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Feeding ecology and trophic impact of the hydroid *Obelia dichotoma* in the Kongsfjorden (Spitsbergen, Arctic)

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Abstract *Obelia dichotoma* is a thecate hydroid with a worldwide distribution, occurring mainly on shallow water hard substrates. Since the trophic ecology of hydroids in polar waters is badly understood, the aim of the present work was to study qualitatively and quantitatively the diet of these organisms in an Arctic environment and to determine their trophic significance. For this purpose, the density of the hydroid population was documented, and simultaneously, zooplankton was sampled in two different years (1997 and 1998). Prey capture rates were estimated by analysing the gastrovascular content of the polyps in a diurnal cycle. Additionally, the digestion time of *O. dichotoma* was measured by laboratory feeding experiments using diatoms as food items. The analyses of the gastrovascular cavities of the polyps sampled during the diurnal cycles showed that *O. dichotoma* fed mainly on faecal pellets, organic matter and microalgae. Zooplankton prey was also observed, but gastrovascular contents and zooplankton abundance did not show any correlation in both years. The consumption rates of the hydroid populations differed between the 2 years. It was almost double (8.9 mg Carbon m^{-2}) in 1998 compared to 1997 (5.5 mg Carbon m^{-2}). The significance of the environmental variability in the feeding ecology and population dynamics of hydroids under Arctic conditions is discussed.

Keywords Trophic ecology · Benthic suspension feeders · Hydroids · *Obelia dichotoma* · Arctic

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Introduction

Hydroids are one of the most abundant zoological taxa among benthic hard substrate communities in shallow water ecosystems (Gili and Hughes 1995). Moreover, several studies have shown the importance of hydroids for bentho-pelagic-coupling processes in shallow marine ecosystems (e.g. Coma et al. 1995; Gili et al. 1998; Coma et al. 1999; Orejas et al. 2000, 2001). During the last three decades, trophic ecology studies on hydroids documented their high impact on the near-bottom seston, being able to consume large amounts of prey, from tropical via temperate to polar seas (e.g. Christensen 1967; Barangé and Gili 1988; Barangé et al. 1989; Coma et al. 1995; Gili et al. 1996a, b, 1998; Coma et al. 1999; Orejas et al. 2000, 2001; Di Camillo et al. 2005; Genzano 2005; Gili et al. 2008).

Hydroids are mainly known as carnivorous organisms, and little is known on the role of prey other than zooplankton (Simkina 1980; Gili and Hughes 1995), except for some specialised associations (e.g. see hydroid-bryozoan associations, Puce et al. 2007). However, although most of

the carbon in several suspension-feeding species originates from zooplankton prey (Ribes et al. 1998; Rossi et al. 2004), different studies reported dinoflagellates, diatoms, detritic particulate organic matter (POM) and bacteria to be part of the hydroid diet (Simkina 1980; Cornelius and Ostman 1987; Barangé and Gili 1988; Barangé et al. 1989; Coma et al. 1995; Gili et al. 1996a; Orejas et al. 2001). Further sedimentation of faecal pellets as a key component of the carbon flux has been already demonstrated (e.g. Wotton and Malmqvist 2001), and faecal pellets have been also recorded as prey for suspension feeders, including hydroids (e.g. Gili et al. 2006, 2008).

Hydroids are common inhabitants of shallow benthic ecosystems also in Polar regions. The taxonomy and biogeography of Arctic hydroids is quite well known and has been widely studied (e.g. Palerud et al. 2004; Ronowicz 2007; Ronowicz et al. 2008, 2011; Voronkov et al. 2010). However, the ecological knowledge on this group in Arctic waters is very scarce, and to our knowledge, there are no published papers on this topic. Nevertheless, hydroid fauna in the Arctic is very conspicuous and abundant in several regions, including Kongsfjorden (Ronowicz et al. 2008), where hydroids might play an important role in the plankton–benthos coupling. In the singular environmental conditions of Polar regions, particularly the presence of ice blocks that scrape the substratum (Holte et al.1996; Barnes 1999; Weslawski et al. 1999; Laudien et al. 2004) and the ice cover, should influence primary and secondary production, playing a role in the feeding dynamics of arctic hydroids and other benthic organisms. Both, sporadic perturbations and strong seasonality, originate temporary decline of populations in areas where they are usually abundant, as it has been documented for Antarctic waters (Bullivant and Dearborn 1967). In a recent paper, Ronowicz et al. (2011) presume a restricted colonisation by hydroids due to iceberg scouring close to a glacier.

Investigations on the trophic ecology especially of polar hydroids are rare. Only three studies on this taxonomic group have been published, all of them from Antarctica: Gili et al. (1996a), Cerrano et al. (2000) and Orejas et al. (2001). In temperate waters, for example, Gili et al. (2008) documented how phytoplankton cells may be digested and easily assimilated by hydroid species, representing an important part of the incoming carbon budget. Also for the Antarctic, Gili et al. (1996a) and Orejas et al. (2001) showed that microalgae and organic matter (OM) contribute a considerable part to the diet of these organisms, and Cerrano et al. (2000) documented diatoms as a prey for an hydroid species. Further, Bluhm et al. (2007) showed a significant relationship between a sympagic hydroid (*Sympagohydra tuuli*), harpacticoid copepods and nematods, all of them potential prey items for this group.

