ*. At least 3 experimental (with copepods) and 3 control (without copepods) bottles were prepared in each experiment and incubated; in addition, 2 initial bottles (control at time 0) were immediately preserved with acid Lugol's (2% final concentration) at the beginning of the experiment to obtain initial prey concentrations.

Experiments were run for approximately 24 hours, and the survival of the females was checked under a stereomicroscope at the end of the incubation. At least 15 females were preserved in 4%-formaldehyde (final concentration) for later sizing and estimation of carbon content. Control and experimental bottles were fixed with acid Lugol's as the initial ones, and kept in a dark room at 4ºC until analysis. The identification and counting of the Lugol's samples (initial, control and experimental) were conducted in the same way as for the vertical profile (*see* above).

Clearance and ingestion rates of *Oithona similis* were calculated according to Frost's equations (Frost 1972) after verification that prey growth rates in experimental bottles were significantly different than those in the control ones (*t-test*, $p < 0.05$). Weight-specific rates were estimated using our measurements of the size of the potential prey (i.e. diatoms, dinoflagellates, and ciliates) and the adult females of *O.similis*, and then converted into carbon using carbon content-size relationships from the literature (*see* above). To determine possible size preferences in the diet of *O.similis*, the different groups of protozooplankton were pooled into size classes of 10 μm intervals (10-20, 20-30, 30-40, and > 40 μm), and clearance rates were then calculated for each size class of ciliates and dinoflagellates.

Egg production measurements

The abundance of ovigerous females in the population was estimated for each depth strata by the sum of attached and detached egg sacs divided by 2 (assuming that all ovigerous females had 2 eggs sacs). The percentage of ovigerous females at each sampling day was then calculated as the quotient of the estimated abundance of ovigerous females with respect to the total number of females. The abundance of eggs was calculated by multiplying the number of egg sacs by the average number of eggs per sac.

Egg production rates (EPR, eggs female^{-1} day^{-1}) were calculated using the egg-ratio method (Edmondson 1971) based on egg and female abundance data from the 4%-formaldehyde samples collected by vertical tows, and on the egg hatching time (*HT*, d) as follows:

$$EPR = \left(\frac{eggs}{females}\right) \times \frac{1}{HT}$$

The egg hatching time (*HT*) was calculated by using the equation given by Nielsen et al. (2002):

$$HT = (0.064 + 0.0145\,T)^{-1}$$

where *T* is water temperature (ºC). Weight-specific egg production was calculated using the egg carbon content that was estimated by using the egg volume conversion factor of 0.14 pg C μm^{-3} (Kiørboe et al. 1985), and the female carbon content estimated by the length-weight relationship provided by Sabatini & Kiørboe (1994). The egg production efficiency (i.e., GGE, %) of adult females of *Oithona similis*, i.e., the fraction of ingested food converted into egg production, was calculated as the quotient of weight-specific egg production and ingestion rate, expressed as percentage.

All parameters used for estimating reproductive parameters were calculated for each depth strata of each sampling day, and then depth-weighted averages were calculated to use in the final estimates of egg production measurements (i.e. number of ovigerous females, number of eggs, carbon content of the females, clutch sizes).

Results

Hydrography

The monitoring station at the entrance of the Godthåbsfjord system (Fig. 1), sampled during winter conditions, is located in a turbulent area, with strong vertical mixing, also influenced by the presence of the intense tidal forces in the region (Mortensen et al. 2011). This is corroborated by the CTD profiles which showed a well-mixed water column (Fig. 2), with salinities between 33-33.5, and temperatures below 1ºC. The very low chlorophyll *a* concentrations found (Table 1), with a uniform distribution in the upper 100 metres, indicated winter conditions, a situation also confirmed by the low diatom concentrations (Fig. 3).

In Disko Bay the structure of the water column was completely different, during the spring bloom and post-bloom. That area is characterized by the presence of sea ice cover during winter, followed by the ice breakup together with the influence of glacier melt water (from Jakobshavn glacier), which results in strong stratification of the water column in spring (Hansen et al. 2012) (*see* Fig. 2). Once the sea ice breaks up, light enters the water column and triggers the phytoplankton growth (Table 1, Fig. 3). The stratification in the water column was characterized by warmer and more saline water in the bottom during the bloom period (Fig. 2). The temperature of the surface increased by ca. 2ºC, due to the increase of solar heating, creating a more-defined surface thermocline situated at 20-30 metres depth during the decaying bloom phase (Fig. 2). Notice that vertical profiles corresponding to 24 April and 17 May are missing in Figure 2 due to technical problems with the equipment in those sampling dates; for the sake of comparison, a profile from 22 April was added to the figure. The concentration of chlorophyll *a* observed in Disko Bay illustrated the transition from the beginning of a bloom to a post-bloom situation (Table 1, Fig. 2).

Potential prey: phyto- and proto-zooplankton

The winter phytoplankton community in the upper 100 metres was dominated by the chain-forming diatoms *Chaetoceros* spp. and *Thalassiosira* spp. (on average 92% of phytoplankton biomass), with lower densities of *Pseudo-nitzschia* spp., *Navicula* spp., *Skeletonema* spp., and undetermined centric diatoms, as well as the silicoflagellate *Dictyota speculum* (data not shown). The integrated average biomass of phytoplankton (98% diatoms) was very low with values that ranged from 0.03 to 0.65 μg C l^{-1} corresponding to February and late March, respectively (Table 2). The protozooplankton community was dominated by small (10 to 40 μm) naked oligotrich ciliates such as *Strombidium* spp., *Strobilidium* spp., and *Lohmaniella* spp., with the presence in lower abundances of *Mesodinium* spp. Tintinnids were either present in low abundances or absent in the samplings. Heterotrophic dinoflagellates were also present, dominated by the athecate genera

Gymnodinium and *Gyrodinium*, and with the presence in lower concentrations of thecate dynophisoid and peridinoid dinoflagellates. The integrated average biomass of ciliates ranged from 0.06 to 0.43 μg C l^{-1}, and the corresponding biomass of dinoflagellates from 0.02 to 0.11 μg C l^{-1} (Table 2). The vertical distribution of protozooplankton in general mirrored the water column structure (Fig. 3).

During spring, the composition of the phytoplankton community was similar to that found in winter, but the abundances were higher. During the spring bloom the dominating diatom was *Thalassiosira* spp., and high abundances of the small flagellate *Phaeocystis* spp. were present. The integrated average biomass of phytoplankton (excluding *Phaeocystis* spp.) ranged from 2.4 to 17.9 μg C l^{-1} in the bloom phase, and from 0.2 to 3.1 μg C l^{-1} in the post-bloom (Table 2). Ciliates, again, dominated the protozooplankton community during the spring bloom and post-bloom (Fig. 3; Table 2); and the most abundant ciliates and heterotrophic dinoflagellates were similar to those found in winter. The integrated average biomass of ciliates ranged from 0.6 to 4.7 μg C l^{-1} during the bloom period, and from 2.9 to 3.9 μg C l^{-1} during the post-bloom; whereas for dinoflagellates the biomass ranged from 0.3 to 2.9 μg C l^{-1} during the bloom, and from 0.8 to 1.9 μg C l^{-1} in the post-bloom phase (Table 2).

The peak abundance and biomass of phytoplankton, dinoflagellates and ciliates were found in the upper 20 m, with a dominance of diatoms in that depth strata during the early phase of the bloom, and a dominance of ciliates later in the decay phase of the bloom (Fig. 3).

The copepod community

Copepods dominated the mesozooplankton, constituting 71%, 94%, and 88% of the total abundance in winter, spring-bloom, and post-bloom periods respectively. The abundance in the different depth strata fluctuated, from a few tens (winter) to 14,000 ind. m^{-3} (post-bloom period) (Fig. 4); and between a few hundreds to 4000 ind. m^{-3} (weighted average) for the whole water column.

During winter the small copepods *Microcalanus* spp., *Microsetella* spp., *Oithona* spp., *Oncaea* spp., and *Pseudocalanus* spp. dominated, whereas the larger copepods *Calanus* spp. and *Metridia* spp.were less abundant (Fig. 4). Average abundances across depths and dates during winter were 105 ind. m^{-3} for *Microcalanus* spp., 120 ind. m^{-3} for *Microsetella* spp., 67 ind. m^{-3} for *Oithona* spp., and 74 ind. m^{-3} for *Oncaea* spp. The group “others” was composed of much-less-abundant copepod species and other mesozooplankton components (e.g. foraminifera, thecostomata and tintinnidae), which accounted for 25-35 % of the total mesozooplankton community. In winter, *Oithona* spp. contributed 10-15% to the total mesozooplankton abundance, and 15-20% to the copepod abundance. The vertical distribution of the copepod community did not follow any specific pattern, probably due to the strong mixing in that dynamic sampling area (Fig. 4).

