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Fatty acid trophic markers and trophic links among seston, crustacean zooplankton and the siphonophore *Nanomia cara* in Georges Basin and Oceanographer Canyon (NW Atlantic)

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SUMMARY: Fatty acid concentrations expressed as percentages of total fatty acid pools in seston, stage V copepodites of *Calanus finmarchicus*, adults of the euphausiid *Meganyctiphanes norvegica*, and the physonect siphonophore *Nanomia cara* were used to elucidate trophic links in Georges Basin and Oceanographer Canyon in September 2003. Seston at both locations was refractory and comprised mainly of saturated fatty acids. Phytoplankton did not contribute significantly to the fatty acid composition of seston or higher trophic levels. Only four fatty acids, i.e. 14:0, 16:0, 16:1 (n–7) and 18:1 (n–7), were transferred from seston to *C. finmarchicus* or *M. norvegica*, which suggested weak trophic interactions. Fatty acids transferred from the two species of crustaceans to *N. cara* included the same four fatty acids, along with three polyunsaturated fatty acids found in relatively high concentrations in both crustaceans, i.e. 20:3 (n–6), 20:5 (n–3) and 22:6 (n–3). In addition, 18:1 (n–9), which occurred in relatively high concentrations only in *M. norvegica*, and 18:0 and 18:2 (n–6), which were found in low concentrations in both crustaceans, also appeared to be transferred to *N. cara*. Overall, fatty acid trophic markers proved useful for identifying trophic links to *N. cara*.

Keywords: fatty acids, trophic relationships, siphonophora, Gulf of Maine.

RESUMEN: ÁCIDOS GRASOS COMO MARCADORES DE LAS RELACIONES TRÓFICAS ENTRE EL SESTON, EL ZOOPLANCTON CRUSTÁCEO Y EL SIFONÓFORO *NANOMIA CARA* EN GEORGES BASIN Y EL CAÑÓN OCEANOGRAPHER (NO ATLÁNTICO). – En este estudio se utilizaron las concentraciones de ácidos grasos (expresadas como porcentajes) para identificar posibles relaciones tróficas entre el seston, el estadio V (copepoditos) de *Calanus finmarchicus*, los adultos del eufáusido *Meganyctiphanes norvegica*, y el sifonóforo fisonecto *Nanomia cara* en Georges Basin y el cañón submarino Oceanographer durante Septiembre de 2003. En ambos lugares el seston era muy refractario y compuesto básicamente por ácidos grasos saturados. El fitoplancton no contribuyó de forma significativa a la composición de ácidos grasos del seston o de niveles tróficos superiores. Sólo cuatro ácidos grasos [14:0, 16:0, 16:1 (n–7) y 18:1 (n–7)] se transfirieron potencialmente del seston a *C. finmarchicus* o *M. norvegica*, lo que sugiere una débil conexión trófica entre estos eslabones de la cadena. Los ácidos grasos transferidos de las dos especies de zooplancton crustáceo a *N. cara* incluyen los mismos descritos más arriba y otros tres ácidos grasos poliinsaturados [20:3 (n–6), 20:5 (n–3) y 22:6 (n–3)] encontrados en concentraciones relativamente elevadas en ambos crustáceos. Además, tanto el 18:1 (n–9) (encontrado en elevadas concentraciones en *M. norvegica*) y los 18:0 y 18:2 (n–6) (encontrados en bajas concentraciones en ambas especies de crustáceos) se transfieren a *N. cara*. Los ácidos grasos demuestran ser una herramienta útil para identificar conexiones tróficas en *N. cara*.

Palabras clave: ácidos grasos, relaciones tróficas, sifonóforos, Golfo del Maine.

INTRODUCTION

Gelatinous zooplankton function as herbivores, carnivores, omnivores or detritivores in all oceans from surface waters to the deep sea (Hartman and Emery, 1956; Pugh, 1975; Biggs *et al.*, 1981; Pagès and Kurbjewit, 1994; Patriti, 1995; Gorsky *et al.*, 2000). Carnivorous gelatinous zooplankters can regulate secondary productivity when they becomes abundant in coastal waters, regions of upwelling, fjords, and submarine canyons (Purcell, 1991; Purcell *et al.*, 1994; Pagès *et al.*, 2001). Therefore, an understanding of trophic links to these predators is crucial for predicting the dynamics of pelagic food webs, especially in systems stressed by anthropogenic impacts, such as chronic overfishing (Mills, 1995).

The roles of gelatinous zooplankton in food webs mainly have been determined from the stomach contents of specimens caught in nets. Unfortunately, such sampling can bias estimates of prey consumption because gelatinous zooplankton may feed on prey concentrated in cod ends, digest stomach contents during tows, or regurgitate prey (Youngbluth and Båmstedt, 2001). In addition, gelatinous plankters are typically abraded or fragmented in nets to an extent that complicates identification and enumeration. In some cases, in situ observations provide reliable data on gut contents of gelatinous predators, but such observations are limited (Robison, 2004).

Analyses of fatty acid trophic markers complement analyses of stomach contents. For example, fatty acid composition integrates feeding behaviour over longer time scales and is not biased by digestion times (Dalsgaard *et al.*, 2003). However, fatty acids are seldom unique to an organism, and changes in environmental conditions that affect metabolic rates can alter the production, storage or conversion of fatty acids (Dalsgaard *et al.*, 2003). Therefore, in the absence of data on metabolism, the most reliable evidence of trophic links arises from the transfer of multiple fatty acids in reasonable quantities, and fatty acid compositions should be viewed primarily as qualitative indicators of trophic links rather than quantitative indicators of the strength of such links (Dalsgaard *et al.*, 2003).

This study examined fatty acids in the physonect siphonophore, *Nanomia cara*, two crustacean zooplankters (stage V copepodites of the calanoid copepod *Calanus finmarchicus* and adult euphausiids, *Meganyctiphanes norvegica*), and seston in an effort to identify trophic links in Georges Basin and Oceanographer Canyon, NW Atlantic. The ecological role of *N. cara* in this coastal region is poorly known, but this species should exert significant effects on its prey and competitors when it reaches densities of 10-100 colonies m^{-3} (Rogers *et al.*, 1978; Mills, 1995; Sommer *et al.*, 2002).

METHODS

Collection of samples

Seston, copepods, euphausiids and siphonophores were collected at depths of between 56 m and 831 m in Georges Basin and Oceanographer Canyon from 11 to 25 September 2003 (Fig. 1; Table 1). At each sampling station, depth, temperature, salinity and dissolved oxygen were measured with Seabird SBE 25 Sealoggers.

Seston was extracted from 1-2 L of water collected in Niskin bottles by filtering it through Whatman GF/F filters that had been precombusted for 5 h at 450ºC. Individual filters with seston were placed into cryotubes and frozen in liquid nitrogen. Four sets of duplicate samples from Georges Basin (n = 8) and three sets of duplicate samples from Oceanographer Canyon (n = 6) were analysed for particulate organic carbon and nitrogen. Fatty acid compositions were determined for three sets of duplicate samples and one unreplicated sample from Georges

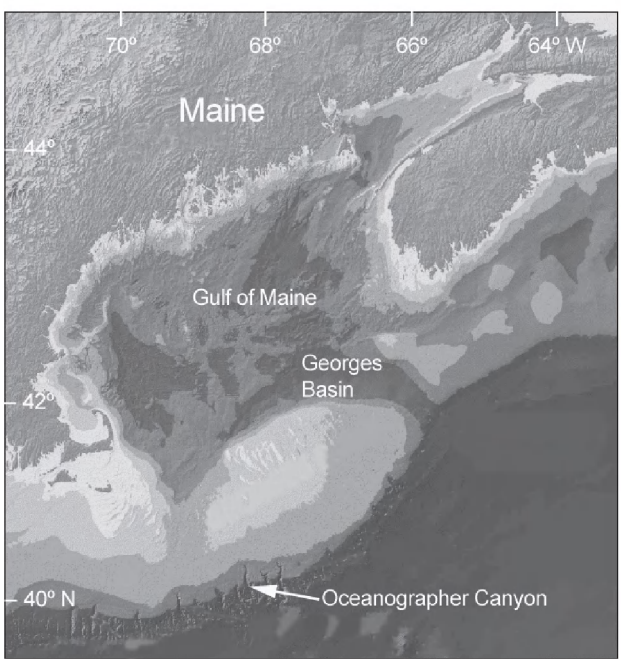

FIG. 1. – Study area showing locations of sampling

TABLE 1. – Details for collection of samples. AM, daytime; PM, nighttime; POC:PON, ratio of particulate organic carbon to particulate organic nitrogen.