Obelia dichotoma (Linnaeus, 1758) is a very common and almost cosmopolitan hydroid species, it can be found on floats, pilings, rocks, shells and other hard substrata. It is a thecate hydroid that forms branching colonies with erect and flexible hydrocauli of 20 till 350 mm height (Cornelius 1982; Bouillon et al. 2004). Polyp diameter ranges from 210 to 275 μm, and polyp height from 215 to 300 μm. The hydrotheca around each hydranth is bell or goblet shaped and has no operculum. Colonies normally grow for 2 to 3 months entering after in a senescent phase, remaining latent as stolons during the adverse environmental conditions. To our knowledge, *O. dichotoma* has been not described at the study site before, and thus, its record in the present study is the first finding of this species in Kongsfjorden. In general, the information on the ecology of Obelia species (especially on benthic stages) is scarce (Marfenin 1993; Orejas et al. 2000), and no information exists on the biology and ecology of this species for the Arctic.

The aim of this paper is to quantitatively study the feeding cycle of the species *Obelia dichotoma* from Arctic Kongsfjorden (Spitsbergen) in the field and in aquaria experiments. Finally, we discuss the possible role of hydroids in this Arctic shallow coastal location. This work presents the first approach to the trophic ecology of a hydroid population in the Arctic.

Materials and methods

Study area

The study was carried out close to Ny Ålesund, located in central Kongsfjorden (79°N 12°E) at the north-western part of Spitsbergen (Svalbard Islands, Norway, Arctic) (Fig. 1). Kongsfjorden is an open fjord under the influence of both, Atlantic water and terrestrial glacial input. The fjord is 26 km long and has a width between 3 and 8 km, and its maximum depth reaches 400 m. The shores consist of a steep rocky bottom as well as weakly declining slopes with, mostly, soft glacier sediments. The tidal range is between 1.5 and 2 m with weak currents (Ito and Kudoh 1997). Four glaciers and a number of glacier run-offs add terrestrial sediments (Elverhøi et al. 1983) and freshwater to the fjord, which may locally reduce salinity from an average 34 psu down to 20 psu. The annual mean water temperature is slightly above 0 °C (Ito and Kudoh 1997); however, in summer maximum temperatures of about 6 °C at the surface and 3.6 °C at 20 m depths have been measured (Hanelt et al. 2001). A summary of the temperature and salinity data recorded during both sampling years is presented in Table 1. Svendsen et al. (2002) and Hop et al. (2002) give a comprehensive overview on the physical

Fig. 1 General view of Spitsbergen, showing Kongsfjorden and the study site (indicated by *star*)
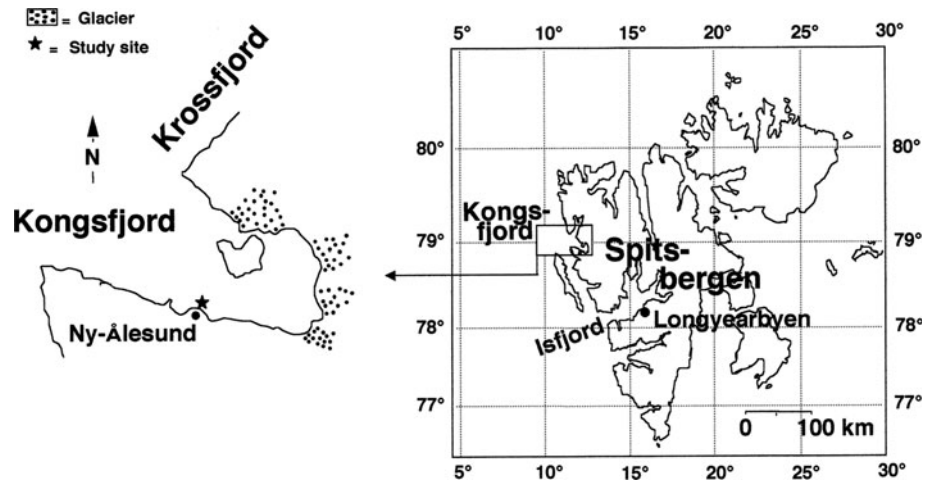

Table 1 Average (±SD) temperature (°C) and salinity (PSU) at 2–3 m depth at the sampling location (Kongsfjorden) during June, July and August of 1997 and 1998

	1997			1998	
	June	July	August	July	August
Temperature (°C)	4.29 ± 1.16	3.97 ± 0.85	4.95 ± 0.26	4.48 ± 0.95	4.37 ± 0.25
Salinity (psu)	34.23 ± 0.20	31.65 ± 0.86	32.71 ± 0.86	31.57 ± 1.98	28.95 ± 0.62

environment and ecological conditions of this area. In central Kongsfjorden, sea ice, if present, regularly breaks up between April and early June, often within a few days (Mehlum 1991; Gerland et al. 1999). While this was the case in 1997 (personal observation), in 1998, the central and inner fjord was covered by ice until the end of June (Bischof et al. 1999), this is a quite exceptional situation, also mentioned by Svendson et al. (2002).

Sampling and field experiments

Population density

Samples were taken from the concrete pier at Ny Ålesund between 3 and 7 m depth in July 1997 and in August 1998. To calculate the density of hydroids, all macroalgal thalli within a sampling frame of 63 cm^2 were collected, taking five and three replicates in 1997 and 1998, respectively. Macroalgal species found were mainly *Saccharina latissima* and *Palmaria palmata* as well as other species of red algae. Samples have been immediately preserved in buffered 4 % formaldehyde. In the laboratory, all hydroids per sampling square were separated from the algae and weighed. From each hydroid sample, three subsamples were taken, weighed, and hydranths were counted. Numbers of hydranths per square metre were calculated. Hydroid samples have been collected exactly in the same location, in two different sampling years (1997, 1998) and

months (July and August) and under different ice coverage conditions.

