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Phytoplankton ingestion by appendicularians in the North Water

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Abstract

We investigated the abundance, body-size distribution, diet, and ingestion rates of appendicularian tunicates at 8 stations in the North Water polynya, northern Baffin Bay, during late June and July 1998. Abundance of appendicularians in the chlorophyll-rich surface layer (40–125 m) ranged from 38 to 11248 m⁻². Body size of individuals ranged from 0.21 to 4.8 mm. Gut chlorophyll content varied from 0 to 84 ng ind⁻¹ and increased with increasing body size. Gut passage time varied from 42 to 104 min (mean ± SD: 58 ± 18 min). Phytoplankton ingestion rates ranged from 0.007 to 2.083 mg chlorophyll m⁻² d⁻¹, with a median of 0.49 mg chlorophyll m⁻² d⁻¹. The median daily grazing impact of the oikopleurid populations was 0.42% and 5.4% of total phytoplankton biomass and primary production, respectively. Since this represents ingested phytoplankton and does not include cells trapped within the mucous houses, the contribution of appendicularian populations to phytoplankton mortality could be 2-fold higher (i.e. ca. 10% of primary production). The faecal pellets of animals incubated onboard in water from the subsurface chlorophyll maximum contained primarily small diatoms at the northern stations, and a mixture of diatoms, dinoflagellates, flagellates, and ciliates at southern stations. The median, daily flow of biogenic carbon from phytoplankton to appendicularian faecal pellets was 8 mg C m⁻², which represents 4% of biogenic carbon export during the month of July. Because the phytoplankton was dominated by small *Chaetoceros* cells, appendicularian ingestion rates were not inhibited by the clogging of the filtration mechanism at high Chl *a* concentrations. Thus, the impact of appendicularians on daily primary production during this season was a simple function of appendicularian abundance, population size structure, and gut throughput rate.

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1. Introduction

Polynyas are mesoscale (i.e. 10 m to 100 km) regions of relatively open water in the midst of ice-covered seas. Polynyas attract polar bears, seabirds, whales, and humans, possibly because they

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provide access to open water, or because of higher biological productivity relative to surrounding ice-covered waters (Stirling, 1997). The North Water polynya is one of the largest and most productive polynyas in the Arctic. A pilot study conducted in May 1991 found a pronounced east–west gradient in hydrography and in the abundance and community structure of phytoplankton (Lewis et al., 1996). However, the effect of these gradients on zooplankton community structure and carbon flux remains unexplored. A central objective of the International North Water Polynya Study (NOW) was to determine the fate of biogenic carbon with respect to physical and biological gradients in the polynya.

Appendicularians are abundant zooplankton in the cold waters of sub-Arctic and Arctic seas, and can contribute substantially to biogenic carbon fluxes (Parsons et al., 1989; Ashjian et al., 1997; Bauerfeind et al., 1997). For example, appendicularians are common in the Northeast Water polynya (northern Greenland Sea), where Ashjian et al. (1997) observed densities as high as $230,000 \text{ ind m}^{-2}$. The discarded mucous-filter houses and faecal pellets of appendicularians comprise about 25% of the annual flux of biogenic carbon to the bottom of the Northeast Water (Bauerfeind et al., 1997). Appendicularians are also abundant in summer in the area of the St. Lawrence Island polynya (Bering Sea), where Deibel and Shiga (unpubl.) observed densities as high as $100,000 \text{ ind m}^{-2}$. Since *Oikopleura vanhoeffeni*, the dominant appendicularian in northern seas, is a stenothermal cryophile (Barrington, 1965), we anticipated that this species would be an important mesozooplankton in the North Water.

Over the past several years, we have developed in situ techniques for the determination of ingestion rates by appendicularian tunicates based on careful tests of assumptions of the gut pigment technique (Bochdansky et al., 1998). These techniques have been used to determine individual rates of ingestion of appendicularians in the Northeast Water (Acuña et al., 1999) and the St. Lawrence Island polynya (Deibel and Shiga, unpubl.). In the Northeast Water, Acuña et al. (1999) found that feeding by individual oikopleur-

id appendicularians was inhibited during phytoplankton blooms characterized by high phytoplankton biomass and the abundance of diatom chains, probably because large cells and colonies can clog the appendicularian mucous feeding mechanism. However, this result was not tested at a population level and it remained to be shown whether inhibition of individual ingestion rates translated into reduced population grazing fluxes. We expected that large chain-forming diatoms would dominate the phytoplankton communities during the productive season in the North Water, as reported by Lewis et al. (1996). Accordingly, our working hypothesis was that individual and population grazing by appendicularians would be a decreasing function of phytoplankton biomass during that period.

2. Methods

2.1. Field procedures

We report individual and population ingestion by appendicularians from 8 stations along a northwest–southeast trophic gradient that existed during the sampling period of the present study (18 June–20 July 1998; Fig. 1). Hydrographic data were collected using a General Oceanics rosette system equipped with 24 Brookes Ocean Technology 10-l sample bottles, a Falmouth Scientific Instrument CTD (FSI-ICTD) and a Seatech fluorometer. Water for gut passage time (GPT) experiments was collected from the depth of the fluorescence maximum (FM), assessed at the time of sampling from the downcast fluorescence profile.

Primary production and phytoplankton biomass (chlorophyll *a*) measurements are described by Klein et al. (2002) and Mei et al. (2002). Water from the FM was passed in parallel through 140 μm , nylon mesh and 5 μm Poretics membrane filters, resulting in total, <140 and <5 μm size fractions. The maximum pore size of the inlet filter of mature *O. vanhoeffeni* is ca. 140 μm (Deibel, 1986). Therefore, the <140 μm fraction was considered to represent ingestible particles. For each size fraction, 300–500 ml subsamples were