DD/MM/YY	Time	Latitude	Longitude	Depth (m)	Samples
Georges Basin					
11/09/03	AM	42°16.27'	-69°30.93'	212	*Calanus finmarchicus* stage V copepodites
				238	*Nanomia cara*
12/09/03	AM	42°19.47'	-67°29.46'	212	Seston (POC:PON and fatty acids = duplicates)
	PM	42°17.50'	-67°30.18'	224	*Nanomia cara*
13/09/03	AM	42°18.51'	-67°29.19'	215	Seston (POC:PON and fatty acids = duplicates)
		42°17.40'	-67°30.19'	224	*Nanomia cara*
13/09/03	PM	42°18.74'	-67°31.16'	195	*Calanus finmarchicus* stage V copepodites
		42°18.74'	-67°32.95'	205	*Nanomia cara*
		42°18.74'	-67°32.95'	214	Seston (POC:PON and fatty acids = duplicates)
21/09/03	AM	42°19.22'	-67°29.24'	213	Seston (POC:PON = duplicates; fatty acids = single sample)
	PM	42°16.06'	-67°31.13'	56	*Nanomia cara*
				207	*Calanus finmarchicus* stage V copepodites
Oceanographer Canyon					
14/09/03	PM	40°17.80'	-68°06.76'	810	*Nanomia cara*
		40°17.25'	-68°07.15'	600	Seston (POC:PON and fatty acids = duplicates)
23/09/03	PM	40°17.38'	-68°06.88'	700	Seston (POC:PON = duplicates; fatty acids = single sample)
24/09/03	AM	40°11.43'	-68°11.34'	831	*Meganyctiphanes norvegica*
					Meganyctiphanes norvegica
25/09/03	PM	40°16.39'	-68°07.04'	700	Seston (POC:PON and fatty acids = duplicates)

Basin (n = 7) and two sets of duplicate samples and one unreplicated sample from Oceanographer Canyon (n = 5).

Fatty acid compositions were determined for pooled samples of *Calanus finmarchicus* stage V copepodites from Georges Basin (n = 3) and pooled samples of adult *Meganyctiphanes norvegica* from Oceanographer Canyon (n = 2). Pooled samples consisted of either 20 *C. finmarchicus* or 1-2 *M. norvegica* that had been placed in separate cryotubes and frozen in liquid nitrogen. Crustaceans for pooled samples were captured with forceps from collections taken with a suction sampler attached to a *Johnson-Sea-Link* submersible (Youngbluth, 1984).

In total, six colonies of the physonect siphonophore *Nanomia cara* were collected in Georges Basin (n = 5) and Oceanographer Canyon (n = 1). Each colony was captured in a different 6.5-L acrylic sampler that had been washed with 1N hydrochloric acid prior to use. Colonies without prey visible in their gastrozooids were kept at 6-10°C on a bed of ice under a dissecting microscope while nectosomes were separated from siphosomes (Fig. 2). Each nectosome or siphosome was placed in a separate cryotube and frozen in liquid nitrogen.

Analysis of particulate organic carbon and nitrogen in seston

Filters containing seston were removed from liquid nitrogen and dried at 60°C for 24 h. Inorganic material was destroyed by keeping the dried filters in air saturated with hydrochloric acid for 48 h (Rossi and Gili, 2005). Filters were dried further at 60°C for

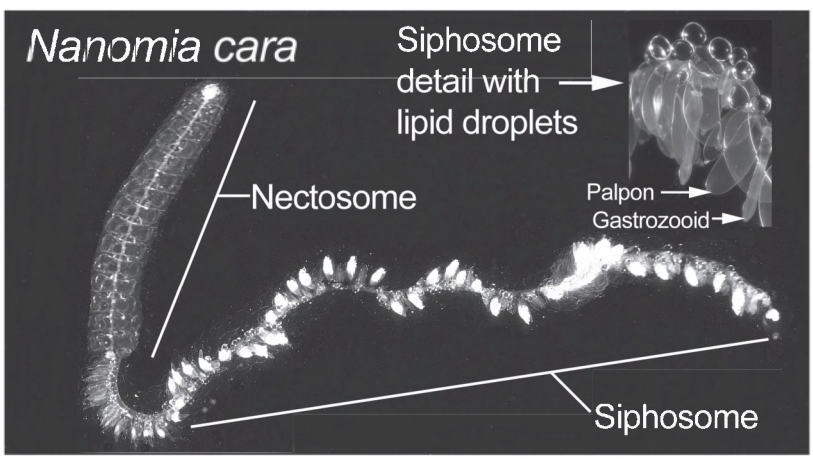

FIG. 2. – *Nanomia cara* showing nectosome, siphosome, gastrozooids, palpons and lipid droplets.

another 24 h. Particulate organic carbon and nitrogen were measured with a Perkin-Elmer 2400 autoanalyser (Doval *et al.*, 1999).

Extraction and quantification of fatty acids

Fatty acids were extracted from samples of seston, copepods, euphausiids and siphonophores that had been lyophilised for 12 h at -100ºC and 100 mbar. After lyophilisation, glass fibre filters with seston were sonicated in 2:1 dichloromethane-methanol three times for 10 min each time. All other samples were ground gently in a 5 ml glass homogeniser, and sonicated three times for 20 min each time in 1 ml of 2:1 dichloromethane-methanol. After each sonication, the solvent was separated from particles by centrifugation. The extracts for each sample were combined, evaporated under vacuum to 0.5 ml, and hydrolysed overnight with 2 ml of 6% potassium hydroxide and methanol. Neutral fractions were recovered with three 2 ml extractions using n-hexane, and then acidic fractions were recovered using n-hexane that had been acidified to pH 2 with aqueous 6N hydrochloric acid. The acidic fractions were reduced to 0.5 ml and esterified overnight with 3 ml of 10% boron trifluoride-methanol. The resulting complexes were destabilised with 2 ml of water, and fatty acids were recovered as their methyl esters by extracting three times with 2 ml of n-hexane (Rossi *et al.*, 2006).

Quantitative gas chromatography was performed with an Agilent 5890 Series II instrument equipped with a flame ionisation detector and a splitless injector. The DB-5 column was 30 m long with an internal diameter of 0.25 mm and a 0.25 μm coating of phenyl-methylpolysiloxane. Helium was used as a carrier gas at 33 cm s^{-1}. The oven temperature was programmed to increase from 60 to 300ºC at 6ºC min^{-1}. Injector and detector temperatures were 270 and 310ºC, respectively. Methyl esters of fatty acids were identified by comparing their retention times to those of standard fatty acids (Supelco®). Fatty acids were quantified by integrating areas under peaks in the gas chromatograph traces, with calibrations derived from an external standard containing different methyl esters.

Evaluation of trophic links

Semi-strong, hybrid multidimensional scaling was used to ordinate relative fatty acid concentrations expressed as percentages of the total pool of fatty acids (Belbin, 1989). Separate ordinations were conducted using data from Georges Basin and Oceanographer Canyon to ensure that differences in fatty acid compositions between locations did not obscure patterns within a location. Means were calculated for duplicate seston samples, which yielded 4 values for seston from Georges Basin and 3 values for seston from Oceanographer Canyon. Ordinations were based on Bray-Curtis dissimilarities, with linear regression applied to dissimilarities below 0.9 and ordinal regression applied to values above 0.9. Ordinations in three dimensions yielded stress values below 0.1, which were considered acceptable representations of the data.

If ordinations indicated that fatty acid compositions of samples within a trophic level were more similar to each other than to different trophic levels, then comparisons of relative concentrations across trophic levels were used to elucidate trophic markers. Fatty acids were classed as potential trophic markers if they: 1) represented approximately 2% or more of the relevant fatty acid pools (Dalsgaard *et al.*, 2003) and 2) occurred in similar percentages in different trophic levels or at a higher percentage in the higher trophic level, which indicated that they were transferred conservatively or accumulated through trophic links.

Table 2. – Environmental conditions during sampling.