Diurnal feeding "in situ"

Diurnal feeding cycles were studied in situ in 1997 and 1998 (following Barangé and Gili 1988; Gili et al. 1996a, b; Coma et al. 1999; Orejas et al. 2000), by analysing zooplankton composition and concentration in the environment, as well as the gastrovascular contents of *Obelia dichotoma* hydranths. In both years, sampling started on the 12th August and was carried out every 4 h (1997:16:00 until 12:00 the next day, 1998: 08:15 until 04:00 the next day). Sampling depth was between 4 and 6 m at the Ny Ålesund pier.

Hydrozoans were collected by scuba divers taking them with a piece of the macroalgae they were growing on. Zooplankton was also sampled by scuba divers towing a hand net (25 cm diameter, mesh size 100 μm; Coma et al. 1994) along the pier, covering about 80-m distance. Total filtered volume calculated for each sample was 3.9 m^3. Hydroid and plankton samples have been preserved in 10 % buffered formaldehyde.

Fifty polyps from each sampling time were dissected under a binocular microscope. Prey found in the gastrovascular cavities of the polyps were identified to the lowest possible taxonomic level, other food items as OM or faecal pellets were recorded, following the methodology applied

by Gili et al. ([1996b](#)). Plankton composition and abundance were analysed from three aliquots of 5 ml each, according to Coma et al. ([1994](#)).

Digestion time

Digestion time for *Obelia dichotoma* was investigated by an aquarium experiment conducted in 1997. Hydroids were collected by scuba divers at the Ny Alesund pier and transferred to the laboratory. For acclimation and to allow digestion of possible food remaining in the guts, hydroids were kept for 26 h in circulating filtered (2 μm) sea water (see Gili et al. [1996a](#)) and maintained at 6 °C, which is close to summer temperature at the sampling location (Hanelt et al. [2001](#)). During this time, water was completely renewed twice. The digestion experiment was started by adding diatoms ad libitum to the water. Diatoms were the most feasible prey items to get in Kongsfjorden and are also one of the main components of the plankton in summer (Piwosz et al. [2009](#)), supplying the system with an important amount of carbon. Samples of 50 polyps each (according to Coma et al. [1994](#)) were taken after 0; 0.5; 1; 1.5; 2; 4; 6 and 10 h from two replicate aquaria. Samples have been immediately preserved in 10 % buffered formaldehyde to stop the digestion process. To analyse gut contents and digestion progress, polyps were dissected using a stereo microscope.

Data treatment and statistical analyses

A Mann–Whitney U test has been conducted, after testing for non-normal distribution of data, to check for possible differences of hydroid density between the 2 years studied.

The number of prey items found in the gastrovascular cavities of the polyps collected during the diurnal cycle sampling was recorded as prey per polyp (prey polyp^{-1}). The different taxonomic groups were expressed as percentage of total prey. To detect possible variations between numbers of prey in the gastrovascular cavities at the different sampling times during the diurnal field experiment, a one-way ANOVA has been conducted for each sampling year. Prey capture rates, expressed as the number of prey items captured per polyp and hour (prey p^{-1} h^{-1}), were calculated from the gut contents of the polyps sampled during the diurnal cycles sampling, using the equation according to Coma et al. ([1994](#)):

$$C = N \left[\sum_{t}^{D} 1 - (t/D) \right]$$

where C = number of prey captured per polyp and hour; N = prey items per polyp; t = time (in hours); and D = digestion time (in hours).

The carbon content of the prey was calculated by estimating zooplankton biomass from its bio-volume (Sebens and Koehl [1984](#)), using conversion factors to wet mass (1.025; Hall et al. [1970](#)), dry mass (13 % of wet mass, Beers [1966](#)) and carbon content (45 % of dry mass, Biswas and Biswas [1979](#)). Carbon (C) content of the hydroid polyps was estimated applying the conversion factors from Paffenhofer ([1968](#)), as described in Barangé et al. ([1989](#)) and recently applied for the hydroid *Eudendrium racemosum* (Rossi et al. [2012](#)): C (mg) = −0.130 + (0.288 × height (cm)).

Results

Population density

The population density of *Obelia dichotoma* differed significantly between the 2 years studied (Mann–Whitney U test, $p < 0.05$). In 1998, the number of polyp m^{-2} was more than three times higher than in 1997: 66,510.8 ± 44,758.4 (SD) polyp m^{-2} in 98 versus 20,689.9 ± 7,047.3 (SD) polyp m^{-2} in 97. These hydroid densities correspond to 772 mg C m^{-2} and 240 mg C m^{-2}, respectively.

In situ feeding diurnal cycle

Gastrovascular contents

In both years, most of the gastrovascular cavities (88 and 93 %, respectively) contained at least one prey item. The most frequent items found in the polyps were faecal pellets, followed by phytoplankton and OM. Other groups were present in much lower proportion as shown in Table [2](#). The ANOVA did not reveal any significant differences between the numbers of prey found in the gastrovascular cavities at different sampling times during the day, in both years (ANOVA: 1997: $F_{5,54} = 0.156$, $p = 0.977$; 1998: $F_{5,54} = 0.779$, $p = 0.569$).