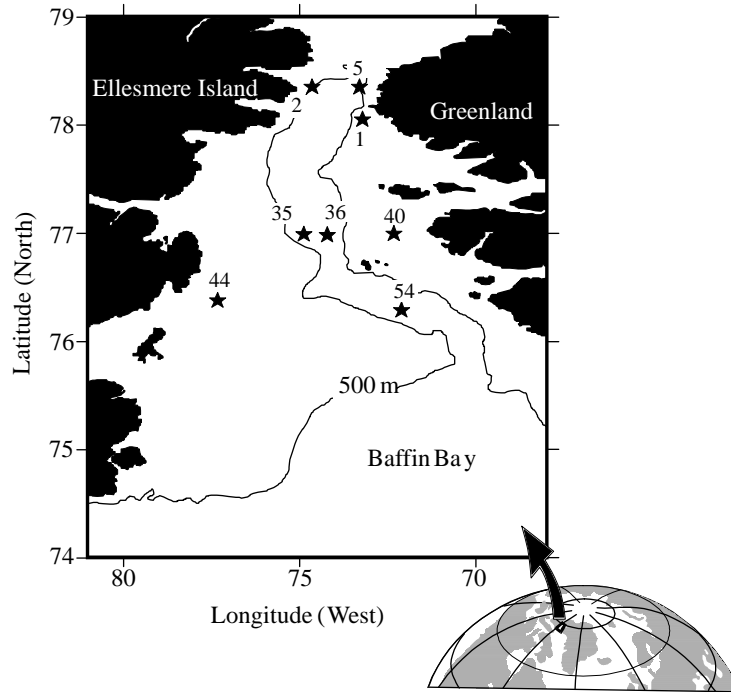


Fig. 1. Location of stations sampled for appendicularian gut chlorophyll analyses in the North Water polynya, 18 June–20 July, 1998.

filtered through Whatman GF/F glass fibre filters. The filters were placed in small, sterile Petri dishes and were stored at -80°C in the dark for up to 7 months before analysis.

Zooplankton samples were collected at each station using vertical tows of paired, 1 m^2 zooplankton nets of $200\ \mu\text{m}$ mesh (Ringuette et al., 2002). The contents of one cod end were immediately fixed in 4% seawater–formaldehyde for the quantification of in situ zooplankton (Ringuette et al., 2002), including appendicularians. Live appendicularians were removed from the second cod end for analysis of gut pigment content. Tow depth (40–125 m) was determined according to the temperature and fluorescence profiles at each station, with the general objective that surface layer tows represent zooplankton located in the stratum where chlorophyll-containing cells were abundant. Previous work indicates that appendicularians are most abundant in the upper 100 m of Arctic waters (Ashjian et al., 1997). The nets were retrieved at $0.3\text{--}0.5\text{ m s}^{-1}$, and a flow meter provided measurements of tow distance for sub-

sequent calculation of the volume filtered during each tow.

The net from which we collected appendicularians for gut pigment analysis was not rinsed after retrieval, in order to minimize stress and damage to animals in the cod end. Contents of the cod end were gently distributed into $\sim 10\text{ l}$ of surface water and transported to a 0°C laboratory. After nets arrived on deck, no more than 26 min elapsed before we finished isolating individual appendicularians. Each animal was removed from the sample using a wide-bore pipette, rinsed twice in 250 ml of filtered seawater, and isolated in a cell of a glass well plate. There was no error introduced by cod end feeding since oikopleurids collected by this method are generally separated from their houses, which are required for food collection. Healthy animals at 0°C released one faecal pellet every 26 min at most (see Results). Therefore, on average, each appendicularian could have defecated a maximum of one pellet before it was placed into the well plates. After isolation, the trunk length of each animal was measured to the nearest

0.06 mm under red light. Trunk length was determined from the lips to the back edge of the stomach, excluding the gonad. Next, the house rudiment and tail were surgically removed. The trunk and any faecal pellets found in the well plate were transferred to a 1.5 ml Eppendorf microcentrifuge tube and flash frozen on a -80°C aluminium block. Onboard, the tubes were stored in the dark at -80°C . Upon arrival at the laboratory, the samples were stored at -80°C in the dark until analysis by HPLC within 9 months of collection. Medium-term (42 day), deep-frozen storage does not affect levels of gut pigment (Morales et al., 1990), and storage periods in the order of the ones used here are common in the gut fluorescence literature.

At five of the eight stations, we used a net with an extra-large codend (diameter = 0.30 m, height = 0.38 m) to collect additional appendicularians for measurement of individual GPT. This net was towed at 0.1 m s^{-1} (Acuña et al., 1999). The advantage of this apparatus is that we can obtain animals feeding actively in their houses. The extra-large codend was transferred to the 0°C cold laboratory, where individual appendicularians were isolated using a wide-bore, acrylic pipette (Acuña et al., 1994). Each appendicularian was placed in a transparent, plastic container filled with ca. 400 ml of water from the FM. These incubation containers were suspended from the ceiling of the laboratory using rubber bands to isolate the animals from ship vibrations (Acuña et al., 1999). Gut throughput dynamics and the time interval between pellets were recorded visually with a stop watch. GPT was calculated according to López-Urrutia and Acuña (1999).

Following GPT observations at five of the stations, 1–2 faecal pellets were collected using a Pasteur pipette and stored fresh in glass vials for microscopic determination of their phytoplankton content, usually within 24 h. Single pellets were measured using an Olympus research microscope. Next, a cover slip was placed on top of the pellet and the squashed pellets were first examined using epifluorescence microscopy, followed in some cases by transmitted light observations. For abundant organisms $<8\text{ }\mu\text{m}$ in size, concentration was extrapolated from counts for a small area of

the pellet. Larger and less abundant organisms were counted over the entire pellet. Both autotrophic and heterotrophic organisms were counted, including diatoms, diatom resting spores, dinoflagellates, dinoflagellate cysts, naked flagellates, silicoflagellates, and oligotrich and tintinnid ciliates. Ingestion rates for non-phytoplankton prey will be reported elsewhere. Dimensions of all cells were recorded in order to calculate biovolume and to estimate carbon content.

2.2. Laboratory analytical procedures

Each quantitative zooplankton sample was split into subsamples using a Motoda Box splitter. Each animal was counted and the trunk length was measured for the first 40 animals encountered. Trunk and tail lengths were multiplied by a factor of 1.18 to correct for shrinkage in formaldehyde (Deibel, 1988). The volume-specific appendicularian abundance was calculated from sample counts after correcting for net-volume sampled using a calibrated flow meter and net mouth area. The areal abundance at each station was then calculated as the product of volumetric abundance and tow depth.

For the analysis of gut chlorophyll content (GCC), 750 μl of cold, 90% acetone were added to the microcentrifuge tubes containing the frozen appendicularians. Samples were homogenized in a iced bath using a manual micropestle. To maximize pigment recovery, the micropestle was rinsed into the original homogenate with 250 μl of ice-cold, 90% acetone. A separate, mixed-source standard was processed in the same way with each sample set to control for any loss of pigment that may have occurred during the procedure. The samples were sonicated at 0°C for 3 min, and passively extracted at -20°C for 10–12 h. After extraction, the samples were sonicated for 3 min at 0°C , followed by centrifugation at 10,000 g for 3 min at 2°C . A 500 μl aliquot of the supernatant was used for pigment analyses by high performance liquid chromatography (HPLC).