Parameter	Georges Basin	Oceanographer Canyon
Water column		
Depth of water column (m)	295	998
Surface temperature (ºC)	15.0-17.5	21.5-23.5
Surface salinity (PSU)	32.0-32.5	34.0-35.0
Surface dissolved oxygen (ml L^{-1})	3.5-4.5	2.5-4.0
Depth at base of thermocline (m)	50	50
Sampling depths		
Temperature (ºC)	5.0-9.0	5.0-10.0
Salinity (PSU)	33.0-35.0	35.5
Dissolved oxygen (ml L^{-1})	2.0-5.0	2.0-4.5

RESULTS

Environmental conditions

All samples were collected below the thermocline, which was at approximately 50 m at both locations (Table 2). At these depths, temperatures, salinities and dissolved oxygen concentrations were

TABLE 3. – Carbon and nitrogen composition of seston. C, carbon; N, nitrogen; SE, standard error.

Location	n	Depth (m)	Mean C (μg L^{-1}) ± SE	Mean N (μg L^{-1}) ± SE	Mean C:N ± SE
Georges Basin	8	200	103.3 ± 3.7	5.5 ± 0.7	23.0 ± 1.7
Oceanographer Canyon	6	700	93.0 ± 3.7	3.8 ± 0.2	26.5 ± 2.4

TABLE 4. – Mean fatty acid concentrations as percentages of the total fatty acid pool, with potential trophic markers in bold. Σ Bacillariophyceae, sum of 16:1 (n–7), 16:4 (n–1) and 20:5 (n–3); Σ Dinophyceae 1, sum of 18:5 (n–3) and 22:6 (n–3); Σ Dinophyceae 2, sum of 20:5 (n–3) and 22:6 (n–3); Σ Prymnesiophyceae, sum of 18:1 (n–9) and 18:4 (n–3).

Fatty acid	Seston		*Calanus*	*Meganyctiphanes*	*Nanomia*			
	Georges Basin (n = 6)	Oceanographer Canyon (n = 6)	Georges Basin (n = 3)	Oceanographer Canyon (n = 2)	Georges Basin		Oceanographer Canyon	
					Nectosome (n = 5)	Siphosome (n = 5)	Nectosome (n = 1)	Siphosome (n = 1)
12:0	5.3	3.5	0.3	0.2	1.8	3.4	0.9	0.3
13:0	0.2		0.1	0.1		0.2		0.1
14:0	**8.3**	**8.0**	**23.9**	**9.3**	**9.5**	**14.0**	**7.2**	**15.2**
15:0	1.2	1.0	1.5	1.4	0.9	0.8		1.2
16:0	**30.7**	**30.5**	**13.7**	**16.2**	**22.1**	**18.8**	**20.6**	**12.9**
17:0	0.8	1.0			0.8	0.3	0.4	0.3
18:0	21.1	34.4	**1.1**	**2.2**	**18.2**	**6.4**	**18.8**	**1.7**
20:0	0.1	0.2	2.1	0.6	0.04	0.04		
22:0	14.7	6.6		0.05	3.1	1.1	20.5	
23:0				0.02	2.1		2.1	
24:0				0.1	2.1		2.7	
26:0					2.3	0.3	0.9	
16:1 (n–7)	**2.2**	**1.7**	**8.6**	**4.2**	**4.6**	**7.8**	**0.3**	**6.7**
18:1 (n–7)	**3.5**	**3.0**	**7.8**	**13.2**	**5.3**	**4.3**	1.9	1.3
18:1 (n–9)	0.2	0.3	**0.4**	**3.8**	**1.2**	**3.5**		**8.4**
22:1 (n–11)	0.1		3.7	6.1				
18:2 (n–6)	0.4	1.6	**1.4**	**1.7**	**2.7**	**2.0**		**8.8**
22:2 (n–6)	0.1				2.8	3.5		8.8
18:3 (n–3)	0.4	0.5	10.6	3.0	1.5	2.8		0.2
20:3 (n–6)		**0.2**	**2.7**	**6.4**	**2.2**	**3.5**	**3.2**	**5.2**
20:5 (n–3)	0.3		**9.0**	**8.7**	**10.0**	**11.2**	**12.1**	**11.8**
22:6 (n–3)	0.8		**4.9**	**11.0**	**9.3**	**8.9**	**7.0**	**8.2**
SFAs	82.4	85.0	42.7	30.0	56.6	51.5	68.7	37.4
MUFAs	5.9	5.1	20.5	27.3	11.1	15.6	2.2	16.4
PUFAs	2.1	2.3	28.6	30.8	28.5	31.9	22.3	43.0
Σ Bacillariophyceae	2.6	1.7	17.6	12.9	14.6	19.0	12.4	18.5
16:1 (n–7)/16:0 – mean ratio	0.1	0.1	0.6	0.3	0.2	0.5	0.02	0.5
20:5 (n–3)/22:6 (n–3) – mean ratio	0.8		1.8	0.8	1.3	1.3	1.7	1.4
Σ Dinophyceae 1	1.2		4.9	11.0	9.3	8.9	7.0	8.2
Σ Dinophyceae 2			13.9	19.7	19.3	20.1	19.1	20.0
18:5 (n–3)/18:3 (n–3) – mean ratio	2.4							
22:6 (n–3)/20:5 (n–3) – mean ratio	0.2	0.3	0.5	1.3	0.8	0.8	0.6	0.7
Σ Prymnesiophyceae	0.4	1.6	0.4	3.8	1.2	3.5		8.4
PUFAs/SFAs			0.7	1.0	0.7	0.6	0.3	1.2
18:1 (n–7)/18:1 (n–9) – mean ratio			21.6	3.4	5.8	6.7		0.2

similar and stable during the sampling period, so spatiotemporal variations in fatty acid metabolism were unlikely.

Characterisation of trophic levels

Carbon and nitrogen concentrations in seston did not vary significantly between locations, which indicated that similar quantities of particulate matter were present (Table 3; F-value for carbon = 3.65, df = 1, 12, p = 0.08; F-value for nitrogen = 3.71, df = 1, 12, p = 0.08). Carbon:nitrogen ratios (C:N ratios) were above 20, which suggested that the particulate organic matter was refractory (Table 3).

In total, samples of seston contained 19 unique fatty acids, with 18 fatty acids found in seston from Georges Basin and 14 fatty acids found in seston from Oceanographer Canyon (Table 4). Across all samples, saturated fatty acids (SFAs) accounted for 73-93% of the total lipids recovered, with 12:0, 14:0, 16:0, 18:0, and 22:0 isolated in the highest concentrations. Monounsaturated fatty acids (MUFAs) typically accounted for less than 10% of the fatty acids isolated from seston, with only 16:1 (n-7) and 18:1

(n-7) extracted from over half of the samples. Polyunsaturated fatty acids (PUFAs) generally represented less than 5% of the fatty acids recovered from seston, and only 18:2 (n-6) and 18:3 (n-3) occurred in more than two samples. Sums and ratios of selected fatty acid concentrations reported to indicate contributions from Bacillariophyceae, Dinophyceae or Prymnesiophyceae suggested that these groups of phytoplankton contributed little to the seston that we sampled (Dalsgaard *et al.*, 2003).

Sixteen and seventeen unique fatty acids comprised the lipids in *Calanus finmarchicus* and *Meganyctiphanes norvegica*, respectively (Table 4). Saturated fatty acids represented 41-45% of all fatty acids in replicate samples of *C. finmarchicus* and 29-32% of all fatty acids in replicate samples of *M. norvegica*, with concentrations of 14:0 and 16:0 being the highest. In both species, MUFAs and PUFAs represented 18-32% of the fatty acids recovered, with 16:1 (n-7), 18:1 (n-7), 18:1 (n-9), 22:1 (n-11), 18:2 (n-6), 18:3 (n-3), 20:3 (n-6), 20:5 (n-3) and 22:6 (n-3) being present in all samples. Sums of selected relative fatty acid concentrations indicated contributions from Bacillariophyceae and Dinophyceae for *C. finmarchicus* and Bacillariophyceae, Dinophyceae and Prymnesiophyceae for *M. norvegica*. In contrast, ratios of selected fatty acid concentrations did not support these interpretations consistently. In addition, the mean ratios of 20:5 (n-3) to 22:6 (n-3), PUFAs to SFAs, and 18:1 (n-7) to 18:1 (n-9) indicated that *M. norvegica* fed at a higher trophic level than *C. finmarchicus* (Dalsgaard *et al.*, 2003).

