Journal of Plankton Research Vol.21 no.9 pp.1593–1611, 1999

The significance of food web structure for the condition and tracer lipid content of juvenile snail fish (Pisces: *Liparis* spp.) along 65–72°N off West Greenland

Lorna Pedersen, Hans Mose Jensen, AnnDorte Burmeister[1] and Benni Winding Hansen[2]

Department of Life Sciences & Chemistry, Roskilde University, PO Box 260, DK-4000 Roskilde, Denmark

[1]Present address: Greenland Institute of Natural Resources, PO Box 570, 3900 Nuuk, Greenland

[2]To whom correspondence should be addressed

Abstract. Plankton community structure was analysed during summer along 65–72°N off West Greenland. The south–north transect mimics a time span of months in the phytoplankton and zooplankton succession during the Arctic summer. In the south, the mixing depth was below the photic zone and the phytoplankton community was dominated by flagellates. North of Disko Bay (69°N), the water column was stratified due to melt water, and the phytoplankton dominated by flagellates and a small amount of diatoms, but with higher biomass and primary production. The copepod community was dominated by *Calanus* spp. and was more progressed in terms of developmental stage composition in the south. The biochemical lipid finger printing in the food chain phytoplankton–mesozooplankton–juvenile planktivorous snail fish (*Liparis* spp.) confirmed the qualitative composition of the phytoplankton, and revealed that the mesozooplankton >400 μm in body size contained lipids originating from a non-diatom diet in the south, whereas it showed mesozooplankton lipids originating from a diatom diet in the north. The C16:1(n-7)/C16:0 ratio increased from 0.3 to 3 for mesozooplankton along the transect, indicating feeding based on diatoms in the north. This ratio was reflected in *Liparis* spp. along the transect. The condition of the juvenile snail fish was generally good (high *b* exponent) along the entire transect based on the relationship: total fatty acids (mg) = 0.0008 × standard length (mm)$^{2.35}$. However, the relationship triacylglycerol:cholesterol was much higher north of Disko Bay, indicating a much better condition and thereby potential starvation tolerance and survival in the north. We conclude that the plankton structure along the south–north transect reflected the yearly succession in phytoplankton with respect to tracer lipids and that juvenile *Liparis* spp. were in a better condition when foraging on wax ester-rich mesozooplankton, which in turn developed ontogenetically during a diatom-based spring bloom in the north.

Introduction

In recent years, studies have indicated that the nutritional quality of copepod prey, i.e. lipid composition, may affect the growth and survival of juvenile fish (e.g. Håkanson, 1989).

Spatial and temporal variation of primary production may create malnutrition of copepods and lead to depletion of lipid or amino acid energy stores and eventually death (e.g. Dagg, 1977). Calanoid copepods from high latitudes are generally rich in wax esters and often have small but significant amounts of triacylglycerols (TAG) (Benson *et al.*, 1972; Sargent, 1976, 1978; Sargent and Henderson, 1986). During starvation, copepods tend to mobilize TAG faster than wax esters (Sargent *et al.*, 1977; Håkanson, 1984). The TAG content of calanoid copepods may reflect the animal's recent nutritional history (several days), whereas the wax ester content may be a measure of the long-term nutritional history (months)

(Håkanson, 1984). Furthermore, it is indicated that the TAG in calanoids are derived more or less directly from dietary lipids (Sargent *et al.*, 1977).

It has been shown that specific fatty acids and fatty acid composition are associated with certain taxonomic classes of phytoplankton, thus having the potential to identify the transfer of phytoplankton production to higher trophic levels (e.g. Sargent, 1978). Species of Chrysophyceae, Haptophyceae and Dinophyceae are characterized by the presence of C18:4(n-3) and C18:5(n-3) fatty acids, which are essentially absent from diatoms (Pohl and Zurheide, 1979; Sargent *et al*., 1987). Diatoms are typified by the fatty acids C16:4 and C20:5 (n-3) (Ackman *et al*., 1964; Chuecas and Riley, 1969; Pohl and Zurheide, 1979) as well as having a higher ratio of C16:1(n-7) to C16:0 fatty acids (>2) than other phytoplankton classes (Ackman *et al*., 1968; Jeffries, 1970; Pohl and Zurheide, 1979). The conservative transfer of these tracer fatty acids into neutral lipids in higher trophic levels has been demonstrated by Falk-Petersen *et al.* (1987). Jeffries (1970) reported a decrease in the ratio C16:1(n-7)/C16:0 in natural phytoplankton–microzooplankton during a diatom to flagellate succession. In a later study of zooplankton and herring larvae held in an enclosed ecosystem, a change in fatty acid composition occurred when the phytoplankton species composition changed from a flagellate to a diatom dominance (Fraser and Sargent, 1989). They reported a reduction in content of C18:4(n-3) (indicative of a non-diatom food resource) and an increase in the ratio C16:1(n-7)/C16:0 (indicative of diatoms as food source). Furthermore, the ratio between TAG and cholesterol (CHOL) has previously been demonstrated to be a good index of fish larval condition (Håkanson, 1989).