Chlorophylls *a*, *b* and *c* were identified and quantified following the procedures of Mantoura and Llewellyn (1983) and Bidigare et al. (1985). Our Beckman HPLC system consisted of a

4.6 × 250 mm reverse phase ODS-C18 column with a pore size of 5 µm, a model 126 quaternary pump, and a model 121 fluorescence detector with an excitation filter of 345–510 nm and emission filter of 610–650 nm. Immediately prior to injection, a 150 µl aliquot of 1 M ammonium acetate was added to the 500 µl sample to improve resolution of the peaks. A 100 µl aliquot of the mixture was injected onto the HPLC using a solvent flow rate of 1550 ml min⁻¹. Chlorophylls *a* and *b* were purchased from Sigma Chemical Co. All other standards were prepared from algal cultures after Wright et al. (1991). Pigment concentrations were quantified by integrating the area under the peaks using Beckman Gold software. The limit of detection for chlorophyll *a* was 0.2 ng ml⁻¹ with reproducibility to ±0.05 ng ml⁻¹. Seven of the 192 animals examined had a GCC below the detection limit. Here we follow the approach by Acuña et al. (1999) in dealing with the effect of body size on GCC, that is, we fit log-transformed GCC and trunk length data to linear functions. This method does not accept 0 GCC values. Dropping values from below the detection limits from our analyses would result in a maximum change to estimates of population ingestion rates of 3%, if all of the discarded data points were from large animals, which was not the case. Thus, the effect of our decision on the estimates of population ingestion rates was <3%.

The gut chlorophyll technique depends upon either complete integrity of the chlorophyll molecule during gut passage or on the ability to recreate the initial amount of chlorophyll ingested from a known and predictable chlorophyll conversion efficiency. We have shown that the conversion of diatom chlorophyll to phaeopigments and colourless products by appendicularians is highly predictable (Bochdansky et al., 1998). We have applied this conversion efficiency to the determination of individual ingestion rates of appendicularians in the Northeast Water polynya (Acuña et al., 1999). Since much of the diet of appendicularians in the North Water consisted of diatoms, individual chlorophyll ingestion rate was determined as

$$IR = \frac{k \cdot GCC}{GPT}, \quad (1)$$

where GCC is the gut chlorophyll content (i.e. the sum of chlorophylls *a* + *b* + *c*, ng ind⁻¹), GPT is the gut passage time (d⁻¹), and *k* = 4.76, based on a conversion efficiency of 79% from ingested chlorophyll to phaeopigments and colourless products (Bochdansky et al., 1998).

To determine the population ingestion rate, we first determined the trunk length of a subsample of up to 40 oikopleurids from the net tows. We then estimated the GCC of each animal in the tow from the power function of individual GCC vs. trunk length. Finally, for each station, we used Eq. (1) in combination with the average GPT observed at that station to calculate the individual ingestion rate for each animal in the tow, and summed these individual rates for all of the animals in the population.

3. Results

3.1. Hydrography and the abundance of oikopleura

In July 1998, the surface layer of the polynya was dominated by relatively oligotrophic Baffin Bay water (Fig. 2; cf. Tremblay et al., 2002). The upper mixed layer at the two northernmost stations (i.e. stations 2 and 5) continued to be dominated by silicate-rich, Arctic water (Fig. 2). While temperature in the upper mixed layer was highest in the central and southwestern polynya, salinity showed no obvious horizontal pattern in the surface mixed layer (Fig. 2). The FM, where we collected water for gut passage observations (see methods section on GPT and defaecation interval) was shallower at the Northeastern stations (Fig. 2). There was no clear trend in the horizontal distribution of *O. vanhoeffeni*, although their abundance was higher in the central and southern regions of the polynya where temperatures were also higher (Fig. 2). The appendicularian populations at these stations were dominated by small, juvenile animals <1.5 mm long (Fig. 3).

3.2. Individual gut chlorophyll content

The GCC of oikopleurid appendicularians ranged from the detection limit of our technique

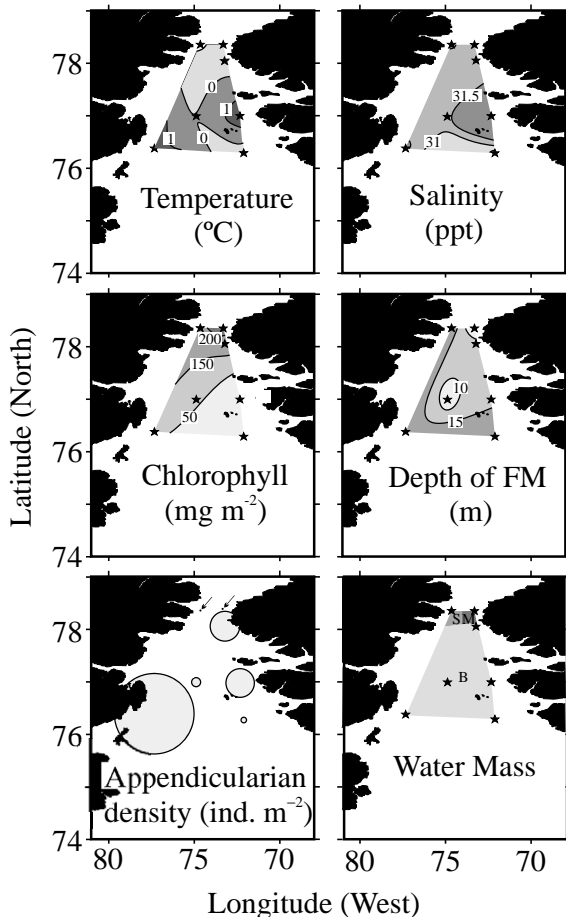


Fig. 2. Distribution over the study area of temperature and salinity at 10 m depth, chlorophyll integrated to the depth of the surface zooplankton tows, depth of the FM where we collected water for gut passage observations, appendicularian density from surface tows (circles are proportional to density, the largest is equivalent to 11248 ind m^{-2}), arrows indicate stations with less than 100 ind m^{-2} , and water mass (S: silicate-rich arctic water; B: Baffin Bay water; M: nutrient characteristics intermediate between S and B; from Tremblay et al., 2002). Data from station 36 were not represented because it was sampled much earlier (18 June) than the others (9–20 July), and because we had no population size distributions to estimate population ingestion rates.