Near-bottom plankton composition

The most frequent taxa in the plankton were nauplii, copepoda and invertebrate eggs, followed in much lower percentage by lamellibranchia, gastropoda, tintinnida, apendicularia, polychaeta, protozoa and some specimens of amphipoda, echinodermata, isopoda and medusa (Fig. [2](#); Table [3](#)). Samples from 1997 comprised 11 taxonomic groups, whereas samples from 1998 included 13 groups. The average plankton concentration was around 60 % higher in 1997 (5,694 ± 4,022 zooplankters m^{-3}) compared to 1998 (3,403 ± 2,144 zooplankters m^{-3}). In 1997, marked daily oscillations in plankton concentration have

Table 2 Food items found in the gastrovascular cavities throughout a diurnal cycle in 1997 (a) and in 1998 (b)

(a)

	12.08.1997 16:00		20:00		0:00		13.08.1997 4:00		8:00		12:00		Total	
	n	Percentage	n	Percentage	n	Percentage	n	Percentage	n	Percentage	n	Percentage	n	Percentage
Faecal pellets	44	29.9	34	34.7	40	28.8	104	57.5	72	47.1	58	18.1	352	41.4
Phytoplankton	40	27.2	10	10.2	24	17.3	7	3.9	19	12.4	8	2.5	108	12.7
Organic matter (OM)	42	28.6	34	34.7	34	24.5	25	13.8	24	15.7	26	8.1	185	21.7
Protozoa	9	6.1	2	2.0	2	1.4	3	1.7	3	2.0	4	1.3	23	2.7
Crustacean fragments	5	3.4	7	7.1	9	6.5	9	5.0	6	4.0	8	2.5	44	5.2
Tintinnids	4	2.7	10	10.2	27	19.4	19	10.5	16	10.5	24	7.5	100	11.8
Copepods	1	0.7	1	1.0	0	0.0	5	2.8	2	1.3	3	0.9	12	1.4
Nauplii	0	0.0	0	0.0	1	0.7	0	0.0	0	0.0	0	0.0	1	0.1
Copepod eggs	1	0.7	0	0.0	1	0.7	2	1.1	3	2.0	1	0.3	8	0.9
Gastropod larvae	1	0.7	0	0.0	0	0.0	4	2.2	2	1.3	1	0.3	8	0.9
Bivalve larvae	0	0.0	0	0.0	1	0.7	3	1.7	6	3.9	0	0.0	10	1.2
Total prey	147		98		139		181		153		133		851	
No. prey/polyp														
Average ± SD	2.9 ± 2.6		2.0 ± 1.9		2.8 ± 1.7		3.6 ± 2.1		3.1 ± 2.4		2.7 ± 2.2		2.8 ± 0.5	

(b)

	12.08.1998 8:15		12:15		16:00		20:20		0:00		13.08.1998 4:00		Total	
	n	Percentage	n	Percentage	n	Percentage	n	Percentage	n	Percentage	n	Percentage	n	Percentage
Faecal pellets	93	38.4	230	43.7	48	26.2	75	43.4	100	43.9	60	18.7	606	36.2
Phytoplankton	50	20.7	146	27.8	89	48.6	62	35.8	18	7.9	163	50.8	528	31.6
Organic matter (OM)	69	28.5	114	21.7	33	18.0	18	10.4	79	34.7	60	18.7	373	22.3
Protozoa	9	3.7	9	1.7	3	1.6	4	2.3	19	8.3	13	4.1	57	3.4
Crustacean fragments	11	4.6	5	1.0	2	1.1	5	2.9	5	2.2	12	3.7	40	2.4
Tintinnids	5	2.1	17	3.2	4	2.2	0	0.0	4	1.8	0	0.0	30	1.8
Copepods	2	0.8	1	0.2	3	1.6	8	4.6	1	0.4	0	0.0	15	0.9
Nauplii	3	1.2	3	0.6	1	0.6	0	0.0	1	0.4	3	0.9	11	0.7
Copepod eggs	0	0.0	0	0.0	0	0.0	0	0.0	1	0.4	10	3.1	11	0.7
Gastropod larvae	0	0.0	1	0.2	0	0.0	1	0.6	0	0.0	0	0.0	2	0.1
Total prey	242		526		183		173		228		321		1,673	
No. prey/polyp														
Average ± SD	4.8 ± 5.7		10.5 ± 5.0		3.6 ± 3.9		3.5 ± 3.0		4.3 ± 3.5		6.4 ± 6.7		5.5 ± 2.6	