To clarify to what extent food quantity and/or quality determine the condition of juvenile *Liparis* spp. along a south–north transect off West Greenland, plankton community structure and the class-specific biomarkers of fatty acids were analysed.

Method

Sampling and biomass measurements

During a cruise with R/V 'Pamiut' from the Greenland Institute of Natural Resources, Nuuk, sampling was carried out off the coast of West Greenland from 17 July until 9 August 1993. A total of 41 stations were examined from 65°N to 72°N, starting at the south (Figure 1 and Table I). Plankton samples <125 μm were pumped (Jolly Jet Model 1100 Marina, 70 l min^{-1}) from the upper 70 m of the water column by raising an 80 m hose with constant speed, and data are presented as mean values. Analysis of chlorophyll *a* concentrations and measurements of area primary production were conducted on integrated water samples (see Jensen *et al.*, 1999). Two hundred millilitres of mixed water were fixed by 1–2% acid Lugol's solution, phytoplankton taxa identified, and cell length and width measured on an inverted microscope. The phytoplankton composition is given as biomass values based on total cell volume from equations in Edler (1979). A volume of 5 l from each sampling with the plankton pump was size fractionated into 20, 45 and 100 μm. The fractions were assumed to represent nanoflagellates

of 0–20 μm, diatoms and dinoflagellates of 45–100 μm, and microzooplankton >100 μm (St John and Lund, 1996). Plankton samples >125 μm were collected by vertical plankton tows to a depth of 70 m with a WP-2 net (125 μm mesh size) equipped with a non-filtering cod end and a flow meter (Digital Model 438 110 Hydro Bios). Mesozooplankton from the WP-2 net were fractionated into 125, 200 and >400 μm fractions, respectively. One half of the fractionated mesozooplankton samples were immediately preserved in 2% buffered formalin and at least 300 individuals were analysed. To distinguish between copepodites of *Calanus* spp., length criteria after Unstad and Tande (1991) were used. The biomasses of all copepod stages and species were obtained from the literature: *Calanus* spp. copepodites and *Metridia longa* from Hirche and Mumm (1992), small taxa like *Acartia* spp., *Pseudocalanus* spp. and *Oithona* spp. from Berggreen *et al.* (1988), Klein Breteler *et al.* (1982) and Sabatini and Kiørboe (1994) and presented as 'others'. If carbon content was not given in the literature cited, the content of *Calanus* spp. copepodite stages I–III and the small-bodied copepod species was assumed to be 50% of the dry weight, while a conversion factor of 60% was used for the older stages, CIV–VI, of *Calanus* spp. (Omori, 1969; Hansen *et al.*, 1994).

Mesozooplankton >400 μm were assumed to be target prey of the juvenile fish and it was assumed that snail fish prefer similar prey size spectra as herring larvae and older stages of cod larvae and smaller juvenile cod (Munk, 1992, 1997).

The fractionated plankton sampled by the plankton pump plus the other half of the fractionated mesozooplankton samples originating from the WP-2 net were concentrated on 4.7 cm GF/F filters (0.2 bar) for lipid extraction. The filters were transferred to screwcap glass vials and filled with deoxygenated chloroform:methanol (2:1 by volume). Chaetognaths, pteropods, medusae and other non-obvious food items for juvenile fish were discarded from the samples.

Sampling of juvenile snail fish was carried out by a 0.56-cm-diameter Bongo net with 500 μm mesh size. The Bongo net was deployed and retrieved at a wire speed of 0.5 m s^{-1} to ~300 m wire length for 20 min while the ship speed was maintained at 3 knots. This resulted in oblique hauls with a towing depth of 100–150 m. The juvenile snail fish caught were identified to genus, standard length measured, and transferred to screwcap glass vials and filled with deoxygenated chloroform:methanol (2:1 by volume). All samples were stored at –20°C during the cruise and thereafter stored at –80°C until analysis.

Fatty acids and lipid classes

All organic solvents used in extraction and analysis were HPLC or glass distilled grade.

Analysis of fatty acids and lipid classes of total lipids in tissue was carried out as follows. For fatty acid analysis, heptadecanoic acid methyl ester (C17:0) was used as internal standard and 1 ml of 0.1 mg ml^{-1} was added prior to homogenizing the samples cooled on ice. Approximately 2–3 ml of the sample were used for quantitation of lipid classes (see later). The samples were evaporated to dryness under nitrogen flow. For saponification, 1 ml of 0.5 M methanolic KOH was added

Table I. Date, positions and water depths at the 41 stations along 65–72°N off West Greenland