Twenty-one fatty acids were isolated from *Nanomia cara*, with siphosomes yielding more fatty acids than nectosomes (Table 4). Fatty acids in individual nectosomes and siphosomes comprised 34-82% SFAs, 7-45% PUFAS and less than 20% MUFAs. Sums of relative fatty acid concentrations indicated contributions from Bacillariophyceae, Dinophyceae and Prymnesiophyceae. In contrast, ratios of selected fatty acid concentrations did not support this interpretation. As expected for a predator, the mean ratios of 18:1 (n-7) to 18:1 (n-9) for *N. cara* were lower than those recorded for their potential prey, i.e. *Calanus finmarchicus* in Georges Basin and *Meganyctiphanes norvegica* in Oceanographer Canyon. In contrast, the mean ratios of 20:5 (n-3) to 22:6 (n-3) and PUFAs to SFAs did not support the conclusion that *N. cara* fed at a higher trophic level than its potential prey.

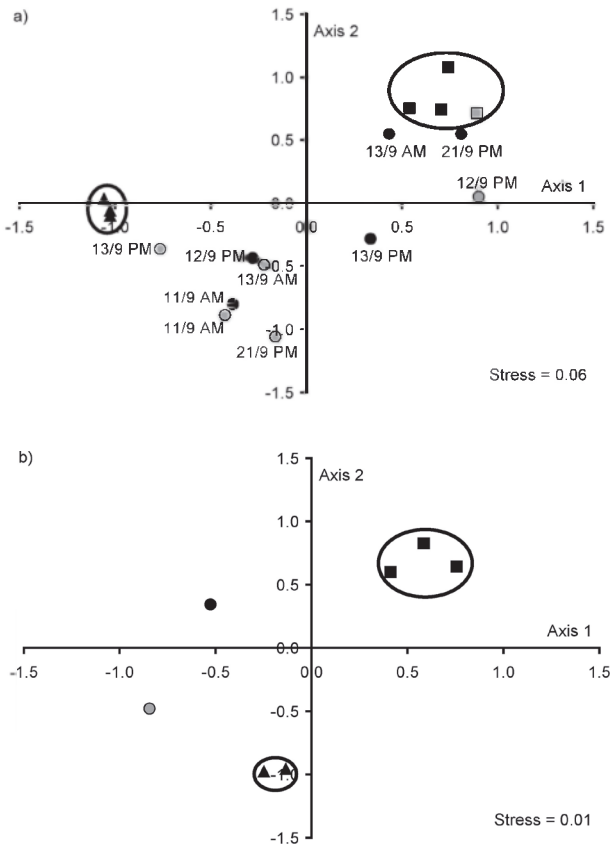

FIG. 3. – Results of ordinations using relative fatty acid concentrations in samples of seston, *Calanus finmarchicus* stage V copepodites, *Meganyctiphanes norvegica* and *Nanomia cara* from Georges Basin and Oceanographer Canyon. Stress values of less than 0.1 indicate an acceptable representation of the data; a) Georges Basin, with dates (dd/m) and times of sampling (AM or PM) shown for *Nanomia cara*: black squares, seston taken during daytime; grey square, seston taken at night; black triangles, *Calanus finmarchicus* stage V copepodites; black circles, *Nanomia cara* nectosomes; grey circles, *Nanomia cara* siphosomes; b) Oceanographer Canyon: black squares, seston taken at night; black trangles, *Meganyctiphanes norvegica*; black circle, *Nanomia cara* nectosome; open circle, *Nanomia cara* siphosome.

Characterisation of trophic links

Three-dimensional ordinations confirmed that samples of seston, *Calanus finmarchicus* stage V copepodites and *Meganyctiphanes norvegica* had fatty acid compositions that were more similar to each other than to samples from different trophic levels (Fig. 3a and b). As shown by the separation of relevant points in the ordinations, samples of *Nanomia cara* nectosomes and siphosomes had the most variable fatty acid compositions (Fig. 3a and b). However, multiple samples of *N. cara* from Georges Basin did not display a consistent pattern related to the date or time of sampling (Fig. 3a). Overall, the data indicated that comparisons of relative fatty acid

concentrations among samples of seston, *C. finmarchicus*, *M. norvegica* and *N. cara* could be used to identify trophic markers.

Analyses of all samples yielded 22 fatty acids (Table 4). Individual fatty acids represented less than 1% to over 30% of total fatty acid pools. In an effort to elucidate trophic markers, fatty acids were classified as: 1) compounds with uncertain value as indicators if they represented less than 2% of every fatty acid pool; 2) trophic markers if they occurred in similar percentages in different trophic levels or at higher percentages in higher trophic levels, which indicated conservative transfer or accumulation; 3) indicators of other food sources or *de novo* synthesis if they were found primarily in a higher trophic level; or 4) compounds that were not transferred conservatively if they appeared primarily in a lower trophic level.

Comparisons of relative fatty acid concentrations among samples from Georges Basin yielded few trophic markers that linked seston and *Calanus finmarchicus* stage V copepodites and numerous trophic markers that linked *C. finmarchicus* and *Nanomia cara* (Table 4). Out of the 19 fatty acids shared by seston and *C. finmarchicus*, only 14:0, 16:0, 16:1 (n-7) and 18:1 (n-7) were classed as trophic markers, with 14:0 and 16:1 (n-7) being accumulated by *C. finmarchicus*. In contrast, ten fatty acids out of 22, i.e. 14:0, 16:0, 18:0, 16:1 (n-7), 18:1 (n-7), 18:1 (n-9), 18:2 (n-6), 20:3 (n-6), 20:5 (n-3) and 22:6 (n-3) were identified as trophic markers that linked *C. finmarchicus* and *N. cara*. Out of these fatty acids, *Nanomia cara* accumulated 18:0 and 18:1 (n-9) beyond levels found in *C. finmarchicus*. Six fatty acids found in *C. finmarchicus* stage V copepodites, i.e. 20:0, 22:1 (n-11), 18:3 (n-3), 20:3 (n-6), 20:5 (n-3) and 22:6 (n-3), were classed as being obtained from food other than seston or synthesised *de novo*. For *N. cara*, five SFAs, i.e. 12:0, 22:0, 23:0, 24:0, 26:0, and one PUFA, i.e., 22:2 (n-6), appeared to come from food other than *C. finmarchicus* or to be synthesised *de novo*. Three SFAs, i.e. 12:0, 18:0 and 22:0, were not transferred conservatively between seston and *C. finmarchicus*, and 20:0, 22:1 (n-11) and 18:3 (n-3) were not transferred conservatively between *C. finmarchicus* and *N. cara*. Six fatty acids, i.e. 13:0, 15:0, 17:0, 18:1 (n-9), 18:2 (n-6) and 22:2 (n-6), occurred in low concentrations in samples of both seston and *C. finmarchicus*, and three SFAs, i.e. 13:0, 15:0 and 17:0, occurred in low concentrations in *C. finmarchicus* and *N. cara*. Three, long-chain SFAs, i.e. 23:0, 24:0 and 26:0, were not found in samples of seston or *C. finmarchicus*.

Samples from Oceanographer Canyon also yielded few trophic markers linking seston and a potential grazer, i.e., *Meganyctiphanes norvegica*, and numerous trophic markers linking *M. norvegica* and *Nanomia cara* (Table 4). The same four trophic markers that linked seston and *Calanus finmarchicus* stage V copepodites, i.e. 14:0, 16:0, 16:1 (n-7) and 18:1 (n-7), were identified as linking seston and *M. norvegica*, with 16:1 (n-7) and 18:1 (n-7) being accumulated by *M. norvegica*. Nine of the ten trophic markers that linked *C. finmarchicus* and *N. cara*, i.e. 14:0, 16:0, 18:0, 16:1 (n-7), 18:1 (n-9), 18:2 (n-6), 20:3 (n-6), 20:5 (n-3) and 22:6 (n-3), also linked *M. norvegica* and *N. cara*. *Nanomia cara* in Oceanographer Canyon accumulated 18:0, 18:1 (n-9) and 18:2 (n-6). In contrast to the results for Georges Basin, 18:1 (n-7) did not link *N. cara* to *M. norvegica*. Six fatty acids found in *M. norvegica*, i.e. 18:1 (n-9), 22:1 (n-11), 18:3 (n-3), 20:3 (n-6), 20:5 (n-3) and 22:6 (n-3), were obtained from food other than seston or synthesised *de novo*. For *N. cara*, three SFAs, i.e. 22:0, 23:0 and 24:0, and one PUFA, i.e. 22:2 (n-6), were obtained from food other than *M. norvegica* or synthesised *de novo*. Three SFAs, i.e. 12:0, 18:0 and 22:0, were not transferred conservatively between seston and *M. norvegica*, and 20:0, 18:1 (n-7), 22:1 (n-11) and 18:3 (n-3) were not transferred conservatively between *M. norvegica* and *N. cara*. Five fatty acids, i.e. 13:0, 15:0, 17:0, 20:0 and 18:2 (n-6), occurred in low concentrations in samples of both seston and *M. norvegica*, and five SFAs, i.e. 12:0, 13:0, 15:0, 17:0 and 26:0, occurred in low concentrations in *M. norvegica* and *N. cara*. The same long-chain SFAs that were absent from samples of seston and *C. finmarchicus* in Georges Basin, i.e. 23:0, 24:0 and 26:0, also were absent from samples of seston and *M. norvegica* in Oceanographer Canyon. In addition, 22:2 (n-6) was absent from samples of seston and *M. norvegica*.