During the spring bloom at Disko Bay the diversity of copepods was similar to that observed in winter at the Godthåbsfjord, but in contrast, larger calanoids dominated the copepod community both in abundance (Fig. 4) and biomass (data not shown). However, during the initial phase of the bloom small copepods were still very abundant, and *Oncaea* spp. and *Oithona* spp. together contributed > 50% of the total copepod abundance (Fig. 4, 19 April). At the peak of the spring bloom there was a decrease in the relative abundance of small copepods due to a large increase in the abundance of *Calanus* spp. (especially nauplii). *Calanus* species reached the maximum abundances in the post-bloom period (Fig. 4). The mean abundance of copepods fluctuated between 1817 ind. m^{-3} during the bloom period, to 2982 ind. m^{-3} during the post-bloom phase (Fig. 4). The maximum abundance of copepods were always located in the upper 50 m, in association with the highest microplankton concentrations (located in the upper 20 m, Fig. 4). *Oithona* spp. contributed 4-15% of the total mesozooplankton abundance during the spring-bloom and post-bloom periods. The other mesozooplankton groups represented less than 10% in all samplings.

It should be mentioned that although some *Oithona atlantica* were observed in the vertical tows, their abundance was negligible and therefore *O. similis* was the target species in this study. From now on we will refer to *Oithona* spp. as *Oithona similis,* considering the presence of other *Oithona* species in the tows as negligible.

Oithona similis stage vertical distribution, abundance and composition

During winter, the vertical distribution of nauplii and copepodites of *Oithona similis* showed no clear pattern, although maximum abundances for both stages were found at the same depth strata at each sampling date (Fig. 5). From the beginning to the end of the winter, the abundance (weighted average) of naupliar and copepodite stages of *O.similis* varied from 41 to 7 nauplii m^{-3}, and from 33 to 4 copepodites m^{-3} (data not shown). During the winter period the most abundant stage (weighted average over dates) was C5 (≈ 8 ind. m^{-3}), followed by N3 (≈ 5 ind. m^{-3}), N5 (≈ ind. 5 m^{-3}) and adult females (≈ 4 ind. m^{-3}) (data not shown). The relative stage composition was diverse but constant throughout the winter period, both nauplii and copepodites accounted approximately for half of the population at each sampling date, with a slight increase in the contribution of nauplii in the last sampling (Fig. 6). The proportion of adult females was quite stable representing approximately 10% of the population (Fig. 6).

In contrast to the winter in Godthåbsfjord, nauplii and copepodites did not show the same vertical pattern during spring in Disko Bay. Nauplii were mainly located in the upper 50 m, whereas copepodites, although also abundant in the upper layers, were comparatively much more abundant in deeper waters (Fig. 5). The abundance of nauplii stages varied between sampling dates with a non-defined trend, although the latest stages (N4-N6) were most abundant (Fig. 5). The abundance of copepodites was clearly dominated by adult females, with abundances (weighted average) between 46 and 122 ind. m^{-3} (data not shown) during the spring. Overall, the stage composition of *Oithona similis* during the spring-bloom and post-bloom periods was dominated by later copepodite stages, with the exception of the last sampling of the post-bloom period, in which the number of nauplii increased reaching 50% of the total stage abundance (Fig. 6). During the bloom, the population of *O.similis* became increasingly dominated by adult females, which were by far the most abundant stage, and contributed 30 to 46% of the total abundance of developmental stages (Fig. 6).

Feeding rates and prey selection of *Oithona similis*

Ciliates were the most abundant components of the protozooplankton community, and the preferred prey for adult females of *Oithona similis*. There was a significant relationship between ingestion and protozooplankton abundance (n = 9, p = 0.03; data not shown). However, the relation was mainly due to the abundance of ciliates, as evidenced when ciliates alone were considered in the feeding rate calculations (Fig. 7, Table 3). Clearance rates on diatoms were always negative (data not shown), and therefore no feeding rates could be computed.

Clearance rates (average ± SE) on ciliates were inversely correlated to ciliate concentration and ranged from 6 ± 6.1 to 51 ± 12.3 ml female^{-1} d^{-1} (Fig. 7A, Table 3). Ingestion rates on ciliates (average ± SE) ranged from maximum values of 199 ± 103 ciliates female^{-1} d^{-1} during the spring bloom, to minimum values of 9 ± 1.4 ciliates female^{-1} d^{-1} during winter (Fig. 7B, Table 3). Ingestion rates, in terms of daily rations (% body carbon ingested per day), were low in winter (1.4%), and reached maximum values of approximately 20-23% during the spring bloom (Fig. 7C; Table 3). Feeding rates were positively correlated with ciliate abundance and biomass (Fig. 7B and 7C).

The highest clearance rates on ciliates were measured when adult females of *Oithona similis* fed on cells between 20 and 40 μm size (equivalent spherical diameter), and reached maximum values (≈113 ml female^{-1} d^{-1}) when feeding on the size range 30-40 μm (Fig. 8A). Ciliates in the size range 20-40 µm were mainly comprised of *Strombidium* spp. and *Lohmaniella* spp., and lower numbers of *Strobilidium* spp. Overall, results of feeding rates on dinoflagellates were inconclusive, with negative values in some replicates, and statistically non-significant values in most of the experiments. The results of feeding rates on dinoflagellates are shown in Table 3 and will be discussed later. Clearance rates on dinoflagellates by sizes tended to be higher on the 10-30 μm prey size range (Fig. 8B). In general, for similar-sized prey, ciliates were cleared more efficiently than dinoflagellates (Fig. 8).

Egg production and egg production efficiency

Egg-carrying females of *Oithona similis* were present both in winter and spring, with values surprisingly high in winter when compared with spring, and most abundant in the post-bloom period (Table 4). The relative abundance of ovigerous females varied from a minimum of 8% (winter) to a maximum of 56% (post-bloom) (Table 4). Clutch sizes (eggs female^{-1}) ranged from 16 to 26 eggs in winter; from 14 to 36 eggs in the spring bloom; from 14 to 38 eggs in the post-bloom period (Table 4). Mean clutch sizes did not show important differences between the bloom phases, and varied on average from 18 (spring bloom) to 22 (post-bloom) eggs per female (Table 4). Variability between average clutch sizes on different sampling dates is reported in Table 4. Egg size did not vary much during the period of the study, averaging 57 ± 3 μm (n= 20) in diameter.

Mean egg production rates varied from 0.09 (winter and spring bloom) to 0.91 (post-bloom) eggs female^{-1} d^{-1}; and weight-specific egg production rates varied approximately from 0.2 to 2 % d^{-1} (Table 4). *Oithona similis* egg production rates (either per capita or weight-specific) were not very variable from winter to the spring bloom, although females found in the tows were slightly smaller in winter (average 0.60 μg C female) than those ones found in spring (average 0.68 μg C). During the post-bloom period, however, egg production rates increased on average 3.8 times the rates found in the earlier periods. On the other hand, egg production efficiencies were relatively high in winter (on average 23%), decreased during the spring bloom (3%), and increased again during the post-bloom (25%) (Table 4).

Discussion

The environmental settings

The CTD profiles revealed a mixed water column during winter, with homogenous and very low chlorophyll *a* concentrations in Godthåbsfjord, in contrast to the development of a stratified water column with increasing chlorophyll *a* during the spring-bloom and post-bloom phases in Disko Bay (Fig. 2). The two localities chosen for the study represented the typical events in the seasonal succession in the oceanography and plankton along western Greenland (Mortensen et al. 2011, Hansen et al. 2012), and can therefore be merged and used to illustrate the winter-spring transition in general. In the present study, the microplankton community of southwestern Greenland was for the first time investigated in winter, showing a clear dominance of ciliates and dinoflagellates. The similar winter importance of protozooplankton in Arctic plankton communities documented further north (Levinsen et al. 2000), enable us to hypothesize that protozooplankton constitute a main food source in the winter feeding of copepods in those latitudes.