Gastrovascular contents of 50 polyps have been analysed at each sampling time. Results are expressed as number of food item (n) and in percentage of total food
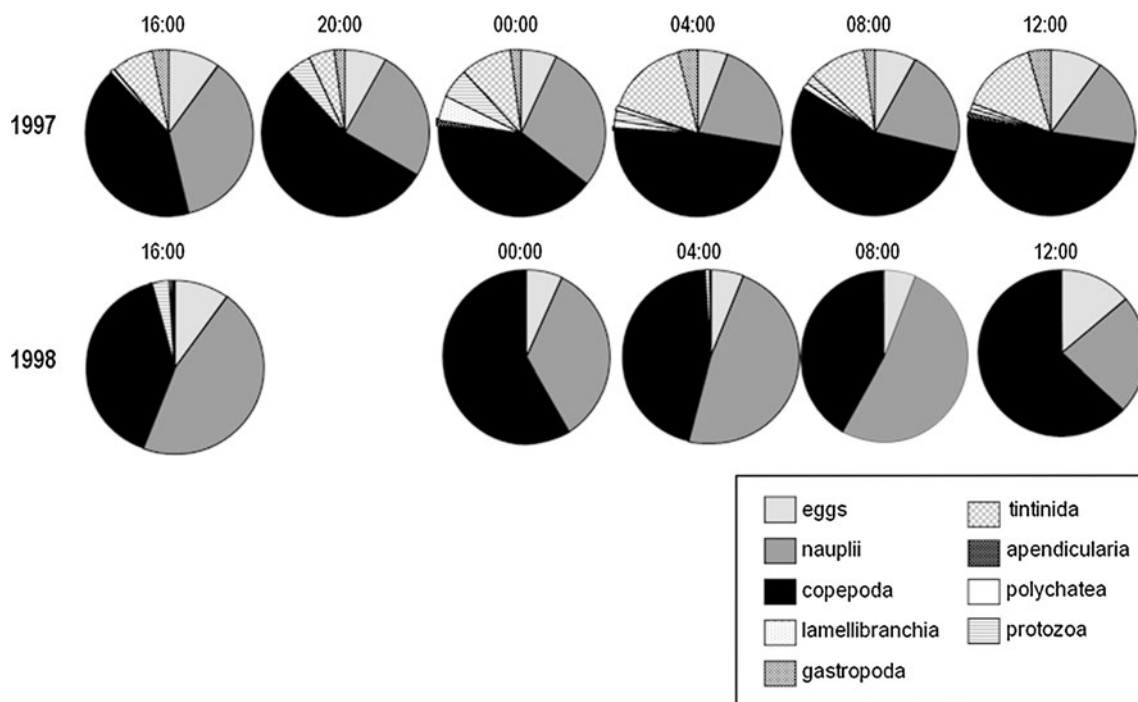
Fig. 2 Variation of zooplankton composition (expressed in percentage) during the course of a day for 1997 and 1998. Results are expressed as average ± Standard deviation (SD)

been recorded with the highest concentration at 20:00 h (Fig. 3). Highest zooplankton concentrations in 1998 were observed at 08:00 and 00:00 h but were less evident than in 1997 (Fig. 3). No daily trend has been observed for total zooplankton concentrations in the water and number of prey found in the gastro vascular system of the hydroids in both years (see, Fig. 3).

Feeding experiment

The digestion of food, investigated by the laboratory experiment, took place mainly during the first 2 h. The decrease of food in the gastro vascular system followed a logarithmic trend as shown in Fig. 4. The number of prey items per polyp declined from 2.28 ± 0.27 (SD) prey polyp^{-1} (time "0") to 1.40 ± 0.19 (SD) after 2 h. After 10 h, 0.88 ± 0.12 (SD) prey items polyp^{-1} were found in the polyp cavities, and after 20 h, the food was almost completely depleted (0.10 ± 0.04 (SD) prey polyp^{-1}). Thus, the digestion time measured for *Obelia dichotoma* from Arctic waters is about 20 h. However, it is important to point out that the present digestion time corresponds to a single prey type (diatoms). Digestion time for other kind of prey (as e.g. zooplankton) may be higher (see discussion). Following the formula described above (Coma et al. 1994), and considering the density of polyps determined at the sampling site (polyp m^{-2}), consumption rates of 5.5 mg C m^{-2} day^{-1} for the population studied in 1997

and 8.9 mg C m^{-2} day^{-1} for the population studied in 1998 were calculated.

Discussion

Hydroids have been largely considered being carnivorous (e.g. Christensen 1967; Paffenhofer 1968; Simkina 1980; Barangé and Gili 1988; Coma et al. 1999). However, *Obelia dichotoma* from Arctic Kongsfjorden show consumption rates of faecal pellets, OM and microalgae, which are similar or even higher than those of zooplankton. These findings agree with previous published results (Gili et al. 2001), which also found that (1) hydroids can be omnivores and (2) for several hydroid species, prey items like faecal pellets, phytoplankton or even benthic microalgae play a dominant role, at least considering its number, in the gastrovascular cavities of the hydroids (Coma et al. 1995; Gili et al. 1996a; Orejas et al. 2000, 2001; Gili et al. 2008; Rossi et al. 2012).

Interestingly, another species of the genus Obelia, *Obelia geniculata,* has been documented to show even opportunistic feeding behaviour (Orejas et al. 2000). In this context, the high consumption rate of faecal pellets, OM and microalgae by *O. dichotoma* is probably an adaptation to high concentrations of these food items in the environment. It has been recorded that microalgae and faecal material presented high concentrations in the water column

Table 3 Plankton groups present in the water column throughout the diurnal cycle sampled in 1997 (a) and in 1998 (b)

(a)

| | 12.08.1997 | | | | | | 13.08.1997 | | | | | |
| | 16:00 | | 20:00 | | 0:00 | | 4:00 | | 8:00 | | 12:00 | |
	$n\,m^{-3}$	Percentage	$n\,m^{-3}$	Percentage	$n\,m^{-3}$	Percentage	$n\,m^{-3}$	Percentage	$n\,m^{-3}$	Percentage	$n\,m^{-3}$	Percentage
Invertebrate eggs	375.0	10.2	932.2	8.2	752.8	7.5	148.1	6.2	407.6	8.5	199.7	10.4
Nauplii	1,318.0	35.9	2,891.6	25.5	2,875.3	28.6	515.0	21.7	1,000.1	20.8	332.9	17.3
Copepods	1,547.7	42.2	6,207.1	54.8	4,084.6	40.6	1,131.9	47.6	2,621.1	54.5	959.3	49.9
Apendicularia	4.1	0.1	40.8	0.4	54.4	0.5	16.3	0.7	21.7	0.5	10.9	0.6
Lamellibranchis	0.0	0.0	0.0	0.0	489.2	4.9	20.4	0.9	31.3	0.7	27.2	1.4
Gastropoda	29.9	0.8	529.9	4.7	644.1	6.4	55.7	2.3	77.5	1.6	19.0	1.0
Polychaeta	1.4	0.0	2.7	0.0	0.0	0.0	12.2	0.5	9.5	0.2	8.2	0.4
Amphipoda	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	0.1
Echinodermata	0.0	0.0	10.9	0.1	8.2	0.1	2.7	0.1	10.9	0.2	4.1	0.2
Tintinnida	301.7	8.2	516.4	4.6	964.8	9.6	377.8	15.9	534.0	11.1	286.7	14.9
Protozoa	93.8	2.6	201.1	1.8	179.4	1.8	97.8	4.1	95.1	2.0	73.4	3.8
Total	3,671.5		11,332.5		10,052.5		2,377.9		4,808.8		1,922.7	