Station	Date	Latitude	Longitude	Depth (m)
South				
1	July 17	64°31′63N	53°14′06W	510
2	July 18	64°53′01N	54°26′50W	nd
3	July 18	65°16′88N	54°59′50W	507
4[a]	July 19	67°36′17N	56°01′17W	120
5[a]	July 19	67°51′06N	55°37′63W	87
6[a]	July 20	67°36′17N	56°01′17W	52
7[b]	July 20	68°42′57N	54°12′76W	347
8[b]	July 21	69°01′07N	54°59′96W	208
9[b]	July 21	69°20′98N	55°25′84W	201
10[b]	July 22	69°30′79N	55°34′52W	250
11[a b]	July 22	69°07′76N	55°03′69W	169
Intermediate				
12[a b]	July 23	69°14′57N	55°29′87W	180
13[b]	July 23	69°08′87N	57°48′02W	275
14[b]	July 23	68°52′22N	57°48′13W	290
15[b]	July 23	68°44′96N	57°39′84W	304
16[b]	July 24	68°41′73N	56°05′61W	322
17[a b]	July 24	68°45′90N	56°01′74W	171
18[a b]	July 25	68°52′28N	56°01′15W	148
19[b]	July 25	68°33′18N	55°27′14W	352
20[b]	July 26	68°25′40N	55°34′73W	459
21[b]	July 26	68°30′39N	55°59′89W	480
22[b]	July 26	68°15′53N	56°03′95W	298
23[b]	July 27	68°09′57N	56°40′15W	249
24	July 30	68°11′23N	56°50′89W	293
25	July 31	68°29′13N	58°14′83W	340
North				
26	July 31	69°05′76N	57°48′32W	286
27	August 1	70°38′97N	58°47′03W	330
28	August 2	71°11′06N	58°30′14W	340
29	August 2	71°17′55N	58°29′79W	276
30	August 3	71°27′08N	58°16′89W	295
31	August 3	71°38′94N	57°57′00W	268
32	August 3	72°16′99N	57°29′50W	372
33	August 4	72°18′76N	57°03′94W	357
34[a]	August 4	71°46′74N	56°48′27W	188
35[a]	August 5	71°41′47N	56°23′55W	155
36	August 5	71°36′20N	55°59′63W	248
37	August 5	71°02′42N	56°37′99W	365
38	August 5	71°03′27N	56°55′80W	186
39	August 6	71°07′04N	57°31′27W	172
40	August 6	70°36′33N	55°43′62W	287
41[a b]	August 6	70°22′50N	55°37′38W	116

nd, no data.
[a]Stations on fishing banks.
[b]No CTD data.

and the samples were kept for 35 min in a water bath at 85°C. For methylation, 1 ml of methanolic boron triflouride was added and the samples were kept for 15 min at 85°C. A volume of 0.5 ml saturated NaCl and 1 ml of *n*-hexane were added. After mixing, the samples were centrifuged to separate aqueous and organic solvent layers, and the lower phase was removed. The samples were washed twice

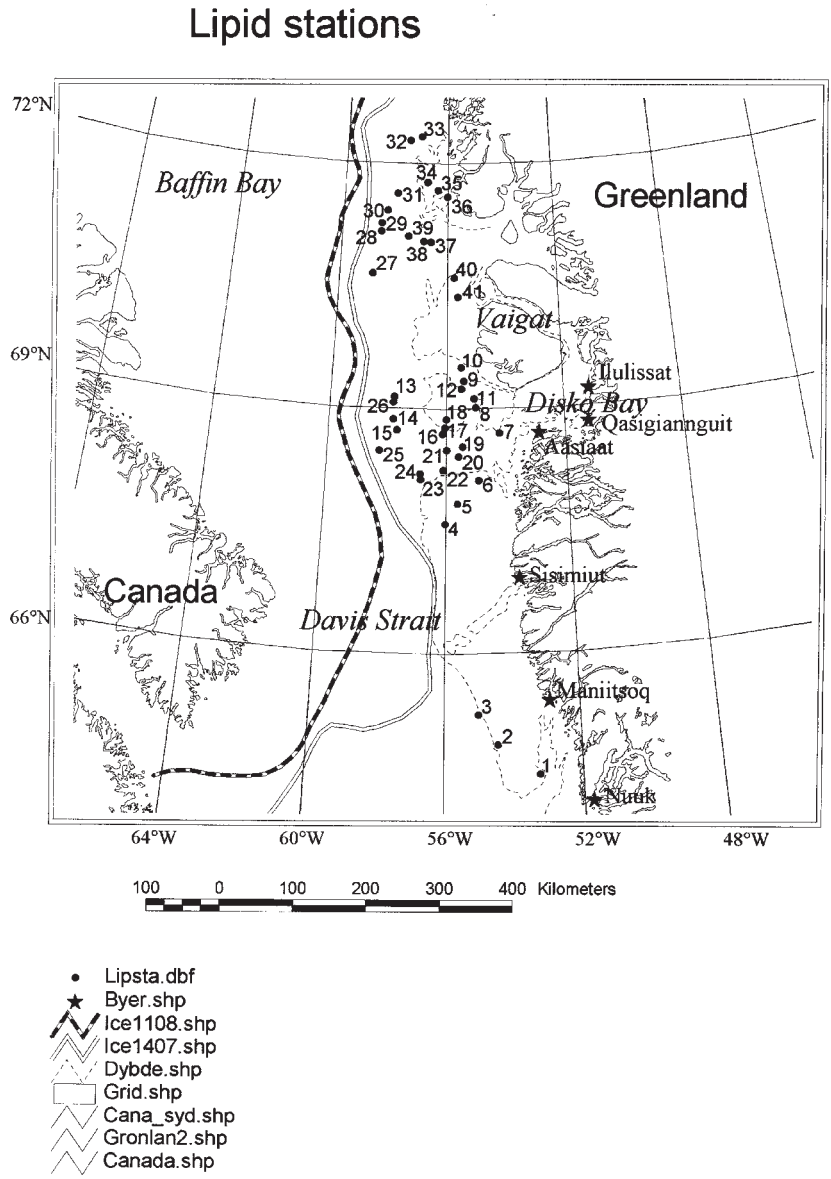


Fig. 1. Map of the study area with sampling stations covering a transect 65–72°N off West Greenland. The double line and broken line refer to the approximate border of close drift ice originating from the West ice on 14 July and 11 August 1993, respectively.