to a maximum of ca. 84 ng ind^{-1} (Fig. 4). GCC increased with increasing body size, with generally higher GCC at a given body size at stations 1, 2, 5 and 36 (Fig. 4). Four of the eight stations had significant, linear regression relationships between log GCC and log trunk length (Fig. 4). The eight

slopes were not significantly different from one another (test for homogeneity of slopes; $F_{7,167} = 0.36$, $p = 0.92$), although intercepts were significantly different (ANCOVA, $F_{7,174} = 10$, $p < 0.001$). Our estimate of the common slope relating GCC and body size for all of the data was 1.57 ± 0.23 ($\pm \text{SE}$). Stationwise intercepts varied between 0.04 and 0.65 ($\log [\text{ng ind}^{-1}]$) and sample sizes between 9 and 38 (Table 1). Results of ANCOVA analysis after balancing the sample sizes to $n = 9$ do not differ substantially from these with unbalanced data.

The exponential of the station-wise intercepts of the log–log regressions between GCC and trunk length (i.e. 10^i) can be used as an index representing the overall level of gut fullness at each station normalized for differences in body size (Acuña et al., 1999), after assuming a common slope of 1.57. Thus, 10^i represents the mean GCC of a hypothetical animal 1 mm long. 10^i increased steadily with chlorophyll concentration from the southern stations (35, 40, 44, 54) to the northernmost stations (1, 2, 5), and then decreased again at the highest chlorophyll concentration of station 36, sampled one month before (Fig. 5).

3.3. Gut passage time and defaecation interval

GPT and defaecation interval were determined for animals collected from five of the eight stations. These animals covered the full range of maturity stages from I to IV (Shiga, 1976), i.e. immature animals lacking any gonad tissue to fully mature, pre-spawning adults (Table 2). In addition, these animals ranged in trunk length from 0.84 to 2.76 mm (Table 2). Water temperature during the 10 incubation experiments was maintained at -1.8°C to $+0.5^\circ\text{C}$ (Table 2). The water from the FM used for the incubations had total chlorophyll *a* concentrations of $0.99\text{--}4.82 \mu\text{g l}^{-1}$ (Table 2). GPT ranged from 42 to 104 min, with a mean value of 58 min. Defaecation interval (i.e. the time between release of successive faecal pellets) ranged from 18 to 46 min, with a mean value of 26 min. Overall, the faecal pellet production rate (i.e. GPT/defaecation interval) was 2.24 ± 0.14 pellets $\text{animal}^{-1} \text{ h}^{-1}$ (mean \pm SD).

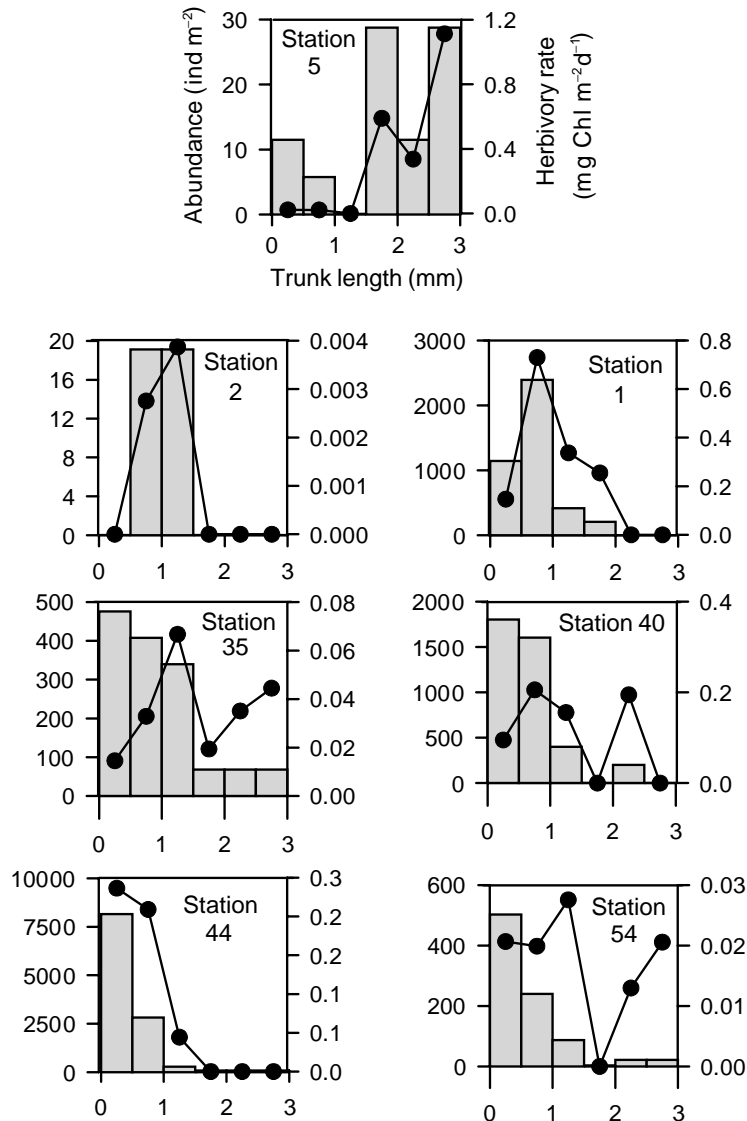


Fig. 3. Histograms for each station sampled showing the areal population abundance density of oikopleurid appendicularians (left Y-axis) in 6 size classes from 0 to 3 mm trunk length (X-axis). Rare, large animals captured from gut pigment tows were generally not encountered in subsamples from quantitative zooplankton tows. Corresponding line plots show the total chlorophyll ingestion rate (right Y-axis) for each appendicularian size class. Axis legends for all panels are the same as for the top panel.