(b)

| | 12.08.1998 | | | | | | 13.08.1998 | | | | | |
| | 8:00 | | 12:00 | | 16:00 | | 20:00 | | 0:00 | | 4:00 | |
	$n\,m^{-3}$	Percentage	$n\,m^{-3}$	Percentage	$n\,m^{-3}$	Percentage	$n\,m^{-3}$	Percentage	$n\,m^{-3}$	Percentage	$n\,m^{-3}$	Percentage
Invertebrate eggs	308.8	5.7	259.5	13.6	252.7	10.0	112.1	8.7	74.1	6.2	328.8	5.5
Nauplii	2,816.8	52.0	440.3	23.0	1,163.1	45.9	409.7	31.7	434.8	36.3	2,887.5	48.5
Copepods	2,278.7	42.1	1,201.2	62.8	997.4	39.4	757.2	58.6	685.5	57.2	2,682.3	45.1
Apendicularia	0.0	0.0	2.7	0.1	10.9	0.4	1.1	0.1	0.0	0.0	5.4	0.1
Lamellibranchis	0.0	0.0	0.0	0.0	6.8	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Gastropoda	1.1	0.0	6.8	0.4	82.9	3.3	2.0	0.2	0.0	0.0	48.9	0.8
Polychaeta	0.0	0.0	0.0	0.0	2.7	0.1	1.0	0.1	0.0	0.0	0.0	0.0
Amphipoda	0.0	0.0	0.0	0.0	8.2	0.3	1.0	0.1	0.0	0.0	0.0	0.0
Echinodermata	7.1	0.1	0.0	0.0	1.4	0.1	1.0	0.1	0.0	0.0	0.0	0.0
Isopoda	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.2	0.0	0.0	0.0	0.0
Medusae	1.1	0.0	0.0	0.0	1.4	0.1	0.0	0.0	0.7	0.1	0.0	0.0
Cladocera	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tinntinida	0.0	0.0	1.4	0.1	6.8	0.3	4.1	0.3	4.1	0.3	1.4	0.0
Total	5,415.5		1,911.8		2,534.2		1,291.2		1,199.2		5,954.3	

Results are expressed as number of zooplankters per m^{-3} (nm^{-3}) and %
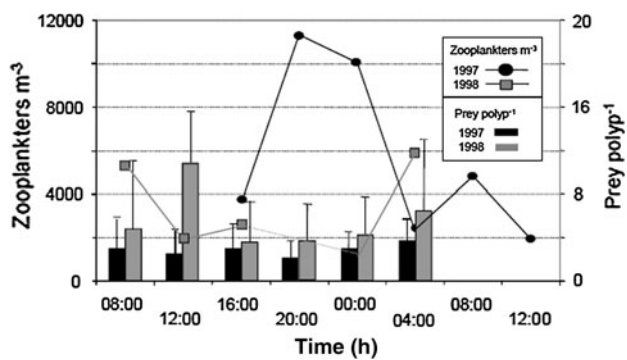
Fig. 3 Number of zooplankters in the water column (expressed as zooplankters m^{-3}) and number of prey found in the polyps of *Obelia dichotoma* (expressed as prey polyp^{-1}) at different times during a day in 1997 and 1998. Results are expressed as average ± SD
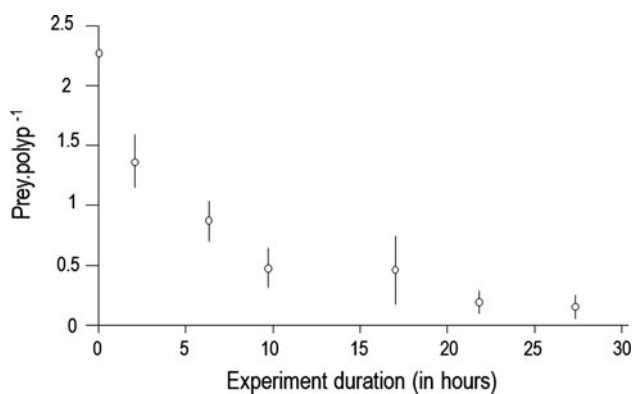