DISCUSSION

The transfer of fatty acids to higher trophic levels is a complex process. Detection of trophic markers is enhanced if higher trophic levels feed extensively on the foods investigated and samples are taken during a period of anabolism rather than catabolism (Falk-Petersen *et al.*, 1987; St. John and Lund, 1996; Kirsch *et al.*,

1998; Fukuda and Naganuma, 2001; Falk-Petersen *et al.*, 2002; Dalsgaard and St. John, 2004).

Without detailed information about metabolism, trophic links should not be derived from fine-scale comparisons of quantitative differences in relative concentrations of fatty acids. Instead, identifying trophic links must rely primarily on the apparent transfer of multiple fatty acids in reasonable quantities among samples collected during a time without significant variation in environmental conditions. We interpreted our results within this context by looking for environmental variability that could mask trophic links, comparing our data to previous reports to establish their reliability, and applying a consistent process to identify trophic markers.

Environmental variability

Environmental variability can alter physiological responses of organisms and mask trophic links. However, fatty acid compositions have been reported to be stable unless environmental conditions changed noticeably. For example, fatty acid concentrations of mixed phytoplankton were stable when the trophic links for *Gadus morhua* larvae were analysed over 9-10 d in the absence of a phytoplankton bloom (Klungsøyr *et al.*, 1989). In addition, changes in fatty acid compositions of fishes, copepods, phytoplankton and seston following phytoplankton blooms remained stable and detectable for 2-3 months (Pedersen *et al.*, 1999; Reuss and Poulsen, 2002; Parrish *et al.*, 2005).

During our 15-d sampling period, environmental conditions remained stable below the thermoclines in Georges Basin and Oceanographer Canyon; therefore, fatty acid compositions were not expected to change to an extent that would mask trophic markers. Ordinations confirmed that the relative fatty acid concentrations of seston, *Calanus finmarchicus* stage V copepodites, adult *Meganyctiphanes norvegica* and *Nanomia cara* did not vary in a consistent pattern across the sampling interval.

Comparisons with previous reports

Seston in Georges Basin and Oceanographer Canyon was sparse and refractory, which indicated that this particulate matter was a poor source of nutrition. In fact, concentrations of particulate organic carbon (93-103 μg C L^{-1}) were low and C:N ratios (25) were high compared with values reported for a mixed water column on Georges Bank between January and June 1999 (150-300 μg C L^{-1}; ratios from 3 to 8; Townsend and Thomas, 2002). One explanation for these findings arises from visual observations made from the *Johnson-Sea-Link* submersible. These observations suggested that marine snow aggregates formed a large percentage of the seston that we sampled. During non-bloom conditions, such particles can become enriched in organic carbon and depleted in nitrogen due to bacterial activity (Silver and Alldredge, 1981; Alldredge and Youngbluth, 1985). Overall, low concentrations of organic carbon and high C:N ratios were consistent with previous reports of low nutrient levels and decreased primary production in the photic layer between June and October accompanied by rapid recycling of elements in shallow water (Roman *et al.*, 1995; Townsend and Thomas, 2002; Bisagni, 2003).

Compared with seven sets of data reported previously, our seston samples contained different fatty acids and different relative concentrations of some fatty acids (Appendix 1). Our coefficients of variation ranged from 0.06 to 2.65, which indicated that the reliability of our measurements was similar to that of reports in the literature, with coefficients of variation ranging from 0.02 to 3.00 (Klungsøyr *et al.*, 1989; Mayzaud *et al.*, 1989; Reuss and Poulsen, 2002; Parrish *et al.*, 2005). Out of 27 fatty acids with relative concentrations of 1% or higher in any report, samples from Georges Basin matched 15 fatty acids reported elsewhere, and samples from Oceanographer Canyon matched 12 fatty acids reported elsewhere. Our samples were the only ones that contained 12:0 in relative concentrations of 1% or more, and 22:0 was found in relative concentrations that were at least 10 times higher in our samples. Sums and ratios of relative concentrations considered indicative of contributions from various classes of phytoplankton yielded inconsistent evidence of such contributions to the seston that we sampled (Fahl and Kattner, 1993; Reuss and Poulsen, 2002; Dalsgaard *et al.*, 2003). In fact, our samples most closely matched those taken from oligotrophic Antarctic waters, with relatively high concentrations of SFAs and low concentrations of PUFAs (Fahl and Kattner, 1993). In addition, fatty acids become saturated as particulate organic matter is oxidised in the water column, especially during periods with low nutrient availability, high levels of detritus, and limited phytoplankton growth (Goutx and Saliot, 1980; Mayzaud *et al.*, 1989; Fahl and Kattner, 1993; Baldi *et al.*, 1997; Parrish *et al.*, 2005).

In contrast to those of seston, relative fatty acid compositions of *Calanus finmarchicus* stage V copepodites and *Meganyctiphanes norvegica* were similar to each other and to reports in the literature (Appendices 2 and 3). The coefficients of variation among our replicates (0.02-1.73) were within the ranges reported elsewhere (0.01-2.25), which demonstrated the reliability of our measurements. Our samples of *Calanus finmarchicus* and *M. norvegica* shared 16 fatty acids that occurred in relative concentrations of 1% or more. In addition, our samples contained approximately 60% of the fatty acids found in relative concentrations of 1% or more in previous studies (14 out of 22 fatty acids for *C. finmarchicus* and 13 out of 21 fatty acids for *M. norvegica*). Our samples of *C. finmarchicus* contained 20:3 (n-6), which had not been reported previously in concentrations of 1% or more, and 3-5 times the relative concentrations of 15:0, 20:0, 18:1 (n-7) and 18:3 (n-3). Our samples of *M. norvegica* contained 20 times the relative concentration of 20:3 (n-6). In addition, our samples of *C. finmarchicus* had approximately twice the relative concentration of SFAs reported in all but two studies. In contrast, relative concentrations of MUFAs were consistent with five of seven previous reports and lower than the other two, and our concentrations of PUFAs were consistent with four previous reports, lower than two and higher than one. The relative concentration of 22:1 (n-11) in *C. finmarchicus* agreed with reports that this fatty acid is synthesised by herbivorous copepods, but 20:1 (n-9), another fatty acid reported to be synthesised by herbivorous copepods, was absent from our samples. The relative concentrations of SFAs, MUFAs and PUFAs in our samples of *M. norvegica* were approximately equal, which was consistent with most other reports.

Our data represent the first report of relative fatty acid concentrations for *Nanomia cara*. In general, the relative concentrations of fatty acids in nectosomes and siphosomes of *N. cara* were similar to those reported for 14 species of gelatinous zooplankton from Arctic and Antarctic regimes (Appendix 4). Coefficients of variation (0.19-2.45) overlapped ranges reported elsewhere (0.03-2.00). In addition, our samples contained 18 out of 30 fatty acids with relative concentrations of 1% or more in any report. *Nanomia cara* contained 22:0, 23:0, 26:0, 22:2 (n-6) and 20:3 (n-6), which had not been reported to occur in relative concentrations of 1% or more in any other species. *Nanomia cara* also had more SFAs than all species other than the ctenophore *Pleurobrachia pileus*, and fewer MUFAs than all other species, which may be related to SFAs being transferred through the trophic web from seston.

In summary, the relative concentrations of fatty acids in our samples provided a reliable, qualitative basis for interpreting trophic links. Our samples confirmed that, in September, seston found below the thermocline in Georges Basin and Oceanographer Canyon was a poor source of nutrition. In general, our samples of *Calanus finmarchicus*, *Meganyctiphanes norvegica* and *Nanomia cara* were qualitatively similar to previous reports. A detailed interpretation of quantitative differences in relative concentrations of fatty acids was obviated by a lack of information about metabolism in all studies.