3.4. Population ingestion rates

Size structure data available for the appendicularian population at seven of the eight stations in our study shows that many of the animals from the net tows were smaller than the minimum size

used to construct the GCC vs. trunk length regression relationships (compare the size distributions in Fig. 3 with the size range in Fig. 4). This was due to the fact that large animals were relatively rare and thus were less likely to be measured during enumeration of the preserved net

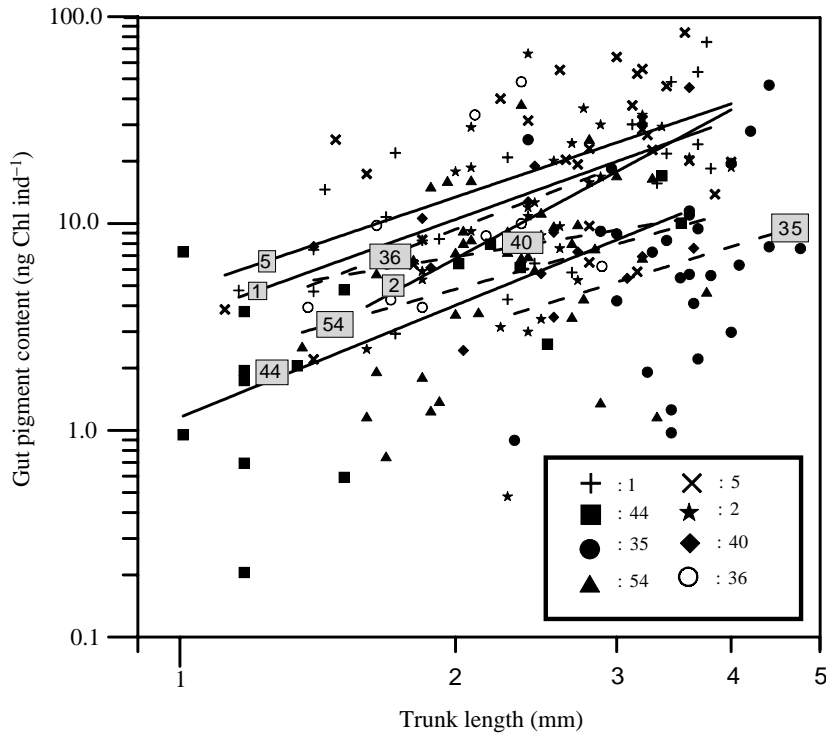


Fig. 4. GCC (i.e. chlorophylls *a*+*b*+*c*) of individual appendicularians versus body size (i.e. trunk length) from the 8 stations shown in Fig. 1. Stations with significant linear regressions between the log of GCC and the log of trunk length are shown as solid lines. Dotted lines depict regressions in which the slopes were not significantly different from 0 ($p > 0.05$). ANCOVA indicated that the 8 slopes were not significantly different from one another ($p = 0.92$) leading to the calculation of a common slope for all the data of 1.57 ± 0.23 .

Table 1
Number of appendicularians sampled for the analysis of individual gut pigment contents at each station, and estimate of the stationwise intercept (i , \pm SE) of the log–log regression between gut pigment content (ng ind^{-1}) and trunk length (mm) after assuming a common slope of 1.57 for all stations (see text)

Station	<i>n</i>	<i>i</i> (log[ng ind ⁻¹])
1	21	0.55 ± 0.13
2	31	0.44 ± 0.11
5	28	0.65 ± 0.12
35	26	0.04 ± 0.14
36	9	0.50 ± 0.14
40	14	0.29 ± 0.13
44	16	0.11 ± 0.10
54	38	0.19 ± 0.10

tow samples. Appendicularians for GCC analysis, on the other hand, were selected by eye from the replicate tow sample, and this process was

apparently biased toward larger trunk lengths. The median trunk length of appendicularians in situ ranged from 0.36 to 1.74 mm at the various stations (with an overall median of 0.56 mm, Table 3). Our estimates of the GCC of small animals could be in error if there was a difference in the diet between small and large animals. However, analyses of gut pigment contents by HPLC indicated no ontogenetic change in diet over a trunk length range of 1–5 mm (see below).

Appendicularian abundance in the upper 50 m varied between 38 and 11,248 ind m^{-2} , and population ingestion rate from 0.007 to 2.08 $\text{mg chlorophyll m}^{-2} \text{d}^{-1}$ (Table 3). The median population ingestion rate was 0.5 $\text{mg chlorophyll m}^{-2} \text{d}^{-1}$ (Table 3). Individuals 0.5–1.5 mm long were the main contributors to total population grazing (Fig. 3).

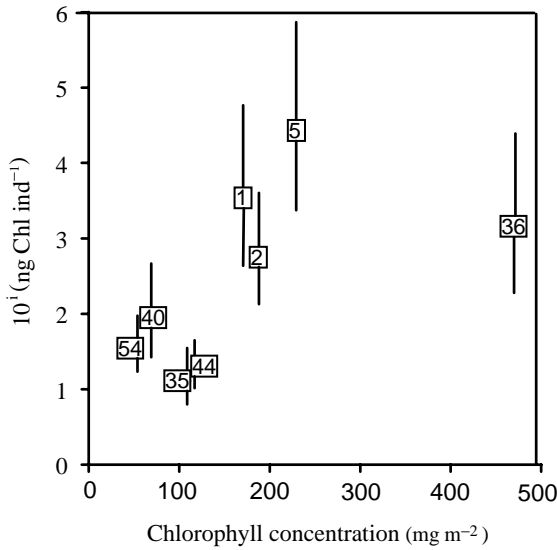


Fig. 5. Plot of the body-size corrected index of GCC (or 10^i) vs. the areal chlorophyll concentration over the upper 50 m of the water column. The error bars represent 10^{i+1SE} and 10^{i-1SE} , respectively. 10^i represents the GCC of a standard appendicularian 1 mm long (see Methods).

3.5. Diet

HPLC analysis of gut pigments suggested a lower Chl *b* content north of the study area (station 1, Fig. 6A) than south (station 54, Fig. 6B). Since microflagellates are the typically Chl *b*-bearing phytoplankton, this suggests a southward shift from a predominantly diatom based to a mixed diet of diatoms and microflagellates. The Chl *b*:Chl *a* ratios of gut contents varied significantly among stations (Fig. 7; ANOVA on arcsin transformed data, $F_{7,181} = 12.6$, $p < 0.001$), and an a posteriori Student–Newman–Keuls test discriminated two groups of stations: stations 40 and 54 in the southeast with high ratios and all other stations with low ratios. However, variances were highly heterogeneous (Bartlett test for heterogeneity of variances, $p < 0.001$). The Chl *a*:Chl *b* ratio was not correlated with trunk length (Fig. 7), suggesting little size-related shifts in diet.