Fig. 4 Digestion process in the gastrovascular cavity of *Obelia dichotoma*. Number of prey items found in the gastrovascular system at different points of the experiment expressed as prey polyp^{-1}. Time 0 = time of feeding. Results are expressed as average ± SD

in the area (e.g. Andreassen et al. 1996, Woelfel et al. 2010), as well as in other Arctic locations (e.g. Auel and Hagen 2002, Turner 2002). In Kongsfjorden, sedimentation rates of faecal pellets are especially high in summer, probably due to the grazing activity of the zooplankton, presenting high abundances and biomass during this season and ranging between 0.64 g C m^{-2} day^{-1} in the inner part of the fjord and 0.75 g C m^{-2} day^{-1} in the outer part (Zajaczkowski unpubl., in Svendsen et al. 2002). Furthermore, the sedimentation rate of seston in the glacially influenced Kongsfjorden is considerably high, filling the water system with high amounts of POM: 1.5–7.4 g m^{-2} day^{-1} (Svendsen et al. 2002). As opportunistic consumers, hydrozoans might take advantage of the organic fraction of the seston, and actually, OM represents a considerable part of *O. dichotoma*'s diet. Thus, the particularly high uptake of OM and faecal pellets in the present study (up to 78 % of the total diet of *O. dichotoma* in 1998, Table 2) is most likely due to the high supply with these items in this Arctic environment. This omnivorous feeding strategy, but especially the preference

of small particles, coincides with the feeding preferences of the planktonic stage of *Obelia* species; contrary to most hydromedusa species, *Obelia* is considered a microphagous-feeding species (Boero et al. 2007).

On the other hand, the high amount of microalgae found in the gastrovascular cavity of *Obelia dichotoma* (3–27 % in 1997; 8–50 % in 1998; Table 2) is surprising. The phytoplankton production in Kongsfjorden is extremely variable during the year with the spring bloom (April–May) representing the only predictable production peak in the fjord (Hop et al. 2002). Only a minor component of the spring bloom, which is dominated by diatoms, sinks from the water column (Wiktor 1999). This bloom is subsequently slowed down by heavy grazing (Eilertsen et al. 1989) resulting in a low sedimentation signal and thus not supporting hydrozoan feeding. Furthermore in the late summer and early autumn, phytoplankton biomass may comprise as little as 15–20 % of the particulate organic carbon (POC) in the water masses (E.N. Hegseth pers. comm.—in Hop et al. 2002). While phytoplankton in Kongsfjorden blooms only for short intervals during spring, microphytobenthic communities are present at least all over the polar day (8–9 months), but probably also during winter time (Woelfel et al. 2009). In a recent study, Woelfel et al. (2009) documented high biomass of benthic diatoms in shallow waters down to 30 m depth all over Kongsfjorden. In addition, the nutritional value of diatoms is usually high due to preferential storage of lipids (e.g. Kuwata et al. 1993; Armbrust 2009). Therefore, benthic diatoms may represent an important food source for zoobenthos in Kongsfjorden in general and for hydrozoans in particular. Actually, Gili et al. (1996a) have shown benthic diatoms to be the main food source for the hydroid *Silicularia rosea* in Antarctic shallow waters (Potter Cove, King George Island). Moreover, diatoms are known to serve as a food source for some Antarctic suspension feeders such as sponges (Gaino et al. 1994) and brittle stars (Kellogg and Kellogg 1982). For a long time, it was not sure whether captured diatoms could be efficiently digested and assimilated by suspension feeders (Widding and Schlichter 2001). However, it has already been demonstrated by Transmission Electron Microscopy (TEM) and labelled carbon, that diatoms are in fact efficiently digested by hydroids (Gili et al. 2008). Although in the present study, it was not investigated in the field experiments whether the microalgae in the gastrovascular cavity of *O. dichotoma* were of benthic or planktonic origin, in the digestion experiments in the laboratory, diatoms were readily consumed by the hydroids.

In 1998, lower average zooplankton abundance in the water column was observed compared to 1997. This could be due to the special situation of sea ice in 1998, since Hop et al. (2002) argue that an extended presence of ice cover has a limiting effect on primary production. However, the

results of the present study show a general lack of correlation between total zooplankton concentration in the water column and prey in the gastrovascular contents of the hydroids. This is surprising, since for an opportunistic suspension feeder, a correlation between zooplankton concentration in the environment and number of zooplankters in the polyps would be highly expected as was already documented by different investigations (Barangé and Gili 1988; Barangé et al. 1989). Especially in late summer, zooplankton abundance should be high in Kongsfjorden (Walkusz et al. 2009) and may represent a major food source for *Obelia dichotoma*. The low portion of zooplankton found in the hydroids might be seen as an adaptation to the considerable variability in zooplankton distribution in terms of abundance and biomass between locations within the fjord as well as between years and months (Hop et al. 2002), making it a highly unreliable food source. The adaptation of hydroids to consume other food sources than zooplankton should be especially important in the Arctic Ocean with its environmental conditions characterised by long and unpredictable oligotrophic periods, when zooplankton is scarce, causing potential problems on the food supply of carnivorous suspension feeders.

Although, compared to microalgae, faecal pellets and OM, zooplankton abundance is low in the gastrovascular cavities of *Obelia dichotoma* from Kongsfjorden, at least 10 % of the hydroids diet were zooplankters, some of them with a high carbon content (e.g. copepods), indicating that zooplankton, even if present in small numbers, may contribute an important part of the carbon input. This was shown for other passive suspension feeders (gorgonians) that capture organic matter and phytoplankton but rely for most of its energy input on prey such as bivalve larvae or copepods (Ribes et al. 1999; Rossi et al. 2004). Thus, to evaluate the impact of a special prey, its carbon content should be taken into account.

Another important factor to interpret and understand the feeding behaviour of hydroids is the size of polyps and colonies, because it is known that large colonies and large polyps are able to capture more and larger prey, as it is the case for *Eudendrium racemosum* (large colony, small polyps) (Barangé and Gili 1988) or *Tubularia larynx* (different colony sizes, but very large polyps) (Gili et al. 1996b). The small colonies (and polyps) of Obelia and Campanularia species seem to capture small prey mainly (e.g. Coma et al. 1995; Orejas et al. 2000), and thus, prey captured and plankton composition are not always as coupled as in other cases (e.g. *T. larynx*, Gili et al. 1996b).