Implied trophic links

Evidence for trophic links between seston and two common crustaceans in Georges Basin and Oceanographer Canyon was inconsistent. Only four fatty acids, i.e. 14:0, 16:0, 16:1 (n-7) and 18:1 (n-7), were classified as trophic markers linking *Calanus finmarchicus* stage V copepodites or *Meganyctiphanes norvegica* to seston. Two of these trophic markers were SFAs, and the relatively high concentrations of SFAs in both our seston and *C. finmarchicus* samples also suggested a trophic link. However, three other SFAs, i.e. 12:0, 18:0 and 22:0 were not transferred from seston to crustacean grazers. Furthermore, both *C. finmarchicus* and *M. norvegica* contained six fatty acids that did not appear to be derived from the seston sampled in this study. In addition, sums and ratios of relative fatty acid concentrations did not indicate strong contributions from Bacillariophyceae, Dinophyceae or Prymnesiophyceae (Pedersen *et al.*, 1999; Reuss and Poulsen, 2002; Dalsgaard *et al.*, 2003). In combination with C:N ratios indicating that the seston was refractory, these results did not strongly suggest a trophic link from seston to crustaceans in Georges Basin or Oceanographer Canyon.

Inconsistent evidence of trophic links between seston and common crustaceans may be related to physiological requirements or feeding behaviour. In September, the metabolic demands and feeding rates of *Calanus finmarchicus* stage V copepodites found below the thermocline may have been decreasing due to the onset of diapause (Miller *et al.*, 1991; Durbin *et al.*, 1997; Saumweber and Durbin, 2006). *Meganyctiphanes norvegica* appeared to feed at a higher trophic level than *C. finmarchicus*, as shown

by mean ratios of PUFAs to SFAs, 18:1 (n-7) to 18:1 (n-9), and 20:5 (n-3) to 22:6 (n-3). In addition, adult *M. norvegica* contained relatively high concentrations of 22:1 (n-11), which has been reported as a trophic marker indicating predation on *C. finmarchicus* (Dalsgaard *et al.*, 2003). Thus, the indications of trophic links to both seston and *C. finmarchicus* confirmed previous reports that *M. norvegica* is omnivorous and preys on copepods (Båmstedt and Karlson, 1998; Lass *et al.*, 2001).

Nine or ten common fatty acids represented potential trophic markers linking *Nanomia cara* to *Calanus finmarchicus* stage V copepodites in Georges Basin and *Meganyctiphanes norvegica* in Oceanographer Canyon, respectively. These trophic markers represented approximately 70-85% of the fatty acid pools for *N. cara*. However, ratios of fatty acids provided inconsistent evidence that *N. cara* fed at a higher trophic level than *C. finmarchicus* or *M. norvegica*, which raises questions about the reliability of such ratios. In addition, as reported for seston and crustaceans, sums and ratios of fatty acid compositions did not indicate that *N. cara* derived fatty acids from Bacillariophyceae, Dinophyceae or Prymnesiophyceae (Pedersen *et al.*, 1999; Reuss and Poulsen, 2002; Dalsgaard *et al.*, 2003).

The transfer of significant amounts of fatty acids from potential prey to *Nanomia cara* was not surprising. Siphonophores are known to assimilate over 90% of the carbon and nitrogen found in their prey (Purcell, 1983). In addition, siphonophores have been reported to prey on small, crustacean zooplankters, with the capacity to ingest 3-69% of available copepod biomass in areas where colonies occurred in high densities (Rogers *et al.*, 1978; Robison *et al.*, 1998; Pagès *et al.*, 2001; Youngbluth *et al.*, personal observation). In fact, gastrozooids of *N. cara* captured in Georges Basin and Oceanographer Canyon contained *Calanus finmarchicus* stage V copepodites and *Meganyctiphanes norvegica* (Youngbluth *et al.*, personal observation). Furthermore, oil sacs have been observed in overwintering *C. finmarchicus* stage V copepodites taken from the Gulf of Maine in autumn and oil droplets have been observed in *N. cara*, particularly in gastrozooids and palpons (Rogers *et al.*, 1978; Fig. 2). Other gelatinous zooplankters also contained highly refractive, lipid droplets in the lumens of their digestive systems, but the droplets we observed were not confined to the digestive system (Larson and Harbison, 1989; Fig. 2). In fact, *N. cara* could have been accumulating fatty acids at the time of our study because we observed evidence of reproduction. Other invertebrates have been reported to accumulate fatty acids before reproducing, especially PUFAs for vitellogenesis and development (Mayzaud *et al.*, 1999; Albessard *et al.*, 2001; Hudson *et al.*, 2004).

In conclusion, our study suggested conservative transfer or accumulation of fatty acids from *Calanus finmarchicus* stage V copepodites and *Meganyctiphanes norvegica* to *Nanomia cara* in Georges Basin and Oceanographer Canyon. The data indicated that these common, secondary consumers contributed significantly to the diet of this siphonophore. In contrast, seston appeared to contribute little to its diet at these two locations.

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APPENDIX 1. – Fatty acid concentrations as percentages of the total fatty acid pool in seston. 1, Norwegian waters after bloom (n = 5; Klungsøyr *et al.*, 1989); 2, North Atlantic coastal waters in August (n = 2; Mayzaud *et al.*, 1989); 3, oligotrophic Antarctic waters (Fahl and Kattner, 1993); 4, Antarctic brown ice dominated by diatoms (Fahl and Kattner, 1993); 5, Antarctic waters in February (Skerratt *et al.*, 1995); 6, Greenland waters after a bloom (n = 10; Reuss and Poulsen, 2002); 7, 220 m in Newfoundland waters in boreal spring and summer (n = 7; Parrish *et al.*, 2005); GB, Georges Basin in September (n = 7); OC, Oceanographer Canyon in September (n = 5). Fatty acids with concentrations ≥ 1.0% in one or more references.

Fatty acid	Mean (standard deviation) or value								
	1	2	3	4	5	6	7	GB	OC
12:0								5.3 (3.5)	3.5 (2.7)
14:0	12.8 (2.9)	10.2 (5.4)	7.1	7.1	11.4	11.2 (2.9)	7.3 (2.1)	8.3 (3.8)	8.0 (1.1)
15:0	1.6 (0.4)	2.1 (0.2)		0.7		1.7 (0.4)	5.6 (4.6)	1.2 (0.6)	1.0 (0.3)
16:0	23.9 (2.1)	20.5 (2.7)	33.6	18.0	17.8	22.1 (3.8)	4.4 (6.1)	30.7 (12.6)	30.5 (4.8)
17:0	1.3 (0.6)	1.0 (0.8)				0.8 (0.1)	0.4 (0.4)	0.8 (1.2)	1.0 (0.6)
18:0	9.7 (2.2)	4.5 (0.5)	25.2	0.9	1.4	8.6 (3.5)	1.3 (0.6)	21.1 (17.8)	34.4 (5.7)
19:0		0.03 (0.04)				1.8 (0.9)			
22:0	0.5 (0.1)	0.4 (0.1)				0.6 (0.4)	0.01 (0.02)	14.7 (11.6)	6.6 (6.4)
16:1 (n–5)		1.8 (0.1)			0.5		0.4 (0.4)		
16:1 (n–7)	6.2 (2.8)	5.4 (0.6)	4.9	31.9	8.4	7.8 (8.7)	22.1 (4.1)	2.2 (1.0)	1.7 (0.4)
16:1 (n–9)	2.7 (0.9)	1.4 (0.3)							
18:1 (n–7)	1.5 (0.5)	3.0 (0.8)	1.4	1.2	6.6	1.7 (0.7)	1.9 (0.9)	3.5 (3.2)	3.0 (3.1)
18:1 (n–9)	10.0 (3.1)	7.5 (2.5)	12.4	11.6	6.7	10.5 (4.4)	4.6 (1.6)	0.2 (0.3)	0.3 (0.4)
20:1 (n–9)	0.8 (0.5)	0.2 (0.0)		0.6		3.0 (2.1)			
22:1 (n–9)		0.1 (0.1)				1.2 (2.2)	0.3 (0.2)		
22:1 (n–11)	0.2 (0.1)					1.8 (0.8)		0.1 (0.2)	
16:2 (n–4)	0.6 (0.2)	0.4 (0.02)					1.6 (0.4)		
16:2 (n–6)		0.01 (0.01)		1.4					
18:2 (n–6)	7.1 (1.2)	4.0 (2.0)		3.6	3.5	7.7 (11.8)	0.9 (0.4)	0.4 (0.4)	1.6 (1.1)
16:3 (n–4)		0.2 (0.3)					1.7 (0.8)		
18:3 (n–3)	2.2 (0.7)			0.3	4.6	1.2 (0.4)	0.3 (0.2)	0.4 (0.4)	0.5 (0.8)
16:4 (n–1)		0.4 (0.5)					4.4 (2.7)		
16:4 (n–3)	1.1 (0.2)	1.3 (1.1)				0.7 (0.4)	0.6 (0.5)		
18:4 (n–3)	5.1 (0.9)	8.0 (1.8)	1.2	3.8	5.5	2.7 (1.1)	2.1 (1.3)		
18:5 (n–3)		4.7 (0.1)					0.01 (0.03)		
20:5 (n–3)	5.1 (0.5)	6.2 (1.6)	1.5	11.2		4.3 (1.7)	12.7 (6.5)	0.3 (0.9)	
22:6 (n–3)	5.4 (2.0)	7.6 (1.7)		2.5	12.6	2.0 (1.3)	2.5 (1.0)	0.8 (1.4)	
SFAs	49.8	38.7	65.9	26.7	30.6	46.7	18.9	82.4 (7.6)	85.0 (5.3)
MUFAs	21.6	19.4	18.7	45.3	22.2	26.1	29.4	5.9 (3.1)	5.1 (3.6)
PUFAs	26.6	32.7	2.8	22.8	26.2	18.4	26.7	2.1 (2.2)	2.3 (0.8)