Microscopic analyses of diet composition supported the trend observed in gut pigment data. More than 97% of the identified faecal pellet volume at the northern and central stations (1, 2

Table 2

Summary of the appendicularian gut passage time observations. Maturity stage is defined by Shiga (1976), with stage I being newly born juveniles and V being mature adults

Sta.	Animal #	Trunk length (mm)	Maturity stage	Temp. (°C)	Chl <i>a</i> <5 μm (mg m ⁻³)	Chl <i>a</i> <140 μm (mg m ⁻³)	Total Chl <i>a</i> (mg m ⁻³)	Gut passage time (min)	Defecation interval (min)
1	1	1.84	I	-0.6	0.26 ± 0.07	4.84 ± 0.46	4.82 ± 0.37	43.0	17.5 ± 9.2 (2)
2	1	2.08	IV	-1.8	0.27 ± 0.04	4.28 ± 0.32	4.23 ± 0.53	104.2 ^a	46.0 (1)
35	1	2.04	II	-0.3	0.18 ± 0.02	2.39 ± 0.61	2.55 ± 0.35	45.0	20.2 ± 0.4 (3)
35	2	2.20	II	-0.8	0.18 ± 0.02	2.39 ± 0.61	2.55 ± 0.35	65.8	29.7 ± 1.3 (3)
35	3	1.88	II	-0.4	0.18 ± 0.02	2.39 ± 0.61	2.55 ± 0.35	53.7 ^a	23.7 (1)
40	1	2.20	III	0.1	0.19 ± 0.03	1.08 ± 0.28	0.99 ± 0.15	42.0	18.7 ± 0.6 (3)
40	2	2.76	III	0.5	0.19 ± 0.03	1.08 ± 0.28	0.99 ± 0.15	58.9 ^a	26.0 ± 0.0 (2)
54	1	1.88	III	-1.6	0.23 ± 0.03	1.36 ± 0.34	1.47 ± 0.35	52.3	21.2 ± 0.1 (3)
54	2	2.40	I	-1.23	0.23 ± 0.03	1.36 ± 0.34	1.47 ± 0.35	54.7	25.6 ± 2.6 (3)
54	3	0.84	Nm	Nm	0.23 ± 0.03	1.36 ± 0.34	1.47 ± 0.35	62.7 ^a	27.7 (1)
Mean		2.01 ± 0.49						58.2 ± 18.0 (10)	25.6 ± 8.2 (10)

The mean defecation interval (±SD) includes the number of observations inside the parentheses. “Nm” indicates not measured.

^a These gut passage times have been estimated from defecation intervals according to the regression equation of gut passage time vs. defecation interval calculated for the other six animals in which gut passage time could be measured: gut passage time = 2.265*defecation interval; SE for the slope = 0.054; $r^2 = 0.997$; $n = 6$; $F = 1771$; $p = < 0.001$.

Table 3

Summary of oikopleurid appendicularian population ingestion rate calculations for those stations in which both gut pigment and population size structure were available (tow depths between parentheses). Chlorophyll concentration is integrated for the tow depth range, and primary production to the euphotic zone. Population chlorophyll ingestion rates were converted to carbon units assuming a C:Chl ratio of 50. Mean values are \pm SD

Sta	Tow depth (m)	Median trunk length (mm)	Population density (ind m ⁻²)	Population gut Chl a content (ng m ⁻²)	Population Chl a ingestion rate (mg m ⁻² d ⁻¹)	Chl a conc. (mg m ⁻²)	Chl biomass ingested daily (%)	Carbon ingestion rate (herbivory) (mg C m ⁻² d ⁻¹)	^a Primary production (mg C m ⁻² d ⁻¹)	Primary production ingested daily (%)
1	40	0.56	4164	9257	1.469	171	0.859	73.44	225	32.64
2	75	0.85	38	101	0.007	188	0.003	0.33	450	0.07
5	125	1.74	86	17685	2.083 ^b	229	0.909	104.14	629	16.56
35	100	0.64	1427	1698	0.213	109	0.195	10.66	1012	1.05
40	50	0.51	4008	4787	0.651	69	0.943	32.55	314 ^c	10.37
44	60	0.36	11248	4160	0.490 ^b	117	0.419	24.50	454	5.40
54	80	0.40	874	836	0.102	54	0.188	5.08	402	1.26
Mean		0.72 \pm 0.48	3121 \pm 3969	5503 \pm 6194	0.716 \pm 0.777	134 \pm 64	0.503 \pm 0.395	35.81 \pm 38.86	498 \pm 259	9.62 \pm 11.77
Median		0.56	1427	4160	0.490	117	0.419	24.50	450	5.39

^aRates of primary production were based on 24h uptake of ¹⁴C bicarbonate (Klein et al., 2002) and were integrated to the 1% light level.

^bNo GPT data were available for these stations, so the mean from other stations (Table 2) was used in the calculations.

^cNo primary production rate data were available, so we assumed the values were equal to the mean values from stations 1 and 54.

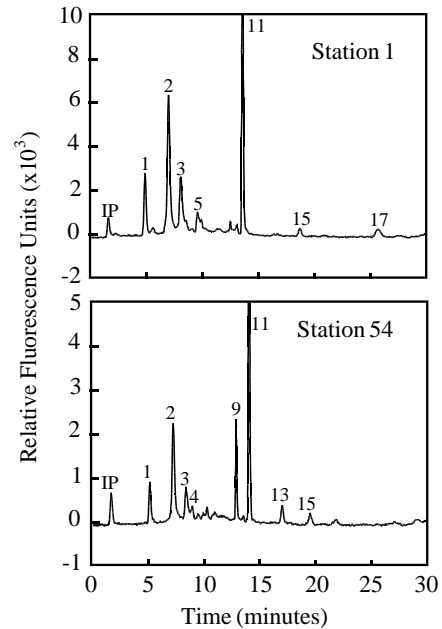


Fig. 6. Chromatograms of acetone extracts of two appendicularians collected at a northern station (upper panel) and a southern station (lower panel). Numbers and symbols identify the pigment responsible for each peak: IP, injection peak; 1, chlorophyllide *a*; 2, chlorophyll *c*; 3, phaeophorbide *a*1; 4, phaeophytin *c*; 5, pyropheophorbide *a*3; 9, chlorophyll *b*; 11, chlorophyll *a*; 13, phaeophytin *b*; 15, phaeophytin *a*; 17, pyropheophytin *a*.