Prey digestion times are highly variable for cnidarians (e.g. Boschma 1925; Yonge and Nicholls 1930; Porter 1974; Sebens and Koehl 1984; Barangé and Gili 1988; Coma et al. 1994). Some of the factors that highly influence the duration of the digestion are prey size and typology (presence or absence of chitinous carapaces, naked prey, shelled larvae, etc.), as shown by Ishii and Tanaka (2001) together with temperature (Rossi et al. 2004, 2012). In this study, digestion times of almost 20 h were found for *Obelia dichotoma* at about 6 °C, digesting diatoms (Fig. 4). Under similar temperatures (4 °C), the hydrozoan *Hydractinia equinata* from the North East Atlantic needed more than 40 h to digest zooplankton prey (Christensen 1967), while the Antarctic shallow water hydroid *Silicularia rosea* digested diatoms in about 12 h at 0–2 °C (Gili et al. 1996a). These different results confirm the high variability of digestion, depending on hydroid species, temperature and on the characteristics of the ingested prey. To determine the most significant variable in this process, more experiments under controlled conditions should be performed.

Considering the density of *Obelia dichotoma* at the sampling site (highly variable between the both studied years) and the number of prey per polyp consumed in both years (Table 2), capture rates of around 134,149 prey items m^{-2} day^{-1} in 1997 and 261,182 prey items m^{-2} day^{-1} in 1998 were estimated. Values in the same range were found for the hydroid *Eudendrium racemosoum* from the Mediterranean Sea (100,000 prey items m^{-2} day^{-1}; Barangé and Gili 1988; Barangé et al. 1989), while *Obelia geniculata* in the upwelling area of the Coliumo Bay (Chile) showed much higher capture rates (>623,000 prey items m^{-2} day^{-1}; Orejas et al. 2000). The quantity of carbon removed from the water column by *O. dichotoma* in Kongsfjorden ranges from 5.5 mg C m^{-2} day^{-1} in 1997 to 8.9 mg C m^{-2} day^{-1} in 1998. These rates are in the lower range compared to those of other species of hydroids in different geographical regions (Table 4). However, the consumption rates of *O. dichotoma*, even if in the lower range for hydroids are still higher than those documented for other suspension feeders, like the gorgonian *Plexaura flexuosa* (1 mg C m^{-2} day^{-1}) from the Caribbean (Ribes et al. 1998) and even for the polychaete species *Lanice conchilega* from the North Sea (2.7 mg C m^{-2} day^{-1}) (Buhr 1976), which is an active filter feeder.

Considering the daily-mass-specific ingestion rate, which means the percentage of the hydroid weight daily ingested, *O. dichotoma* from Kongsfjorden showed very similar values (7.5–12.1 %) compared to *Silicularia rosea* (12.6 %) from Antarctic waters (Gili et al. 1996a, Table 4). Brey and Clarke (1993), and Arntz et al. (1994) assumed that low environmental temperatures cause a shift towards low basal metabolic rates in Antarctic invertebrates and may enable a better survival during the seasonally high fluctuation levels of food. The results of the present study indicate that this may also count for Arctic hydroids. Thus to correctly interpret the trophic ecology of these

Table 4 Impact on the water column (expressed as mg C removed per m^{-2} per day^{-1}) of different hydroid species from different geographical areas

Species	Geographical area	mg C removed m^{-2} day^{-1}	Diel mass-specific ingestión rate (in percentage)	Source
Silicularia rosea	King George Island (Antarctica)	66	12.6	Gili et al. (1998)
Nemalecium lighti	Panamá (Caribbean Sea)	6	136	Gili et al. (1998)
Campanularia everta	Spain (NW Mediterranean)	6.4	19	Gili et al. (1998)
Eudendrium racemosum	Spain (NW Mediterranean)	12	39.1	Gili et al. (1998)
Tubularia larynx	Scotland (NE Atlantic)	89.9	89.9	Gili et al. (1998)
Obelia geniculata	Chile (SE Pacific)	113.2	113.2	Gili et al. (1998)
Obelia dichotoma	Kongsfjord (Spitsbergen, Norway)	5.5–8.9	7.5–12.07	This work

organisms, it is important to consider not only the number of prey, but especially their carbon content, as well as the daily-mass-specific ingestion rate and the environmental conditions of the area. Further, caution should be taken before generalisation to define ecological roles, which may be variable according to different ecological situations (see, Piraino et al. 2002).

Obelia dichotoma in Kongsfjorden has shown comparably high capture rates at the investigated site. Beside soft sediments, hard substrates overgrown by macroalgae are found at several locations in Kongsfjorden. Thus, macro algal communities are a typical component of the Fjord not only at the sampling spot (Hop et al. 2002; Wiencke et al. 2004), indicating a relevant trophic impact of associated hydrozoans. Since modelling exercises for Kongsfjorden as a model ecosystem are taking place currently (Hop et al. 2002), organisms with filtration rates in the range of *O. dichotoma* are not to be neglected in assessments of matter flux in the "model ocean" Kongsfjorden. At the present stage, the data obtained using the pier as a model area for Kongsfjorden eulittoral of course cannot be extrapolated to the whole hard-bottom area of the fjord. However, no data particularly on the distribution and density of *O. dichotoma* throughout the fjord are available at the present stage. To include the trophic impact of *O. dichotoma*, or hydroids in general, into ecosystem modelling, data of their distribution, density and activity have to be collected including annual and seasonal variability.

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