The winter copepod community described in this study in the southwest of Greenland was dominated by small copepods, as previously documented in the same area for the late summer (Tang et al. 2011), and for the periods of the year when *Calanus* spp. are not present in the surface layer in Disko Bay (Madsen et al. 2008). Our study documents the abundance of small copepods in winter, suggesting they comprise an important food web component, often unconsidered, outside the period of the main bloom. The even vertical distribution of different species of copepods found in winter could be explained by the turbulent regime in the area (Mortensen et al. 2011), which could blur the “natural” distribution patterns of species separated vertically in less-energetic systems (Haury et al. 1990). However, during the spring bloom and post-bloom, when *Calanus* spp. took over the surface water, the smaller copepods were more abundant in deeper waters.

Population dynamics of *Oithona similis*

Even though it is one of the most abundant copepods in Arctic and subarctic regions (Auel & Hagen 2002, Hopcroft et al. 2005, Møller et al. 2006, Madsen et al. 2008, Svensen et al. 2011), the population dynamics of *Oithona similis* have not been investigated thoroughly in Greenland. In this study, we found all developmental stages of *O.similis* present during the period of sampling. The presence of egg-carrying females during winter confirmed the year-round reproduction strategy described for *O. similis* from lower latitudes (Kiørboe & Nielsen 1994, Sabatini & Kiørboe 1994). Moreover, the presence of the earliest nauplii stages in winter evidenced a successful recruitment despite unfavourable food conditions. In spring, *O.similis* females were present in the entire water column but the younger stages were mostly found near the surface. We observed an increase in nauplii abundance by the end of May (post-bloom), parallel to an increase in ovigerous females abundance indicating that the peak production of *O.similis* must occur later in the season. The eggs produced by females late in the period will form the basis of the high abundance of *O.similis* normally observed in summer-autumn (Hansen et al. 1999, Madsen et al. 2008, Zamora-Terol et al. unpubl.). However, 2010 was a historically warm year in Greenland (Jensen & Rasch 2011), which could result in an early initiation of the high productive period. Periods of low productivity are rarely included in studies of copepod life history, in that sense our study is unique because included the pre-bloom population dynamics of *O.similis*, thereby improving our knowledge on the ecology of this copepod in the period of the year when it dominates the plankton community.

Feeding rates and prey selection

In all the feeding experiments carried out in the present study we found that *Oithona similis* had a clear preference for medium-sized ciliates (20-40 μm). Preference for ciliates has been reported from ecosystems at lower latitudes, not only for *O.similis* (Nakamura & Turner 1997, Castellani et al. 2005*a*) but also for other *Oithona* species (Atienza et al. 2006: *O.nana*, Zamora-Terol et al. unpubl.: *O.attenuata*). Experiments with *O. similis* feeding on natural plankton populations found that when dinoflagellates were as abundant as ciliates, *O. similis* still preferred ciliates (Nakamura & Turner 1997, Castellani et al. 2005*a*), confirming the pattern observed in this study and suggesting the active selection for ciliates by *Oithona* spp. In this context, our grazing rates of *O.similis* on dinoflagellates were controversial throughout the different experiments. We observed no significant ingestion (*t-test* > 0.05) in most of the experiments conducted, occasionally resulting in negative clearance values in some replicates, probably as a consequence of trophic cascade effects. Therefore, we cannot fully discard that *O.similis* grazed on dinoflagellates, but in any case predation on ciliates seemed to be more important.

As expected, we found no ingestion of diatom, in agreement with most previous studies (Uchima 1988, Lischka & Hagen 2007, Nishibe et al. 2010). Although occasionally in the literature reports on diatom consumption by *Oithona* spp. can be found (Lampitt & Gamble 1982, Atkinson 1996, Atienza et al. 2006, Pond & Ward 2011), it is not clear what mechanisms are involved. In this regard, the work by Svensen & Kiørboe (2000) suggests that ambush raptorial copepods as *Oithona similis* should rely on hydromechanical signals for detecting individual prey; and Kiørboe & Visser (1999) further showed that the hydromechanical signals from non-motile and slow-sinking particles are not in the detection threshold of *O.similis*.

In the case of size preference, there are also different opinions on the capability of *Oithona* spp. to feed on very small or large prey. We did not check the ingestion of small flagellates (<5μm), but we observed that small (<5-10 μm) single diatoms were not ingested in any of the experiments. In the present study, *Oithona similis* captured particles mainly within the 10-40 μm size range, what is in agreement with previous investigations on the same species (Drits & Semenova 1984, Castellani et al. 2005*a*, Nishibe et al. 2010); however, wider range of sizes has also been reported (4-300 μm for *O.nana*, Lampitt & Gamble 1982). It is very likely that in natural environments, size preferences will be influenced by the abundance and type of prey comprised in that range, in particular *Strombidium*-like and *Strobilidium*-like ciliates.

Daily rations (% body C ingested d^{-1}) of *Oithona similis* found in this study were positively correlated with the abundance of ciliates, and were in average 1.4% in winter, 16% during the spring bloom, and 6% in the post-bloom. Assuming that metabolic costs would account for 1.4% d^{-1} (at 4ºC, Castellani et al. 2005*b*), the ingestion rates measured in spring were more than enough to cover respiration costs at mean temperature encountered in Disko Bay. For the winter period, however, ingestion rates were rather low and only occasionally could be sufficient to cover metabolic requirements, suggesting the need to use lipid reserves to ensure the winter survival strategy of *O.similis* (Narcy et al. 2009). In contrast to large calanoid copepods that go into diapause, during the winter *O.similis* appears to be actively feeding and reproducing (*see* below), even if at low rates, despite the low temperatures and nutritionally diluted environment.

Egg production rates and efficiency

Overall, the fecundity of *Oithona similis* in the present study did not respond strongly to the development of the spring bloom and associated microbial community (Fig. 9A and 9B), and it was only during the post-bloom that a substantial increase in egg production occurred.

The proportion of ovigerous females found here (8-56%) was in the range of reported values in other high latitude environments (0-67% Ward & Hirst 2007, 22-52% Dvoretsky & Dvoretsky 2009*b*). The maximum percentage of ovigerous females (56%) was observed at the end of May (post-bloom), and was close to the maximum values reported for *O. similis* in the Southern Ocean (67%, Ward & Hirst 2007). The presence of ovigerous females in winter also suggests they are reproductively active throughout the year, as previously reported in other polar environments (Fransz & Gonzalez 1995, Metz 1995, Lischka & Hagen 2005).

Clutch sizes found for *Oithona similis* were within the range reported in the literature (18-26 eggs per female, Castellani et al. 2007, Dvoretsky & Dvoretsky 2009*a*). Despite the changes in food availability throughout the study period, clutch size did not vary much (16-24 eggs $female^{-1}$), in agreement with previous studies that also reported little variation throughout the year (Danish coastal waters: Kiørboe & Nielsen 1994; Barents Sea: Dvoretsky & Dvoretsky 2009*a*; Southwest Atlantic: Temperoni et al. 2011). We could not find a correlation between clutch size and food availability (Fig. 9A) or any other factors, suggesting that clutch size is weakly dependent on environmental factors. Egg production rates in the present study (0.1-0.9 eggs $female^{-1}$ day^{-1}) are within the range of the lowest values reported in earlier studies on the same species from lower (Castellani et al. 2005*a*, Ward & Hirst 2007), and similar (Dvoretsky & Dvoretsky 2009*b*) latitudes.

Egg production rates are influenced by different factors, and food availability has been considered one of the most important factors driving feeding and egg production rates for calanoid copepods (Kiørboe & Nielsen 1994, Saiz & Calbet 2011). We did not find any clear relationship between food availability and any reproductive parameter of *Oithona similis*. In fact, average egg production rates were the same in winter and during the spring bloom, 0.2 eggs $female^{-1}$ day^{-1}. However, an increase of the egg production (0.5-0.9 eggs $female^{-1}$ day^{-1})

was observed during the post-bloom phase, very likely due to a delay between coupling of food availability (which increased during the spring bloom) and fecundity. These observations are in agreement with studies that covered a longer part of the reproductive season for *O.similis*, and that reported reproductive peaks in summer or early autumn (Lischka & Hagen 2007, Madsen et al. 2008, Dvoretsky & Dvoretsky 2009*a*). In this regard, we should not ignore the temperature as an important factor controlling the egg production of *Oithona* spp. Maximum egg production rates in egg-carrying copepods are greatly determined by hatching times, which are at the same time dictated by temperature (McLaren et al. 1965; Nielsen et al. 2002). Studies on the egg production of *Oithona* spp. have described the strong effect of water temperature on hatching times and egg production rates (Sabatini and Kiørboe 1994, Uye and Sano 1995, Drif et al. 2010), as has also been documented in calanoid copepods (*see* Mauchline 1998).