with $NaHCO_3$ removing the lower phase. After washing, the upper phase was transferred to a GC vial. Samples containing wax esters were saponified using potassium-*t*-butoxide (Lee *et al.*, 1971) and the alcohols were separated as described by Christie (1989). Analysis of fatty acid methyl esters was carried out

using a Hewlett Packard gas chromatograph (5090 Series II) fitted with a polar DBWax column (Supelco). Splitless injection at an injection temperature of 250°C, a helium flow of 1.0 ml m^{-1} and a temperature programme of 160°C in 5 min to 240°C, with a rate of 1°C min^{-1}, was used. Fatty acid methyl esters were identified by comparison with the retention time of methyl esters of lipids of interest obtained from Sigma and Larodan.

For quantitation of lipid classes, samples were separated by thin layer chromatography (TLC) on glass plates (20 × 20 cm) coated with silica gel G, 0.25 mm thick. In order to remove any impurities, the TLC plates were pre-washed in a saturated glass chamber using hexane–diethyl ether–formic acid as the developing solvent (80:20:2 by volume) (Christie, 1972). The samples were filtered through a 25 mm GF/F filter to remove impurities. The lipid classes were separated from total lipids along with known standards of tripalmitin, CHOL, phosphatidylcholine and wax ester ($C_{40}H_{78}O_2$) (Sigma). The TLC plates were developed for 30 min within a sealed glass chamber. The TLC plates were then stained with copper acetate–phosphoric acid reagent as described by Fewster *et al.* (1969) and charred by heating in an oven for 60 min at 180°C. Lipid class compositions were estimated using a Camag TLC Scanner II densitometer connected with a Hitachi D2000 integrator under conditions where the absorbance of each zone was directly proportional to the mass of the lipid on the TLC plate. To improve linearity, a correction factor was used (Owen, 1973).

Condition of the snail fish (Liparis spp.)

A condition factor K_n was calculated for the snail fish along the transect as $K_n = W_{obs}/W_{exp}$, where W_{obs} is the observed fatty acid content and W_{exp} is the expected fatty acid content from a regression describing total fatty acid content versus standard length (Le Cren, 1951).

Analysis for statistical significance of the C16:1(n-7)/C16:0 ratio and TAG/CHOL ratio in snail fish between north and south stations was performed by *T*-test (see Results for a definition of north and south along the transect).

Results

Physical oceanography

The transect was divided into south, stations 1–11 (64°31′63N–69°30′79N), intermediate, stations 12–25 (68°09′57N–69°14′57N) and north, stations 26–41 (north of 70°22′50N) (Figure 1 and Table I), based on the change in chlorophyll *a* concentration and primary production reflecting the prevailing hydrography and ice situation (see Jensen *et al.*, 1999). Representative salinity and temperature profiles revealed water masses of rather constant salinity with a decreasing temperature from around 10 m and down to 40 m where it was rather constant towards the bottom in the southern part of the transect. This indicates a vertical mixing depth below the photic zone (named south in Figure 2) (see Jensen *et al.*, 1999). Further north and off Disko Bay towards the middle of Davis Strait (intermediate, Figure 2), the water masses were characterized by a slight increase in

salinity and a decrease in temperature around 8–10 m depth with a weaker pycnocline. North of Disko Bay (north, Figure 2), the salinity increased from low surface values (31.7 p.p.t.) due to the influence of melt water to maximum salinity below 40 m (33.5 p.p.t.). The temperature decreased from high values in the upper 15 m (3.9°C) to a minimum temperature below 40 m (–1.7°C) with a well-defined pycnocline around 15 m. The mixed water masses collectively called the Polar Current (East Greenland Polar Current and Irminger Current; see the map in Jensen *et al.*, 1999) prevailed from the south to the Disko Bay area, whereas the stations north of Disko Bay appeared to be influenced by melt water from glaciers and from cold water masses originating in Baffin Bay. Unfortunately, the CTD was out of order just in this dynamic intermediate region, making it impossible to verify hydrographical discontinuities here (see Table I).

Plankton biomass and abundance of juvenile snail fish (Liparis spp.)