and 35) was composed of diatoms, while at the most southeasterly station (54), about half of the identified faecal pellet volume was contributed by the heterotrophic, tintinnid ciliate *Ptychocylis* spp. (Table 4). The composition of faecal pellets from two animals from station 40 in the southeastern region, supported a general trend of increasing volume of protozoan prey in the appendicularian diet from north to south, with a predominance of heterotrophic forms (Table 4). Flagellates, considered characteristic of “post-bloom” phytoplankton assemblages, were present in the diet in significant amounts only at the southeastern station 54 (Table 4). Although all of the diatoms listed in Table 4 are known to form chains, almost all of the cells found in the water column during July occurred as single cells or short chains (Booth et al., 2002). This observation is consistent with our data showing that essentially all chlorophyll *a*

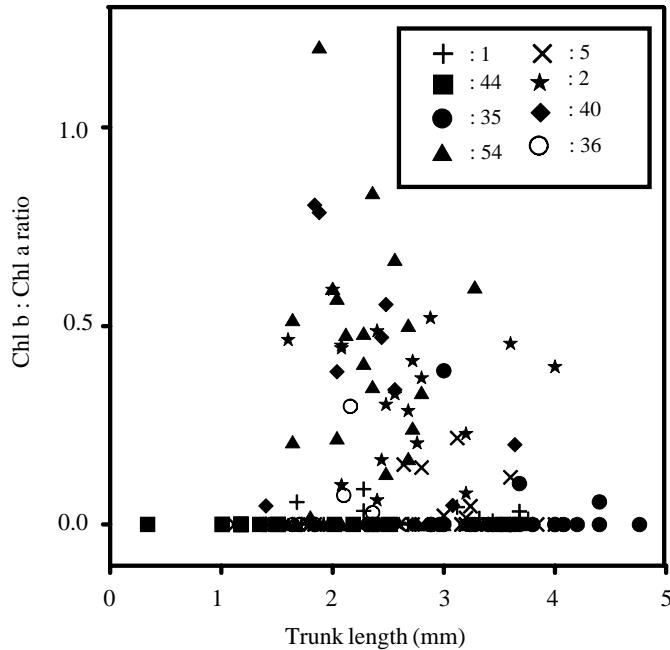


Fig. 7. Plot of the ratio Chl *b*:Chl *a* vs. trunk length for all appendicularians collected in the North Water for gut pigment analysis. There was no significant correlation between these two variables (Spearman rank correlation coefficient, $p = 0.943$, $n = 183$).

Table 4

Faecal pellet contents of appendicularians in the North Water polynya. Data are the relative volume (in percentage) of eight selected species and of broad taxonomic categories. Only those species showing relative abundances >10% are shown, while the relative abundance in the broad categories was calculated using all of the species present in the faecal pellets. Data represent the mean (\pm SD) for replicate pellets within each animal. “N” is number of pellets observed per animal

Station	1		2		35		40		54	
Animal #	1		1		1	2	1	2	1	
N	4		3		1	1	1	3	3	
Selected species										
<i>Chaetoceros hyalochaete</i>	0.0 \pm 0.0		53.8 \pm 47.8		0.0	0.0	0.1	0.0 \pm 0.0	0.0 \pm 0.0	
<i>Chaetoceros socialis</i>	0.0 \pm 0.0		0.2 \pm 0.3		0.0	0.0	0.0	11.3 \pm 19.5	0.0 \pm 0.0	
<i>Chaetoceros socialis</i> r.s.	49.3 \pm 21.7		25.3 \pm 43.9		0.0	0.0	74.0	36.2 \pm 50.8	4.8 \pm 8.3	
<i>Thalassiosira</i> 18 μ m	0.0 \pm 0.0 \pm		0.0 \pm 0.0		2.5	0.2	0.4	0.2 \pm 0.3	25.2 \pm 43.6	
<i>Thalassiosira</i> > 25 μ m	3.6 \pm 7.1		5.2 \pm 8.1		0.0	12.4	15.8	0.0 \pm 0.0	1.2 \pm 2.1	
<i>Thalassiosira antarctica</i>	0.0 \pm 0.0		0.0 \pm 0.0		0.0	26.5	0.0	0.0 \pm 0.0	0.0 \pm 0.0	
<i>Thalassiosira bioculata</i>	20.6 \pm 41.3		3.2 \pm 5.6		85.5	59.9	6.6	19.7 \pm 34.1	15.8 \pm 27.4	
<i>Ptychocylis</i> sp.	0.0 \pm 0.0		0.0 \pm 0.0		0.0	0.0	0.0	19.4 \pm 33.6	32.5 \pm 56.2	
Broad taxonomic categories										
Diatoms	92.2 \pm 6.5		98.5 \pm 2.4		97.4	99.6	98.8	76.6 \pm 37.8	49.1 \pm 42.5	
Autotrophic dinoflagellates	0.0 \pm 0.1		0.0 \pm 0.0		0.4	0.3	0.9	0.4 \pm 0.4	2.1 \pm 3.6	
Heterotrophic dinoflagellates	4.1 \pm 5.4		0.0 \pm 0.0		2.2	0.1	0.3	0.7 \pm 0.9	2.0 \pm 3.5	
Autotrophic flagellates	0.0 \pm 0.0		0.0 \pm 0.0		0.0	0.0	0.0	0.0 \pm 0.0	8.5 \pm 8.5	
Heterotrophic flagellates	0.0 \pm 0.0		0.1 \pm 0.1		0.0	0.0	0.0	0.1 \pm 0.1	2.3 \pm 3.4	
Ciliates	3.7 \pm 7.3		1.4 \pm 2.5		0.0	0.0	0.0	22.2 \pm 38.5	36.0 \pm 53.5	

biomass was contained in $<140\ \mu\text{m}$ particles at five stations (Table 2) and thus ingestible by *O. vanhoeffeni*.

4. Discussion

GCCs of individual appendicularians measured in the North Water (Fig. 4) are similar to those reported for oikopleurids in other arctic polynyas and boreal waters. Maximum values in the Northeast Water and St. Lawrence Island polynyas were ca. $100\ \text{ng ind}^{-1}$ (Acuña et al., 1999; Deibel and Shiga, unpubl.) and values for animals in coastal Newfoundland waters ranged from 90 to $135\ \text{ng ind}^{-1}$ (Redden, 1993; Bochdansky et al., 1998). The method we used in this study to estimate individual ingestion rate was developed for *O. vanhoeffeni* fed diatoms (Bochdansky et al., 1998), and this approach appears suitable to circumstances in the North Water, where diatoms dominated the diet of appendicularians, especially at northern stations (Table 4; Figs. 6 and 7). This was probably because most of the diatoms occurred as single cells within the ingestible size range of *O. vanhoeffeni* (i.e. $<140\ \mu\text{m}$ in size, Table 2). Moreover, GPTs measured here (58 min; Table 2), using a recently developed, non-intrusive technique (López-Urrutia and Acuña, 1999), are similar to values for *O. vanhoeffeni* determined using diatoms and cornstarch markers in laboratory experiments (47 min, Bochdansky et al., 1998).