Weight-specific egg-production rates reported in this study for *Oithona similis* (0.2-2% d^{-1}) are in agreement with previous investigations on the same species (0-2% d^{-1} Ward & Hirst 2007, 0.5-4% d^{-1} Dvoretsky & Dvoretsky 2009*b*), and slightly higher than values found for *Oithona* spp. in the same area during the same time of the year (0.004-1.5 % d^{-1}, Madsen et al. 2008). In general, our maximum weight-specific egg-production rates are in good agreement with previous studies in high latitude environments at temperatures similar to ours (Ward & Hirst 2007, Dvoretsky & Dvoretsky 2009*b*).

Surprisingly we found that the egg-production efficiency (i.e. gross growth efficiency, GGE) was high during winter and very low during the spring bloom (Table 4). As mentioned above, it is very likely that females of *Oithona similis* were using lipid reserves in winter to compensate for the low food concentration, and these reserves contributed to fuel egg production. In this regard, it has been observed how *O.similis* exhibit low content of lipids in spring in the Arctic (Lischka & Hagen 2007). This fact would explain that the high feeding rates in spring do not translate into high egg production, but are very likely allocated to refuel the lipid reserves. Although some studies have investigated reproduction of *O. similis*, very few have compared feeding with egg production and calculated their growth efficiencies (Castellani et al. 2005*a*). The egg production efficiency (i.e. GGE) found in this study was in average 15%, whereas Castellani et al. (2005*a*) reported 47% in the North Atlantic. Difference in estimations, however, could be due to the use of egg-production rates calculated from the population, instead of individual females measurements. The GGE found in this study was in good agreement with the value estimated in the laboratory for *O.davisae* (16%) based on individual female incubations (Zamora-Terol & Saiz 2013).

In this study we have documented how *Oithona similis* is actively feeding and successfully reproducing during winter. We have also confirmed the preference of *Oithona* spp. for ciliates as prey items, highlighting their key role in pelagic food webs as a link between the microbial food web and higher trophic levels. This role is especially relevant in Arctic and subarctic plankton webs when larger *Calanus* spp, are not active in the water column. In conclusion, the capability of *Oithona* spp. to survive and succeed when unfavourable conditions are present in the water, might explain the success of the genus, not only in polar environments but also in marine environments worldwide.

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Legends to figures

Fig.1. Map showing the sampling stations on the west coast of Greenland. One located at the entrance of the Godthåbsfjord, in Nuuk; and the other one situated approximately 2 km off Qeqertarsuaq, in Disko Bay.

Fig. 2. Vertical profiles of temperature and salinity (top panel), and fluorescence (bottom panel). The asterisk (*) indicates a sampling date replacing the sampling of 26 April. Notice a different scale and bottom depth in the winter samplings.

Fig. 3. Vertical distribution of diatom, dinoflagellate, and ciliates biomass (μg C l^{-1}) in the upper 100 m. Note different scales for each period.

Fig. 4. Vertical distribution of copepod abundance (ind. m^{-3}) in winter (0-50, 50-100, 100-200 and 200-300 m depth strata) and in spring (0-50, 50-100, 100-150, 150-200, 200-250 m depth strata). Each date of sampling is indicated. Note that the scale for 17 and 24 May goes up to $1.5 \cdot 10^4$ ind. m^{-3}.

Fig. 5. Vertical distribution of nauplii and copepodites of *Oithona similis* (ind. m^{-3}) during winter, spring bloom and post-bloom. Depth strata as in Fig. 4.

Fig. 6. Relative stage composition of *Oithona similis* (%) for each sampling date.

Fig. 7. Feeding rates of *Oithona similis* adult females on ciliates. (A) Clearance rate (*F*, ml female^{-1} d^{-1}), (B) ingestion rate (IR, cells female^{-1} d^{-1}), and (C) daily ration (DR, % body carbon ingested female^{-1} d^{-1}). Each point represents the mean value (± SE) of 3-4 replicates. Cil-C: ciliate concentration, either in cells or carbon. Asterisk (*) indicates a date not included in the fitted equations, because the presence of negative values.

Fig. 8. Size dependent clearance rates (ml female^{-1} d^{-1}) of adult females of *Oithona similis* on (A) ciliates and (B) dinoflagellates. Symbols are for the different sampling dates. Each point represents the mean value (± SE). Asterisk (*) indicates statistically significant grazing rate (t-test, $p < 0.05$).

Fig. 9. *Oithona similis* adult females. (A) Clutch size (eggs female^{-1}) and (B) weight-specific egg production rates (%, d^{-1}) plotted against the average biomass of ciliates (μg C l^{-1}); dash lines show linear regressions. (C) Egg production efficiency (i.e. GGE); continuous line indicates 30% GGE.

Figures and tables

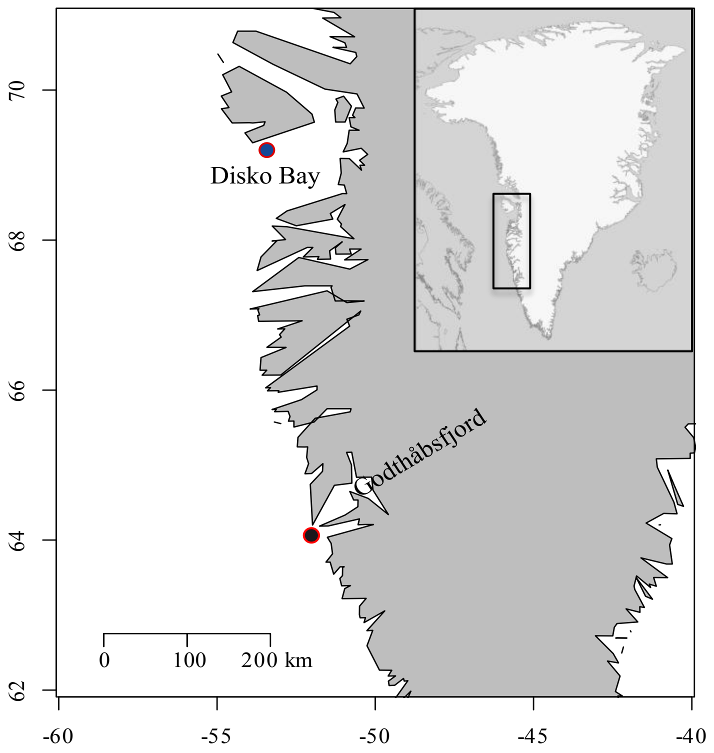
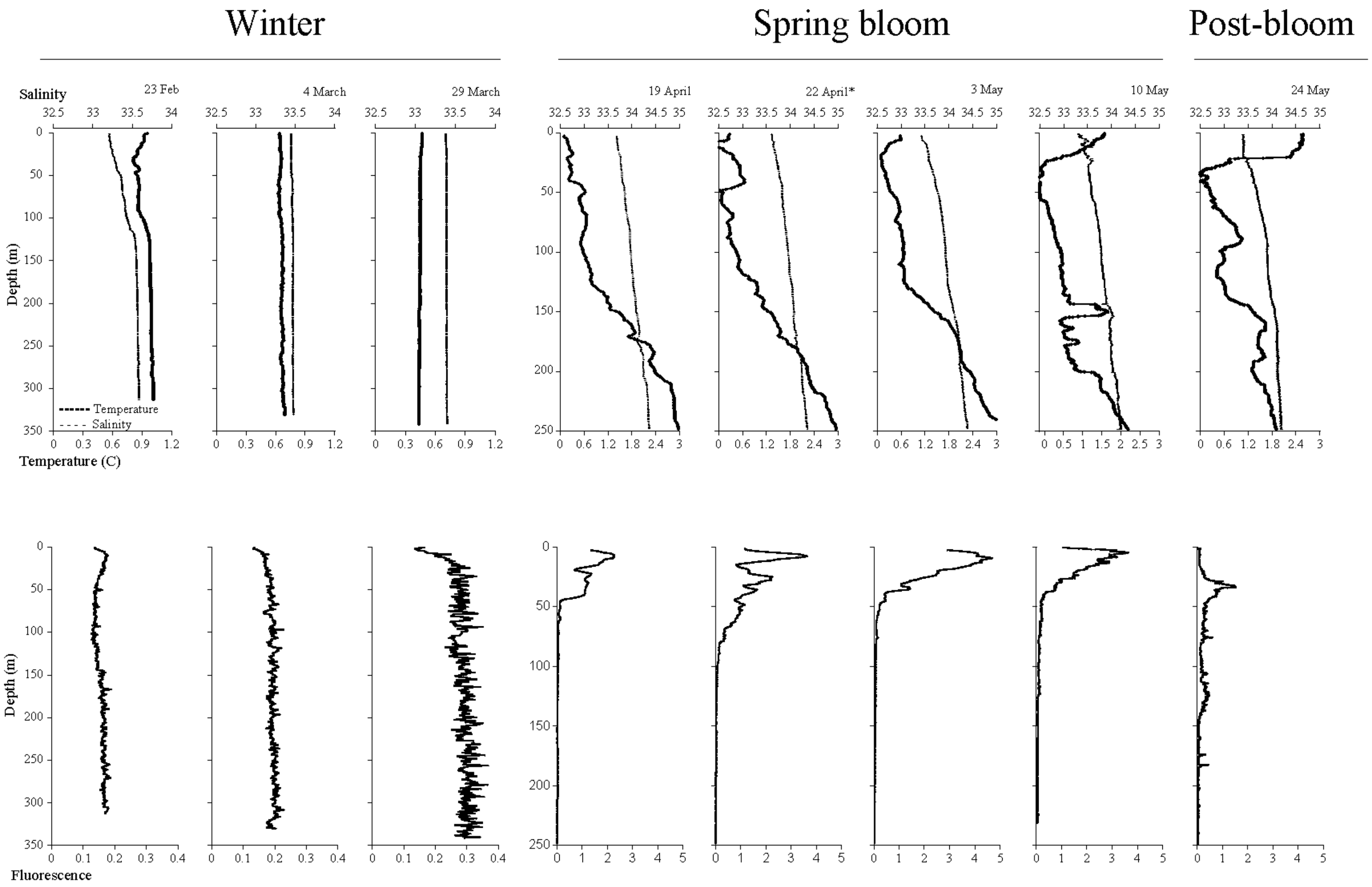