There were no obvious differences in phyto- and mesozooplankton biomass whether the sampling station was positioned on or off fishing banks (Table I). The mean chlorophyll *a* as well as the mean primary production increased from south

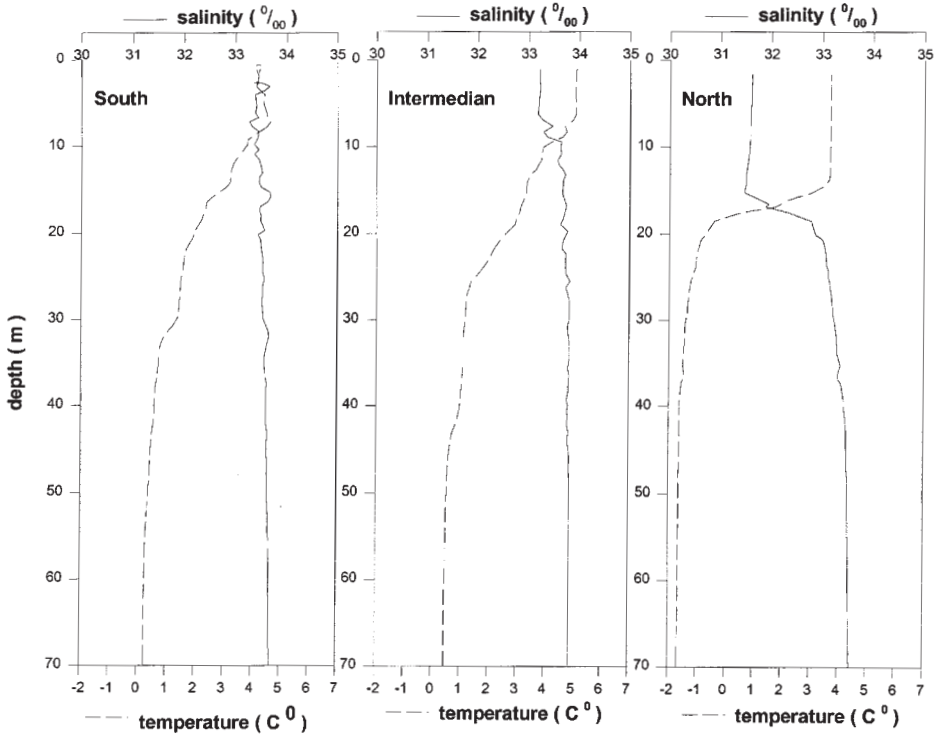
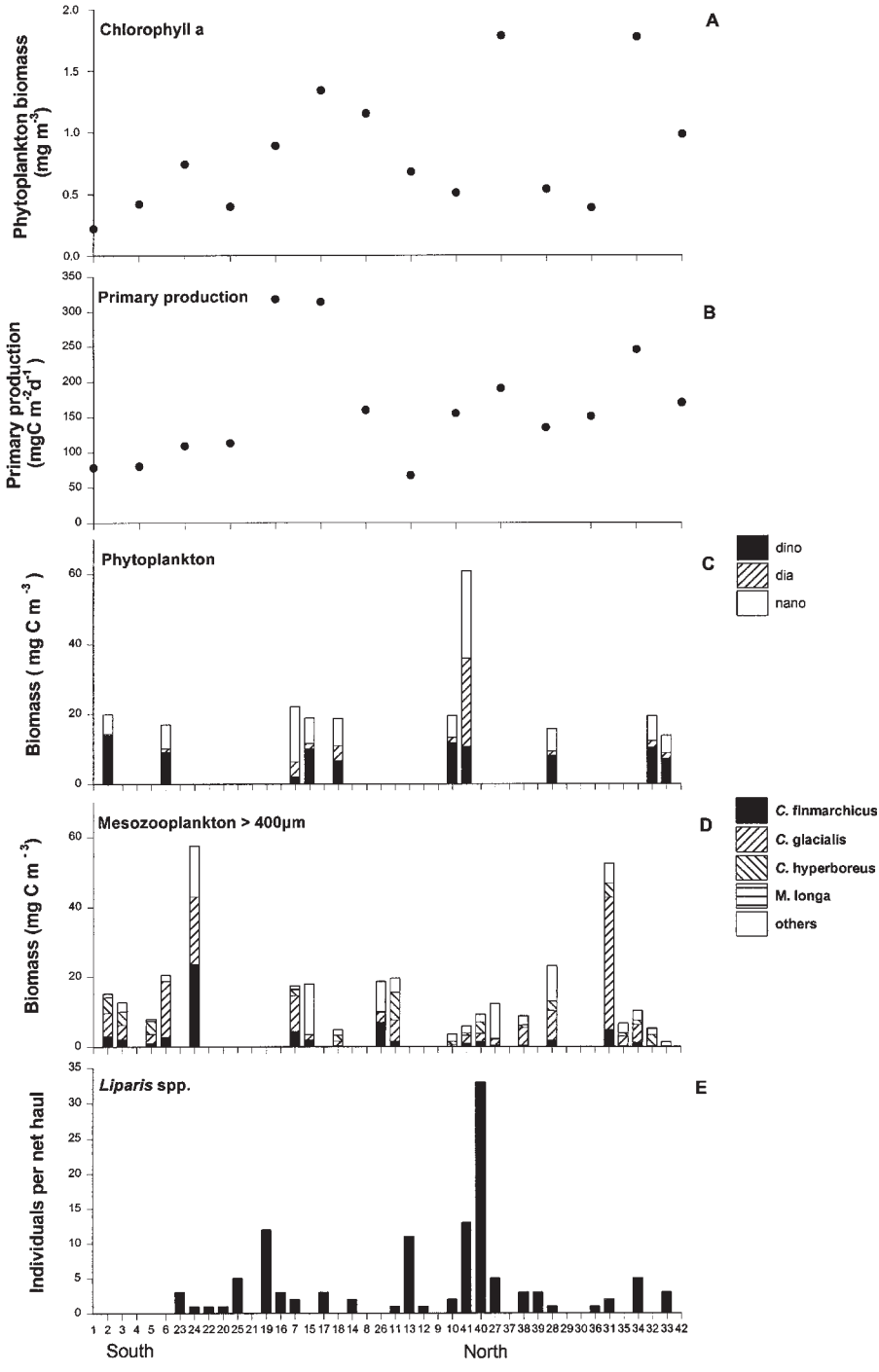