APPENDIX 2. – Fatty acid concentrations as percentages of the total fatty acid pool for *Calanus finmarchicus* from the literature and this study. 1, Balsfjorden in October (Falk–Petersen *et al.*, 1987); 2, North Sea in April and May (n = 4; Kattner and Krause, 1987); 3, Fram Strait in June and July (n = 4; Kattner *et al.*, 1989); 4, Greenland Sea in June and July (Graeve *et al.*, 1994); 5, Fram Strait in June and July (n = 2; Albers *et al.*, 1996); 6, Kongsfjorden from August to September (Scott *et al.*, 2000 in Falk-Petersen *et al.*, 2002); 7, Kongsfjorden from August to September (n = 22; Scott *et al.*, 2002); 8, Arctic Ocean (n = 24; Dalsgaard *et al.*, 2003); GB, Georges Basin in September (n = 3). Fatty acids with concentrations ≥ 1.0% in one or more references.

Fatty acid	Mean (standard deviation) or value								
	1	2	3	4	5	6	7	8	GB
14:0	8.5	11.5 (0.4)	15.5 (2.6)	16.1	26.3 (4.0)	5.3	9.1 (3.5)	16.9 (5.1)	23.9 (0.4)
15:0		0.4 (0.2)			0.7 (1.0)	0.5		0.7 (0.4)	1.5 (0.2)
16:0	15.5	8.3 (0.7)	8.5 (0.7)	7.8	9.8 (1.3)	7.7	7.1 (3.2)	12.7 (2.4)	13.7 (1.0)
18:0	1.2	0.9 (0.1)		1.1	0.9 (0.0)	0.5	0.4 (0.2)	1.5 (0.8)	1.1 (0.2)
20:0		0.4 (0.1)							2.1 (1.8)
16:1 (n–7)	11.9	5.7 (2.1)	4.9 (1.4)	2.7	6.7 (2.0)	14.4	23.0 (3.1)	6.2 (2.0)	8.6 (0.9)
18:1 (n–7)	0.8	0.9 (0.2)		0.2	0.3 (0.4)	2.0	1.5 (3.3)	0.4 (0.9)	7.8 (0.4)
18:1 (n–9)	6.1	2.4 (0.7)	4.6 (0.5)	4.3	5.3 (1.3)	2.2	2.6 (0.7)	5.3 (1.2)	0.4 (0.1)
20:1 (n–7)				0.9	0.9 (0.5)	1.7	1.9 (1.6)	1.0 (0.5)	
20:1 (n–9)	9.6	6.3 (1.0)	8.1 (2.0)	6.5	7.8 (2.0)	26.1	14.5 (2.1)	7.7 (3.8)	
22:1 (n–9)	0.9	1.7 (2.0)		0.5	0.2 (0.3)	0.9	1.4 (1.8)	0.3 (0.3)	
22:1 (n–11)	13.6	8.7 (3.2)	9.9 (2.6)	9.0	7.0 (0.8)	25.3	9.7 (3.9)	8.0 (4.1)	3.7 (1.2)
16:2 (n–6)					0.6 (0.2)		1.5 (0.4)[a]	0.9 (0.3)	
18:2 (n–6)	1.7	0.6 (0.2)		0.7	1.2 (0.1)	0.7	0.8 (0.5)	1.8 (0.6)	1.4 (0.2)
16:3 (n–3)					0.9 (0.4)		1.5 (0.6)[a]		
18:3 (n–3)	1.6	1.5 (0.3)		2.0	1.5 (0.1)	0.3	0.6 (0.9)	1.1 (0.4)	10.6 (0.9)
20:3 (n–6)									2.7 (0.4)
16:4 (n–3)		5.6 (2.1)					1.0 (0.7)[a]		
18:4 (n–3)	4.8	4.8 (1.1)	14.6 (4.0)	21.5	13.7 (1.2)	1.3	2.7 (1.9)	9.5 (6.5)	
20:4 (n–6)				1.4	0.4 (0.5)	0.3	0.6 (0.6)		
20:5 (n–3)	10.7	23.3 (3.3)	12.1 (3.5)	12.9	11.4 (0.9)	5.5	11.5 (2.7)	13.2 (5.8)	9.0 (0.8)
22:6 (n–3)	2.1	10.2 (0.7)	9.0 (1.0)	9.5	2.2 (0.6)	0.7	1.4 (0.9)	11.6 (6.3)	4.9 (0.5)
SFAs	25.2	21.5	24.0	25.0	37.7	14.0		31.8	42.5 (2.4)
MUFAs	42.9	26.1	27.6	24.1	29.1	72.6		29.3	20.4 (2.1)
PUFAs	21.6	46.0	35.6	48.0	33.1	8.8		37.2	28.6 (1.3)

[a] Position of initial double bond not reported.

APPENDIX 3. – Fatty acid concentrations as percentages of the total fatty acid pool in *Meganyctiphanes norvegica*. 1, North Atlantic from fin whale stomachs in October and November (n = 3; Ackman *et al.*, 1970); 2, Balsfjorden, Norway in November and December (Sargent and Falk–Petersen, 1981); 3, Mediterranean Sea in November (n = 2; Mayzaud *et al.*, 1999); 4, northeastern Atlantic Ocean in June, July, February and March (Virtue *et al.*, 2000); 5, North Sea in July and March (Virtue *et al.*, 2000); 6, Mediterranean Sea in April and September (Virtue *et al.*, 2000); OC, Oceanographer Canyon in September (n = 2). Fatty acids with concentrations ≥ 1.0% in one or more references.

Fatty acid	Mean (standard deviation) or value						
	1	2	3	4	5	6	OC
14:0	5.8 (1.0)	6.8	3.2 (0.1)				9.3 (2.7)
15:0	1.2 (0.1)		1.4 (0.3)				1.4 (0.1)
16:0	20.4 (3.7)	26.8	16.1 (3.8)				16.2 (3.6)
17:0	0.9 (0.1)		1.5 (0.02)				
18:0	2.0 (0.6)	1.8	2.1 (0.01)				2.2 (0.8)
16:1 (n–7)	2.2 (1.1)	4.3	1.8 (0.1)	5.8	10.8	2.6	4.2 (0.7)
16:1 (n–13)				0.4	0.8	1.0	
18:1 (n–7)	5.5 (1.1)	7.6	4.4 (1.3)	6.9	7.2	4.8	13.2 (4.2)
18:1 (n–9)	12.2 (0.7)[a]	11.4	9.3 (0.9)	12.1	12.7	12.0	3.8 (0.8)
20:1 (n–7)	0.5 (0.3)			1.0	1.0	0.4	
20:1 (n–9)		6.3		7.7	5.2	2.8	
22:1 (n–11)	3.6 (2.3)	2.9		2.2	3.0	0.6	6.1 (1.0)
18:2 (n–6)	1.9 (0.3)	2.2	1.6 (0.2)	1.6	1.6	2.2	1.7 (0.3)
18:3 (n–3)	1.0 (0.2)	1.7	1.0 (0.1)	0.7	0.6	1.4	3.0 (2.2)
20:3 (n–6)	0.3 (0.3)						6.4 (1.4)
16:4 (n–3)	0.1 (0.05)			1.5	1.8	0.1	
18:4 (n–3)	1.6 (0.7)	0.6	1.3 (0.2)	2.5	1.4	3.0	
20:4 (n–6)	0.7 (0.4)		2.2 (0.7)				
18:5 (n–3)					0.03	1.0	
20:5 (n–3)	10.1 (1.9)	8.7	15.9 (0.4)	14.6	9.5	7.8	8.7 (1.1)
22:6 (n–3)	16.7 (8.8)	7.3	31.8 (3.3)	10.4	7.9	19.6	11.0 (0.4)
SFAs	31.0 (4.6)	35.4	24.2	26.2	29.4	34.9	30.2 (1.9)
MUFAs	32.4 (7.7)	32.5	16.2	39.0	44.4	26.2	27.3 (5.4)
PUFAs	36.7 (11.3)	20.5	53.8	33.5	24.5	37.8	30.9 (1.8)

[a] Small proportion was 18:1 (n–11).