Fig.1.



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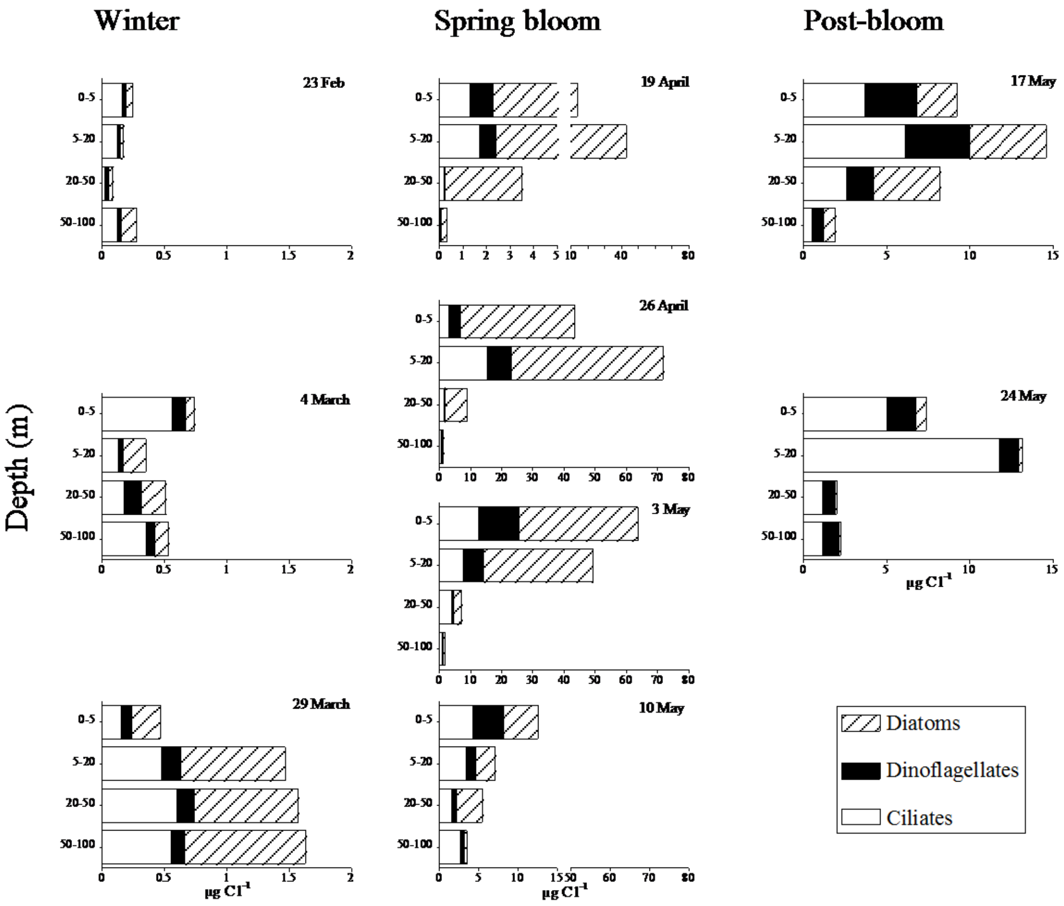
Winter
Spring bloom
Post-bloom
Depth (m)
23 Feb
4 March
29 March
19 April
26 April
3 May
10 May
17 May
24 May
0-5
5-20
20-50
50-100
0
0.5
1
1.5
2
0 1 2 3 4 5 10 40 80
0 10 20 30 40 50 60 70 80
0 5 10 15 50 60 70 80
0 5 10 15
µg Cl-1
Diatoms
Dinoflagellates
Ciliates

Fig. 3.

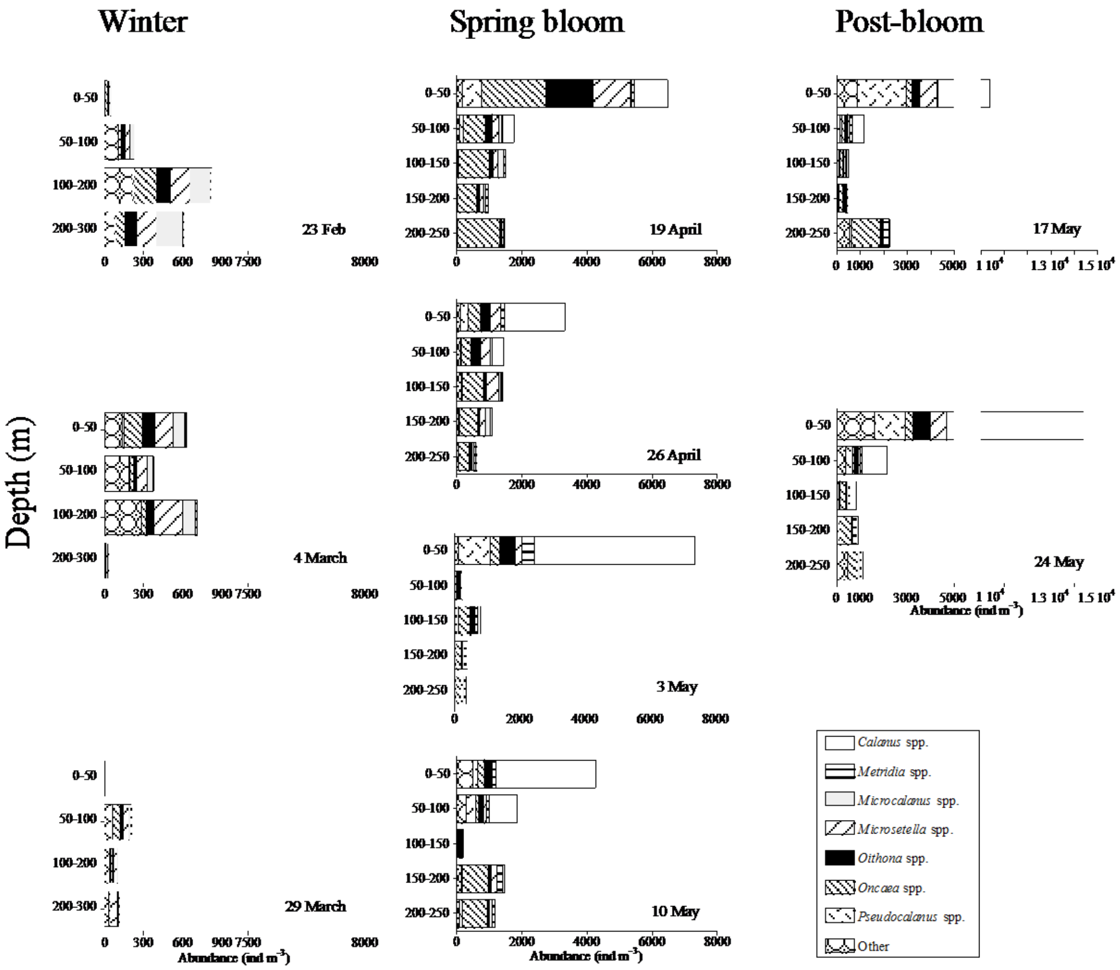
Winter
Spring bloom
Post-bloom
Depth (m)
0-50
50-100
100-200
200-300
100-150
150-200
200-250
23 Feb
4 March
29 March
19 April
26 April
3 May
10 May
17 May
24 May
0
300
600
900
7500
8000
2000
4000
6000
1000
3000
5000
$1\ 10^4$
$1.3\ 10^4$
$1.5\ 10^4$
Abundance (ind m^{-3})
Calanus spp.
Metridia spp.
Microcalanus spp.
Microsetella spp.
Oithona spp.
Oncaea spp.
Pseudocalanus spp.
Other