Fig. 2. Representative hydrographical data from south, an intermediate location off Disko Bay, and from north along the transect 65–72°N off West Greenland.


A
Chlorophyll a
Phytoplankton biomass (mg m-3)
2.0
1.5
1.0
0.5
0.0
B
Primary production
Primary production (mgC m-2d-1)
350
300
250
200
150
100
50
0
C
Phytoplankton
Biomass (mg C m -3)
60
40
20
0
dino
dia
nano
D
Mesozooplankton > 400µm
Biomass (mg C m -3)
60
40
20
0
C. finmarchicus
C. glacialis
C. hyperboreus
M. longa
others
E
Liparis spp.
Individuals per net haul
35
30
25
20
15
10
5
0
1 2 3 4 5 6 23 24 22 20 25 21 19 16 7 15 17 18 14 8 26 11 13 12 9 10 41 40 27 37 38 39 28 29 30 36 31 35 34 32 33 42
South
North

towards north with values ranging from 0.22 to 2.82 µg chlorophyll *a* l^{-1} and from 67 to 251 mg C m^{-2} day^{-1}, respectively (Figure 3A and B).

The phytoplankton standing crop was dominated by dinoflagellates (*Gyrodinium*/*Gymnodinium* spp., *Dinophysis* spp. and *Prorocentrum* spp.), nanoflagellates and a small amount of diatoms (*Chaetoceros* spp., *Thalassiosira* spp., *Nitzschia* spp., *Fragilaria* spp. and *Leptocylindrus* spp.) (Figure 3C). The diatoms were less significant in the southern part of the region. Maximum biomass was found at station 41, the only station where diatoms constituted the main part of the biomass together with nanoflagellates. The relative distribution of the total phytoplankton biomass along the transect revealed that dinoflagellates constituted 54.0 ± 9.7% (mean ± SD), nanoflagellates 36.2 ± 6.3% and diatoms 9.5 ± 4.5%, except for station 7 where nanoflagellates constituted 71% of the biomass.

The mesozooplankton were dominated by copepods, with the genus *Calanus* being predominant (Figure 3D). *Calanus finmarchicus*, *Calanus glacialis* and *Calanus hyperboreus* collectively constituted 71 ± 24.3% (mean ± SD) of the biomass in the southern part and 77 ± 14.7% in the northern part of the transect. *Calanus glacialis* was the most abundant among the three species and constituted 36 ± 20.8% of the total *Calanus* spp. biomass.

Liparis spp. is common along the west coast of Greenland and juveniles were caught semiquantitatively at most of the stations (Figure 3E). The maximum number of individuals per Bongo net haul was caught at stations 40 and 41 where the maximum phytoplankton biomass was also found.

Stage composition of Calanus spp.

The relative developmental stage composition of the *Calanus* species revealed no CVI males (Figure 4). The stage composition of *C.finmarchicus* was generally dominated by CI–CIII. Additionally, females were more common at the north and no apparent difference in composition of the other developmental stages between the southern and the northern part of the transect was observed. *Calanus glacialis* was in general dominated by CII–CIV, where CIII dominated the southern area (34 ± 14%) and CII the northern part (37 ± 8%). The proportion of CVI females was greater at the northerly stations (10 ± 27.7%). The stage composition of *C.hyperboreus* was dominated by CIV in both the southern and northern part where it constituted 47 ± 39 and 41 ± 35%, respectively.

Lipid content of phytoplankton, mesozooplankton and juvenile snail fish

A high proportion of the C18:4w3 fatty acids in the south indicated a flagellate-dominated phytoplankton community (size fraction 0–20 and 20–45 µm), and also among the phytoplankton grazers (zooplankton fractions 45–400 µm) (Table II).

Fig. 3. (**A**) Mean chlorophyll *a* concentrations (data from Jensen *et al.*, 1999), (**B**) area primary production (data from Jensen *et al.*, 1999), (**C**) composition of the phytoplankton biomass, (**D**) biomass of mesozooplankton >400 µm in body size and (**E**) a semiquantitative presentation of *Liparis* spp. (individuals caught per Bongo net haul) along the transect. South = stations 1–11; north = station 26 and northwards (see the text and Table I).