APPENDIX 4. – Fatty acid concentrations as percentages of the total fatty acid pool for gelatinous zooplankton. 1, *Atolla wyvillei* 1997; 2, *A. wyvillei* 1998 (n = 2); 3, *Beroe cucumis*; 4, *Beroe forskalii*; 5, *B. forskalii* (n = 3); 6, *Bolinopsis infundibulum* (n = 2); 7, *Calycopsis borchgrevinki*; 8, *Dimophyes arctica* (3 pooled samples); 9, *Diphyes antarctica* (18 pooled samples); 10, *D. antarctica* (n =3); 11, *Pleurobrachia pileus*; and 12, *Stygiomedusa gigantea* from Antarctic waters in January and February (Nelson *et al.*, 2000). 13, *Mertensia ovatum* and 14, *B. cucumis* from Kongsfjorden, Norway in August and September (Falk-Petersen *et al.*, 2002). Nectosomes, *Nanomia cara* nectosomes (n = 6) and Siphosomes, *N. cara* siphosomes (n = 6) from Georges Basin and Oceanographer Canyon in September. Fatty acids with concentrations ≥ 1.0% in one or more references.

Fatty acid	Mean (standard deviation) or value															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Nectosomes	Siphosomes
12:0	0.6		0.1	0.3	2.7 (0.7)		0.5		0.8		0.5				1.6 (2.0)	2.9 (6.2)
14:0	6.1	2.0 (1.0)	4.4	4.5	5.0 (0.7)	6.5 (0.7)	2.5	3.9	5.7	7.6 (0.8)	5.4	6.6	7.9	6.9	9.1 (3.1)	14.2 (3.2)
15:0	0.6	0.5 (0.1)	0.7	0.7	0.4 (0.1)	1.0 (0.1)	0.3	0.8	1.0	1.1 (0.3)	0.8	0.6	0.6	0.5	0.7 (0.6)	0.9 (0.7)
16:0	20.8	16.0 (2.2)	19.9	23.4	17.4 (1.6)	14.3 (9.2)	16.6	18.9	20.1	18.0 (2.7)	25.8	12.1	11.5	11.1	21.8 (4.2)	17.8 (5.9)
18:0	2.8	11.9 (9.4)	4.6	9.9	2.3 (0.1)	10.5 (1.6)	4.8	9.3	7.6	8.8 (3.7)	20.0	4.9			18.3 (12.1)	5.6 (6.4)
22:0															6.0 (8.2)	0.9 (1.6)
23:0															0.02 (0.04)	2.1 (1.0)
24:0													0.7	1.1	0.08 (0.1)	2.2 (0.7)
26:0															0.05 (0.1)	2.1 (1.7)
16:1 (n–7)	5.3	2.6 (1.4)	1.8	2.3	2.2 (0.2)	0.7 (0.0)	9.2	15.3	3.8	4.0 (2.8)	1.4	10.2	4.9	7.3	3.9 (3.4)	7.6 (2.4)
18:1 (n–5)	0.8	1.1 (0.2)	0.3	0.5	0.7 (0.1)	0.4 (0.1)	1.9	0.4	1.0	0.9 (0.1)		0.5				
18:1 (n–7)	7.2	4.1 (2.3)	2.1	3.2	4.9 (0.7)	2.2 (0.3)	3.7	4.1	4.1	2.0 (1.8)	10.7	5.8	1.2	1.4	4.7 (2.9)	3.8 (2.8)
18:1 (n–9)	11.8	9.0 (4.2)	6.0	8.8	6.4 (2.6)	4.9 (0.5)	26.4	17.2	7.3	8.7 (4.8)	10.2	18.6	8.6	8.4	1.0 (1.0)	4.3 (3.8)
19:1[a]	0.5	1.3 (1.4)	1.2	0.8	0.5 (0.1)	1.9 (0.3)	0.6	0.2								
20:1 (n–7)	1.4	3.1 (1.0)	4.2	1.7	4.2 (1.4)	2.6 (0.5)	2.8	1.0	0.6	3.6 (5.1)		3.0	0.4	0.1		
20:1 (n–9)	3.2	4.2 (5.1)	2.8	2.2	1.3 (0.8)	2.5 (0.5)	2.5	1.1	1.7	1.2 (1.3)	2.7	2.6	21.6	21.2		
22:1 (n–7)	0.2		0.2	0.4	0.3 (0.2)	1.2 (1.7)			0.3	0.3 (0.5)		0.2				
22:1 (n–9)		0.5 (0.2)	2.1	1.3	1.1 (1.0)	3.0 (3.5)		1.3		0.1 (0.1)		0.3	0.1			
22:1 (n–11)	0.2				0.3 (0.5)	3.7 (5.2)				0.2 (0.4)		0.1	21.1	20.6		
18:2 (n–6)	2.5	1.4 (0.4)	1.4	1.3	1.7 (0.3)	0.7 (0.1)	1.5	1.0	1.9	2.2 (0.3)	0.9	1.0	1.4	1.6	2.2 (3.5)	3.1 (3.9)
20:2 (n–6)	0.3	0.4 (0.5)	0.6	0.6	1.0 (0.0)	0.5 (0.1)	0.6		0.4	0.1 (0.1)	1.3	0.8				
22:2 (n–6)															2.3 (2.3)	4.4 (3.7)
18:3 (n–3)	1.0	0.5 (0.5)	0.2		1.2 (0.3)		0.2	0.1	0.2	0.3 (0.3)		0.3	1.1	0.9	1.2 (1.8)	2.4 (3.4)
20:3 (n–6)															2.4 (2.1)	3.8 (2.0)
18:4 (n–3)	5.0	0.9 (1.2)	0.3	0.7	2.3 (0.1)		0.1	0.2	0.6	2.1 (2.9)		1.3	9.4	8.7		
20:4 (n–6)		4.2 (6.0)	2.0	1.5		0.5 (0.7)	1.4		1.2	1.4 (0.2)	2.6					
22:4 (n–6)	0.3	1.3 (0.9)			0.1 (0.1)		0.9					0.7				
20:5 (n–3)	16.6	15.0 (6.2)	17.4	14.6	21.3 (2.9)	17.1 (3.4)	9.6	8.2	19.1	16.5 (1.3)	7.2	20.8	4.1	4.6	10.4 (4.4)	11.2 (4.0)
22:5 (n–3)	2.4	9.7 (8.7)	0.2	0.2	0.4 (0.1)		2.1	0.1	0.3	0.2 (0.2)		1.9	0.4	0.4		
22:6 (n–3)	5.6	3.9 (0.6)	24.8	18.0	16.8 (0.5)	22.7 (3.9)	7.0	10.4	17.6	16.9 (5.3)	9.1	4.2	1.7	1.8	8.9 (5.4)	8.7 (3.2)
SFAs	30.9	30.4 (12.7)	29.7	38.8	27.8 (3.2)	32.3 (11.6)	24.7	32.9	35.2	35.5 (7.5)	52.5	24.2			58.5 (19.0)	49.3 (16.7)
MUFAs	30.6	25.9 (15.8)	20.7	21.2	21.9 (7.6)	23.1 (12.6)	47.1	40.6	18.8	21.0 (16.9)	25.0	41.3			9.7 (6.3)	15.7 (3.3)
PUFAs	34.2	39.5 (28.1)	47.3	37.1	45.1 (4.6)	41.5 (8.1)	24.1	20.0	42.3	39.7 (10.6)	21.1	31.0			27.4 (15.3)	33.7 (13.3)

[a] Position of double bond not given.