Fig. 4.

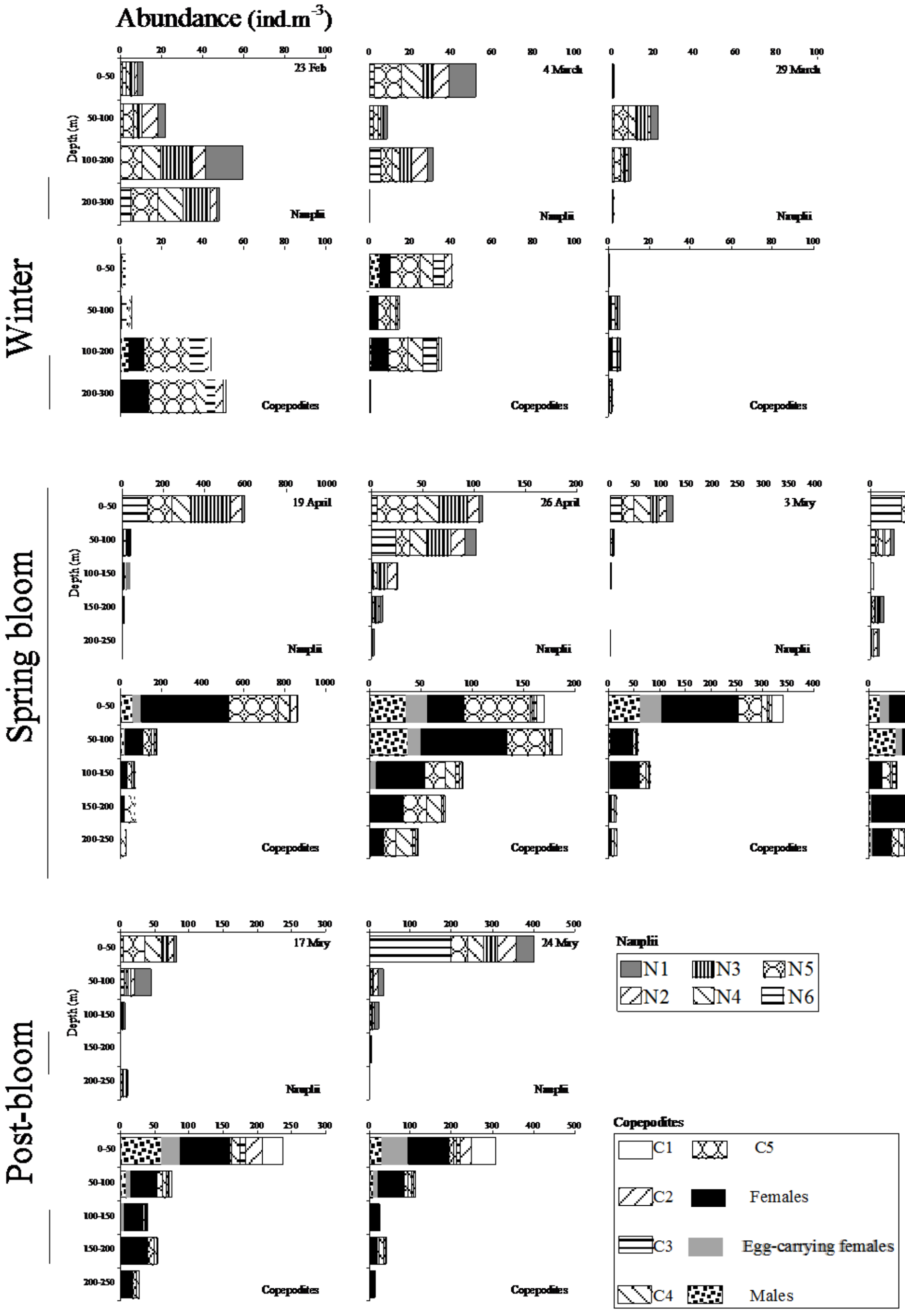
Abundance (ind.m^{-3})
Winter
Spring bloom
Post-bloom
Depth (m)
0-50
50-100
100-200
200-300
100-150
150-200
200-250
23 Feb
4 March
29 March
19 April
26 April
3 May
10 May
17 May
24 May
Nauplii
Copepodites
N1
N2
N3
N4
N5
N6
C1
C2
C3
C4
C5
Females
Egg-carrying females
Males

Fig. 5.

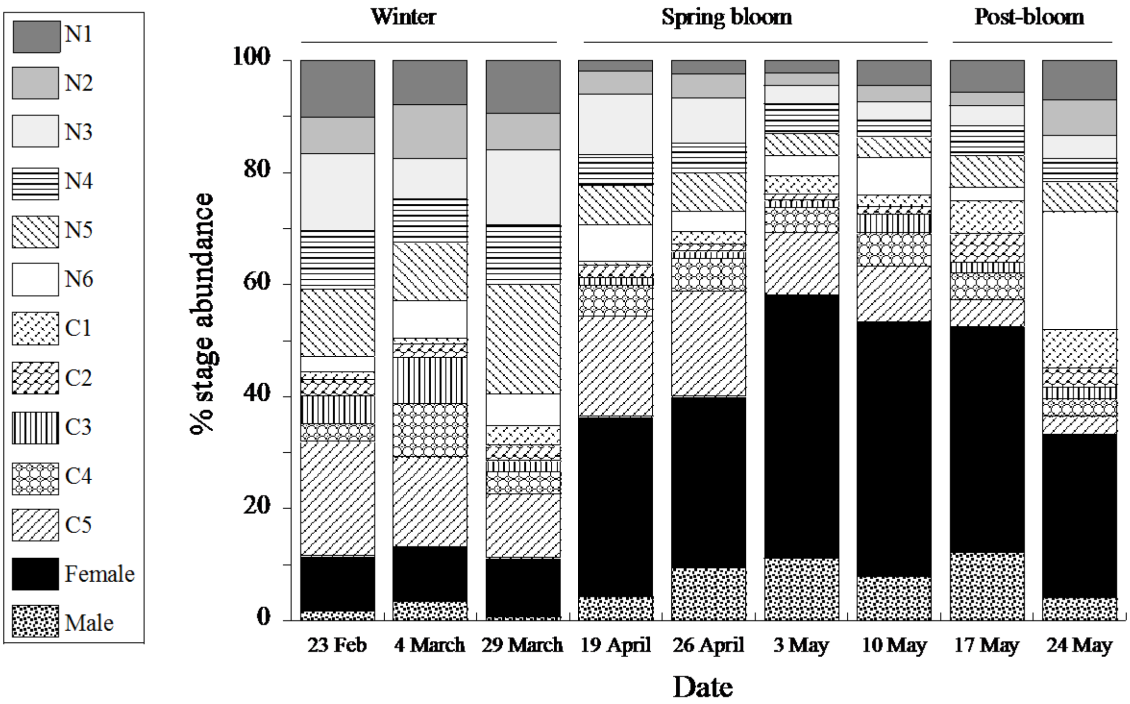
N1
N2
N3
N4
N5
N6
C1
C2
C3
C4
C5
Female
Male
Winter
Spring bloom
Post-bloom
% stage abundance
100
80
60
40
20
0
23 Feb
4 March
29 March
19 April
26 April
3 May
10 May
17 May
24 May
Date

Fig. 6.