Table II. The ratio C16:1(n-7) versus C16:0 and the fatty acids C18:4(n-3) for Chrysophyceae, Haptophyceae and Dinophyceae, C20:5(n-3) for Bacillariophyceae (diatoms), and C22:6(n-3) for Dinophyceae and Haptophyceae from size-fractionated plankton samples in the southern and the northern part of the transect along 65–72°N off West Greenland. Data represent the mean ± SD weight% of total lipid content

Plankton fraction	South				North			
	C16:1/C16:0	C18:4(n-3)	C20:5(n-3)	C22:6(n-3)	C16:1/C16:0	C18:4(n-3)	C20:5(n-3)	C22:6(n-3)
0–20 µm	0.43 ± 0.35	8.4 ± 6.7	13.1 ± 6.1	8.4 ± 5.8	0.45 ± 0.18	4.6 ± 2.5	8.7 ± 3.3	5.2 ± 1.9
20–45 µm	0.51 ± 0.72	5.1 ± 2.3	11.1 ± 7.4	15.1 ± 21.0	0.55 ± 0.41	7.2 ± 5.2	5.4 ± 3.5	2.2 ± 0.6
45–100 µm	0.40 ± 0.48	8.5 ± 4.6	12.8 ± 5.9	8.0 ± 5.5	0.63 ± 0.81	5.9 ± 2.6	5.4 ± 1.9	nd
125–200 µm	1.21 ± 0.31	4.6 ± 4.1	14.0 ± 6.6	11.0 ± 6.1	1.33 ± 0.54	2.7 ± 2.6	14.8 ± 6.6	7.9 ± 4.4
200–400 µm	1.29 ± 0.59	2.2 ± 3.3	18.4 ± 4.1	16.2 ± 5.6	1.36 ± 0.35	1.2 ± 0.9	19.6 ± 2.8	12.7 ± 4.5
>400 µm	1.37 ± 0.88	1.2 ± 1.8	21.9 ± 7.4	20.0 ± 7.8	2.61 ± 0.23	1.9 ± 2.7	20.5 ± 5.0	9.5 ± 2.6
Mean ± SD	0.87 ± 1.46	5.0 ± 10.1	15.2 ± 15.6	13.1 ± 25.2	1.16 ± 1.15	3.9 ± 7.4	12.4 ± 10.15	7.5 ± 7.1

nd, no data.

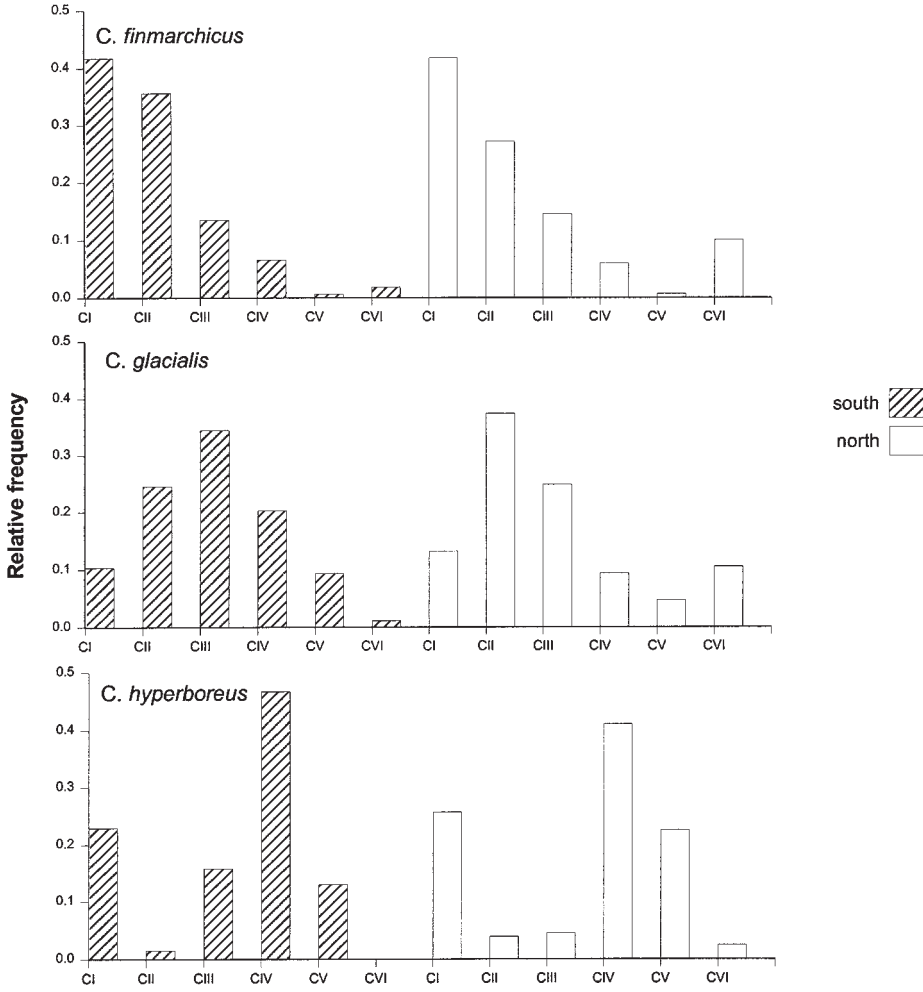


Fig. 4. Mean relative developmental stage composition of *C.finmarchicus*, *C.glacialis* and *C.hyperboreus* in south and north along the transect. South = stations 1–11; north = station 26 and northwards.