The daily impact of appendicularian herbivory on phytoplankton during early mid-summer in the North Water (July) was moderate (0.003–0.94% of the chlorophyll standing stock and 0.07–32.64% of PP, Table 3). Median appendicularian phytoplankton consumption was $0.49\ \text{mg chlorophyll m}^{-2}\ \text{d}^{-1}$, $24.5\ \text{mg C m}^{-2}\ \text{d}^{-1}$ or 0.4% of phytoplankton standing stock and 5% of daily primary production (Table 3). However, our pigment-based technique gives an estimate of only the phytoplankton ingested by the animal. Ten to 60% of the phytoplankton removed from suspension by appendicularians remains stuck within the mucous filters of the house and is not ingested (Gorsky, 1980; Acuña and Kiefer, 2000). There-

fore, the impact of appendicularian populations on phytoplankton in the North Water could be up to 2 times higher than the above estimates of ingested chlorophyll. Using a different technique based on the removal of marker beads which takes into account the fraction that remains attached to the filter house, Deibel (1988) estimated daily population ingestion rates of 13% of phytoplankton biomass and up to 10% of primary production in Newfoundland coastal waters during the spring phytoplankton bloom. Using a similar bead technique, Alldredge (1981) estimated that 10–100% of the primary production was removed daily by appendicularians in subtropical waters. Using literature values for individual ingestion rates, Pesant et al. (1998) estimated that appendicularian populations removed up to $500\ \text{mg C m}^{-2}\ \text{d}^{-1}$ during spring and summer in the Northeast Water polynya. However, this figure may be inflated because they used mean trunk length data for animals collected visually with pipettes for gut pigment analyses (Acuña et al., 1999), a procedure that neglects some of the smaller animals. In addition, these authors did not consider the potential negative effect of large phytoplankton on the individual ingestion rates of appendicularians (Knoechel and Steel-Flynn, 1989; Acuña et al., 1999).

Sediment-trap evidence from the Northeast Water polynya indicates that the annual peak of appendicularian grazing does not occur until late August and September in the Arctic (Bauerfeind et al., 1997). Thus, our mid-summer measurements may not have documented the annual maximum population ingestion rate of appendicularians in the North Water. Discarded appendicularian filter houses containing egested faecal pellets sink at several hundred metres each day and can reach great depths (see review by Gorsky and Fenaux, 1998). In this regard, at least part of the mucilaginous material that clogged sediment traps during the summer months in the North Water (Hargrave et al., 2002) could have an origin in the discarded houses of oikopleurid appendicularians. We can estimate the potential vertical flux of appendicularian faeces in July in the North Water from the median population ingestion rate of $24.5\ \text{mg C m}^{-2}\ \text{d}^{-1}$ (Table 3) and assuming an

absorption efficiency of 67% measured for *O. vanhoeffeni* (Bochdansky et al., 1999). Thus, the potential vertical flux of appendicularian faeces in the North Water was $8 \text{ mg C m}^{-2} \text{ d}^{-1}$, much higher than the zooplankton faecal pellet flux during late spring in the North Water ($0.52 \text{ mg C m}^{-2} \text{ d}^{-1}$ in late June 1998; Sampei et al., 2002), where both large and small elliptical pellets clearly suggest an appendicularian origin. Moreover, this flux is similar to the vertical flux of appendicularian faecal pellets and filter houses determined by sediment traps in the Northeast Water (i.e. $5 \text{ mg C m}^{-2} \text{ d}^{-1}$, Bauerfeind et al., 1997). During July the maximum estimated potential export of particulate organic carbon from the euphotic zone (E_{POC}) was $196 \text{ mg C m}^{-2} \text{ d}^{-1}$ (Table 5 in Klein et al., 2002, computed using pelagic food web characteristics in Tremblay et al. 1997). Based upon a median vertical faecal flux of $8 \text{ mg C m}^{-2} \text{ d}^{-1}$, appendicularians would account for 4.1% of the E_{POC} . This is certainly an underestimate of the contribution of this group to the vertical carbon flux since these estimates do not include the heterotrophic portion of the diet or the carbon contained in or attached to, the discarded filter houses (Gorsky, 1980; Acuña and Kiefer, 2000).

The present data do not support our initial hypothesis that appendicularian individual and population ingestion rates should be lower in the presence of diatom blooms. The most likely reason in this case is that, by our study period in July 1998, the diatom bloom was dominated by small, ingestible cells (July–September; e.g., *Chaetoceros socialis*; Booth et al., 2002), as opposed to larger chain-forming taxa that typically dominate diatom blooms during the spring (May–June; e.g., *Fragilariopsis*, *Thalassiosira*). Under these circumstances, the gut contents, and consequently the individual ingestion rates of oikopleurids, increased with chlorophyll concentration according to a pattern resembling the functional response of appendicularians in the laboratory (Acuña and Kiefer, 2000). The maximum population ingestion rate was observed at stations 5 and 1 (Table 3) where we also found the highest gut content values (Fig. 5). This illustrates that not only population abundances

and size structure, but also feeding ecophysiology are important in determining the magnitude of grazing fluxes associated with appendicularian populations.

According to current conceptual models, copepods are the primary mesozooplanktonic grazers during diatom blooms (see Cushing, 1989), while appendicularians are especially suited to thrive on the small cells in the microbial loop (Cushing, 1989; Gorsky and Fenaux, 1998). However, recent evidence (including this study) may lead to a modification of this paradigm. Large appendicularian species typical of cold oceans have been found to ingest relatively large diatoms during the spring bloom (Urban et al., 1992, 1993). In the North Water, we have found a significant flow of small, nanoplanktonic diatoms into appendicularian populations during a summer bloom which lasted for up to 3 months (see Booth et al., 2002). Thus, when diatom blooms are dominated by small cells, removal by mucous-web feeders could be significant.

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