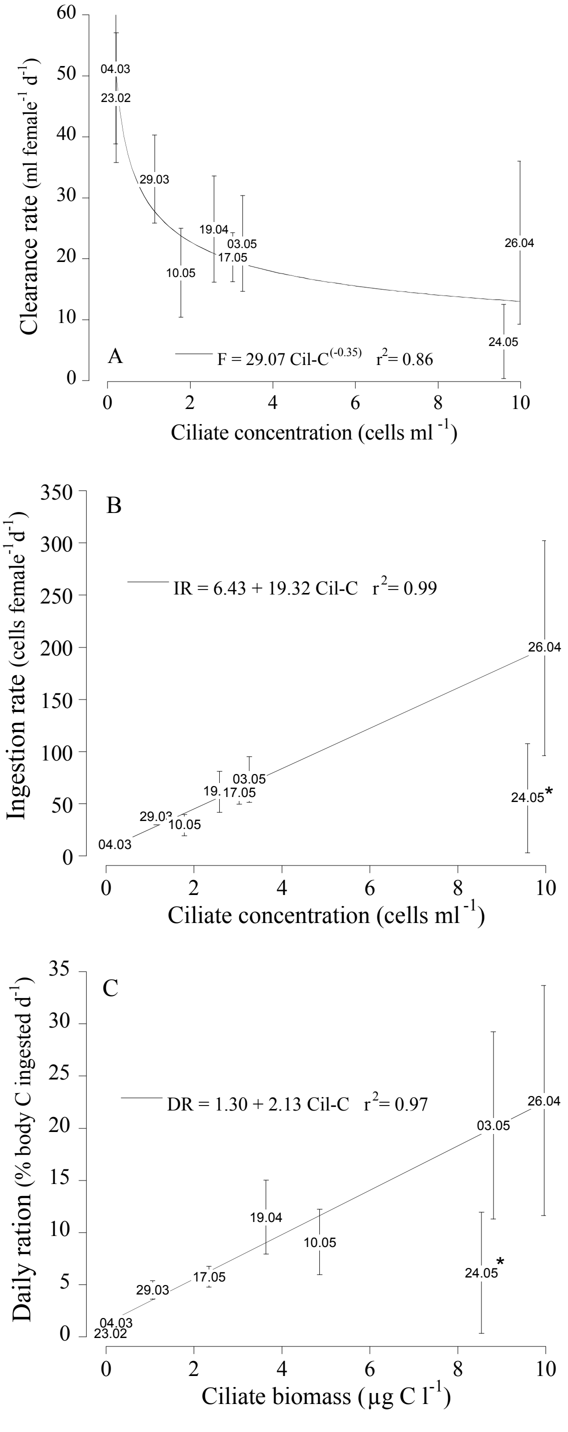
A
Clearance rate (ml female^{-1} d^{-1})
F = 29.07 Cil-C$^{(-0.35)}$ r^2= 0.86
Ciliate concentration (cells ml^{-1})
0
10
20
30
40
50
60
0
2
4
6
8
10
04.03
23.02
29.03
19.04
03.05
17.05
10.05
26.04
24.05
B
Ingestion rate (cells female^{-1}d^{-1})
IR = 6.43 + 19.32 Cil-C r^2= 0.99
Ciliate concentration (cells ml^{-1})
0
50
100
150
200
250
300
350
0
2
4
6
8
10
26.04
03.05
19.
17.05
29.03
10.05
04.03
24.05*
C
Daily ration (% body C ingested d^{-1})
DR = 1.30 + 2.13 Cil-C r^2= 0.97
Ciliate biomass (µg C l^{-1})
0
5
10
15
20
25
30
35
0
2
4
6
8
10
26.04
03.05
19.04
10.05
24.05*
17.05
29.03
04.03
23.02

Fig. 7.

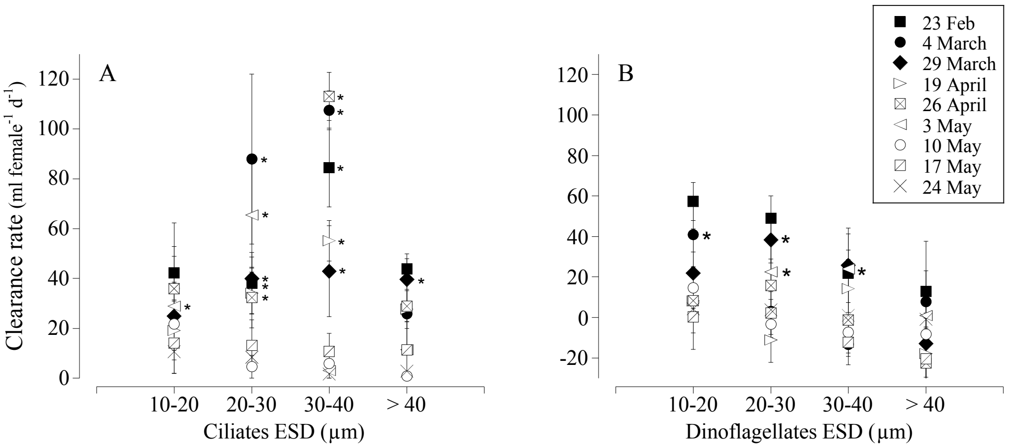
A
B
Clearance rate (ml female^{-1} d^{-1})
0
20
40
60
80
100
120
-20
10-20
20-30
30-40
> 40
Ciliates ESD (µm)
Dinoflagellates ESD (µm)
■ 23 Feb
● 4 March
◆ 29 March
▷ 19 April
⊠ 26 April
◁ 3 May
○ 10 May
▨ 17 May
× 24 May
*

Fig. 8.

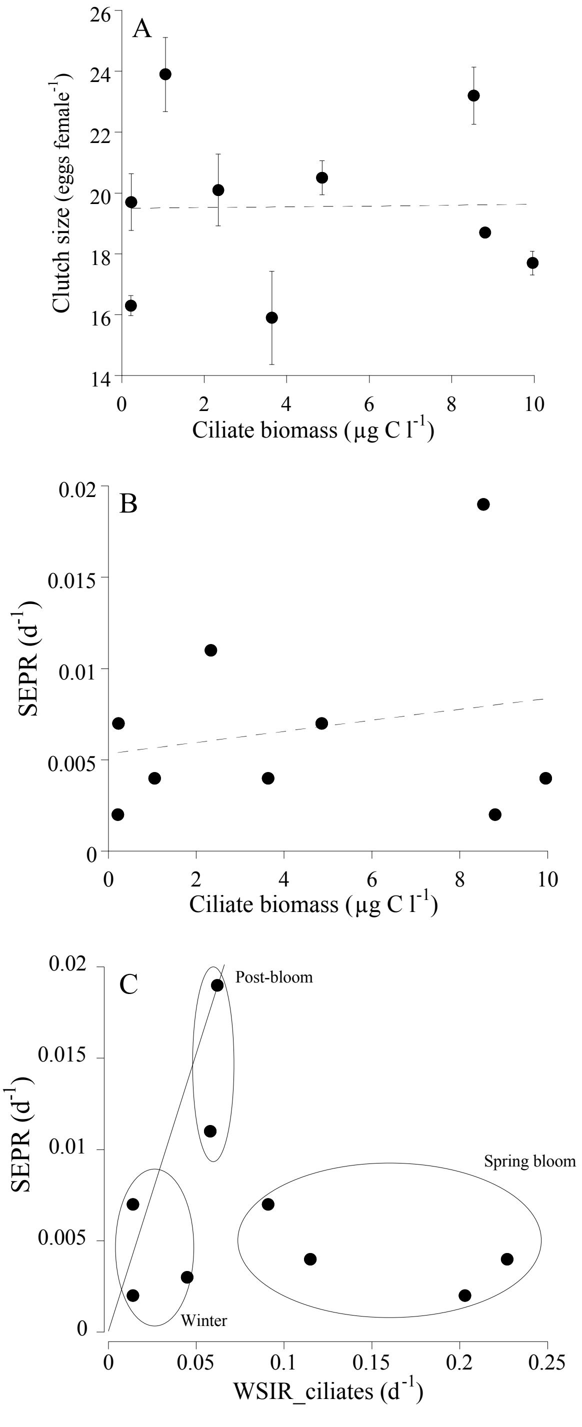
A
Clutch size (eggs female^{-1})
26
24
22
20
18
16
14
0
2
4
6
8
10
Ciliate biomass (µg C l^{-1})
B
SEPR (d^{-1})
0.02
0.015
0.01
0.005
0
0
2
4
6
8
10
Ciliate biomass (µg C l^{-1})
C
SEPR (d^{-1})
Post-bloom
Spring bloom
Winter
0.02
0.015
0.01
0.005
0
0
0.05
0.1
0.15
0.2
0.25
WSIR_ciliates (d^{-1})

Fig. 9.

Tables

Table 1. Mean (± SE) chlorophyll *a* concentrations (μg l^{-1}) in the upper 100 metres from each sampling date.

Water depth (m)	Winter			Spring bloom				Post-bloom	
	23 Feb	5 March	29 March	19 April	26 April	3 May	10 May	17 May	24 May
1	0.07	0.07	0.13	8.3 ± 0.09	20.4 ± 2.23	12.8 ± 1.86	10.0 ± 1.13	5.2 ± 0.51	0.9 ± 0.09
15	0.07	0.07	0.14	6.6 ± 0.27	17.9 ± 2.66	14.7 ± 2.78	9.0 ± 1.52	8.2 ± 1.07	1.5 ± 0.21
50	0.08	0.08	0.14	0.9 ± 0.02	5.0 ± 1.02	1.8 ± 0.01	4.3 ± 0.59	8.3 ± 1.08	2.4 ± 0.32
75	0.07	0.07	0.14	0.3 ± 0.09	1.5 ± 0.28	0.8 ± 0.24	1.4 ± 0.22	1.5 ± 0.21	1.4 ± 0.03
100	0.07	0.07	0.14	0.1 ± 0.06	0.8 ± 0.03	0.5 ± 0.04	0.9 ± 0.23	0.9 ± 0.16	1.4 ± 0.20

Table 2. Mean depth integrated abundance (cells ml^{-1}) and biomass (μg C l^{-1}) in the upper 100 m of each potential prey category (diatoms,dinoflagellates, and ciliates) by sampling location and date.

			Diatoms		Dinoflagellates		Ciliates	
Location	Date	Period	Biomass μg C l^{-1}	Abundance cells ml^{-1}	Biomass μg C l^{-1}	Abundance cells ml^{-1}	Biomass μg C l^{-1}	Abundance cells ml^{-1}
Godthåbsfjord	23 Feb	Winter	0.03	0.14	0.02	0.07	0.06	0.06
	4 March		0.14	0.51	0.08	0.13	0.18	0.15
	29 March		0.65	1.63	0.11	0.17	0.43	0.38
Disko	19 April	Spring bloom	12.25	17.73	0.27	0.52	0.61	0.47
	26 April		17.93	39.96	2.28	2.82	4.68	3.41
	3 May		12.83	22.18	2.91	3.70	4.62	3.31
	10 May		2.38	6.15	0.91	1.60	2.06	1.54
Disko	17 May	Post-bloom	3.07	5.20	1.93	4.19	2.93	3.98
	24 May		0.17	0.39	0.78	2.30	3.86	9.42

Table 3. Experimental conditions of the feeding experiments. For each experiment the number of replicates (*n*), concentration of adult females of *Oithona similis* in the bottles, and female body weight are indicated. Initial concentration of dinoflagellates (dino.) and ciliates in cell and biomass is shown. Mean (± SE) clearance and ingestion rates of dinoflagellates and ciliates are shown, as well as the percentage of body carbon ingested per female and day (daily ration).

				Female		Initial concentration				Clearance rate		Ingestion rate		Daily ration	
Location	Date	Period		concent.	weight	Dino.	Ciliates	Dino.	Ciliates	Dino.	Ciliates	Dino.	Ciliates	Dino.	Ciliates
			n	females l^{-1}	μg C	cells ml^{-1}		μg C l^{-1}		ml cop d^{-1}		cells cop d^{-1}		% body C ingested d^{-1}	
Godthåbsfjord	23 Feb	Winter	3	15	0.71	0.16	0.21	0.09	0.22	19.0 ± 7.8 *	46.4 ± 10.6 *	2.8 ± 1*	9.4 ± 1.4*	0.21 ± 0.08	1.4 ± 0.2
	4 March	Winter	3	15	0.81	0.15	0.2	0.08	0.23	8.8 ± 4.7	51.2 ± 12.3 *	1.2 ± 0.6	9.9 ± 1.9*	0.08 ± 0.04	1.4 ± 0.3
	29 March	Winter	3	15	0.77	0.27	1.14	0.14	1.06	21.3 ± 11.3	33.1 ± 7.2 *	5.5 ± 2.7	37.3 ± 7.2*	0.38 ± 0.19	4.5 ± 0.9
Disko	19 April	Spring bloom	3	18	0.75	6.45	2.58	2.77	3.64	-1.3 ± 15.7	24.9 ± 8.7 *	n.v.	61.4 ± 19.8*	n.v	11.5 ± 3.54
	26 April	Spring bloom	3	18	0.86	14.34	9.98	11.81	9.96	7.7 ± 23.0	22.6 ± 4.9	7.7 ± 301.9	199.2 ± 103	n.v.	22.7 ± 11.0
	3 May	Spring bloom	4	18	0.89	7.33	3.26	11.68	8.81	8.3 ± 4.5	22.5 ± 6.7*	60.5 ± 32.5	73.2 ± 21.8*	15.0 ± 5.8	20.3 ± 8.9
	10 May	Spring bloom	4	18	0.81	4.25	1.78	4.15	4.86	4.6 ± 3.2	17.7 ± 7.3*	18.4 ± 13.1	29.6 ± 10.2*	2.1 ± 1.5	9.1 ± 3.1
Disko	17 May	Post-bloom	4	18	0.81	4.81	3.03	2.42	2.34	2.4 ± 3.1	20.3 ± 4*	10.3 ± 14.3	60 ± 10.2*	0.7 ± 0.9	5.8 ± 1.0
	24 May	Post-bloom	3	18	0.81	4.41	9.59	1.98	8.54	2.2 ± 5.0	6.4 ± 6.1	7.9 ± 22.6	55.3 ± 52.3	0.4 ± 1.3	6.1 ± 5.8

* Significant rates (*t-test* $p < 0.05$)
n.v.: negative value

Table 4. Fecundity of *Oithona similis*. Proportion of ovigerous females, clutch size, egg production rates (EPR), and weight-specific egg production rates (SEPR) are based in weighted average values from WP-2 net and multinet samples. Egg production efficiencies (GGE) are estimated from weight-specific ingestion rates only on ciliates.

Location	Date	Period	Temperature (ºC)	Ovigerous females	Clutch size		EPR	SEPR	GGE
				%	eggs female^{-1}	average and range	eggs female^{-1} d^{-1}	% d^{-1}	%
Godthåbsfjord	23 Feb	Winter	1.0	8	16.3 ± 0.33**	20 (16-23)	0.09	0.2	16
	4 March	Winter	0.7	24	19.7 ± 0.93**		0.30	0.7	47
	29 March	Winter	0.4	14	23.9 ± 1.22**		0.17	0.4	9
Disko	19 April	Spring bloom	0.3	15	15.9 ± 1.53	18 (14-36)	0.17	0.4	3
	26 April	Spring bloom	0.4 *	29	17.7 ± 0.39		0.19	0.4	2
	3 May	Spring bloom	0.2	12	18.7 ± 0.10		0.09	0.2	1
	10 May	Spring bloom	1.0	31	20.5 ± 0.56		0.30	0.7	7
Disko	17 May	Post-bloom	1.5 *	36	20.1 ± 1.18	22 (14-38)	0.51	1.1	20
	24 May	Post-bloom	2.3	56	23.2 ± 0.94		0.91	1.9	31

* Temperature not estimated from CTD profiles

** Clutch sizes estimated from n < 10 egg sacs dissected