From the southern to the northern part of the transect, an increase in the C16:1 (n-7)/C16:0 ratio from <2 to 3 was observed in the >400 μm mesozooplankton samples (Figure 5A, Table II). This is indicative of utilization of a diatom food source by mesozooplankton to the north.

Each juvenile snail fish (>10 mm total length) was analysed for the ratio of the fatty acids [C16:1(n-7)/C16:0] as well as for total fatty acid content. The C16:1 (n-7)/C16:0 ratio in *Liparis* spp. followed the same pattern as in the mesozooplankton with a highly significant increase (*T*-test, $P < 0.001$, $n = 90$ individuals) in this ratio in the northern part of the transect compared to the southern part (Figure 5B).

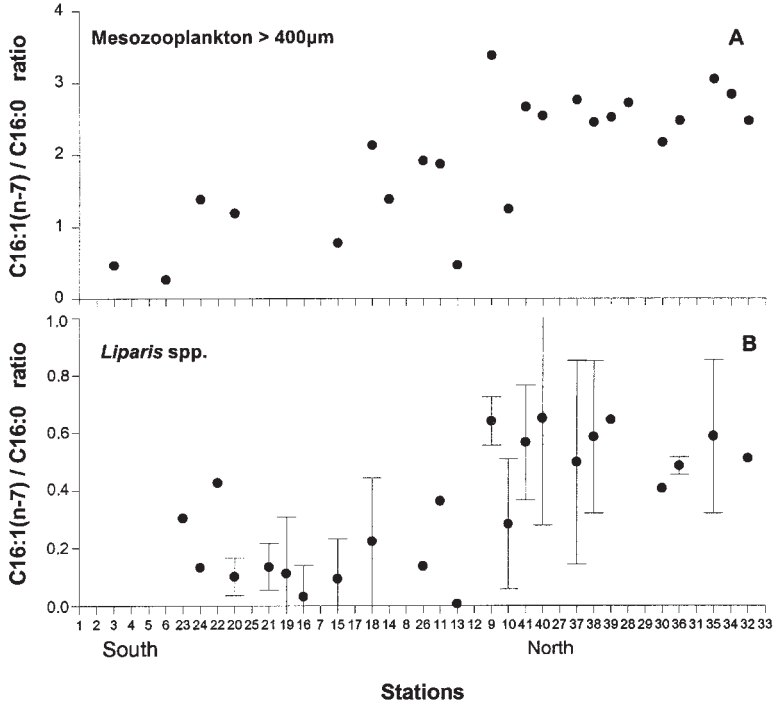


Fig. 5. Ratio between C16:1(n-7) and C16:0 for (**A**) mesozooplankton >400 µm in body size and (**B**) for *Liparis* spp. along the transect 65–72°N off West Greenland.

The total fatty acid (TFA) content increased with standard length (9–34 mm) of juvenile snail fish following the power function: TFA (mg) = $0.0008L$ (mm)$^{2.35}$. There was no difference in fish size distribution throughout the transect (*T*-test, $n = 93$) and the high *b* exponent (2.35) indicates a general good condition (St John and Lund, 1996) (Figure 6).

To evaluate the condition of the juvenile snail fish [TAG/CHOL ratio versus C16:1(n-7)/C16:0, and by K_n versus C16:1(n-7)/C16:0 for all fish samples; $n = 93$; Figure 7], each individual was analysed for neutral lipids (TAG) and structural lipids (CHOL). The condition of the snail fish clearly increased as a function of elevated C16:1(n-7)/C16:0 ratio. Additionally, the condition of the snail fish based on C16:1(n-7)/C16:0 increased significantly (*T*-test, $P < 0.001$, $n = 90$) to the north (with a mean ± SD ratio of 49.8 ± 37.8) as compared with the condition in the south (mean ± SD 11.5 ± 9.7). The condition factor (K_n; see Method) showed the same tendency, although not significantly, as TAG/CHOL (Figure 8).

Discussion

The present investigation was based upon analysis of the linear food chain phytoplankton–mesozooplankton–juvenile *Liparis* spp. Large-scale hydrography and

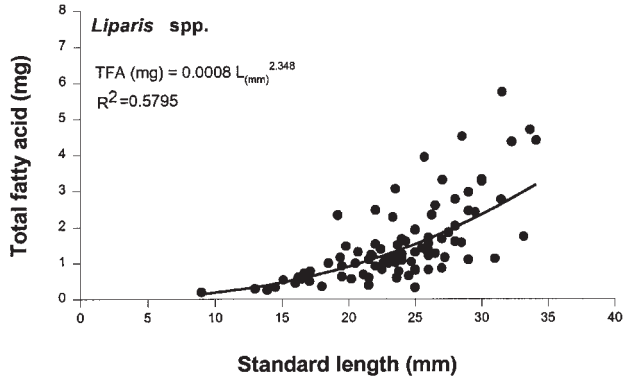


Fig. 6. Total fatty acid content versus standard length of juvenile *Liparis* spp. caught along the entire transect. $n = 93$.

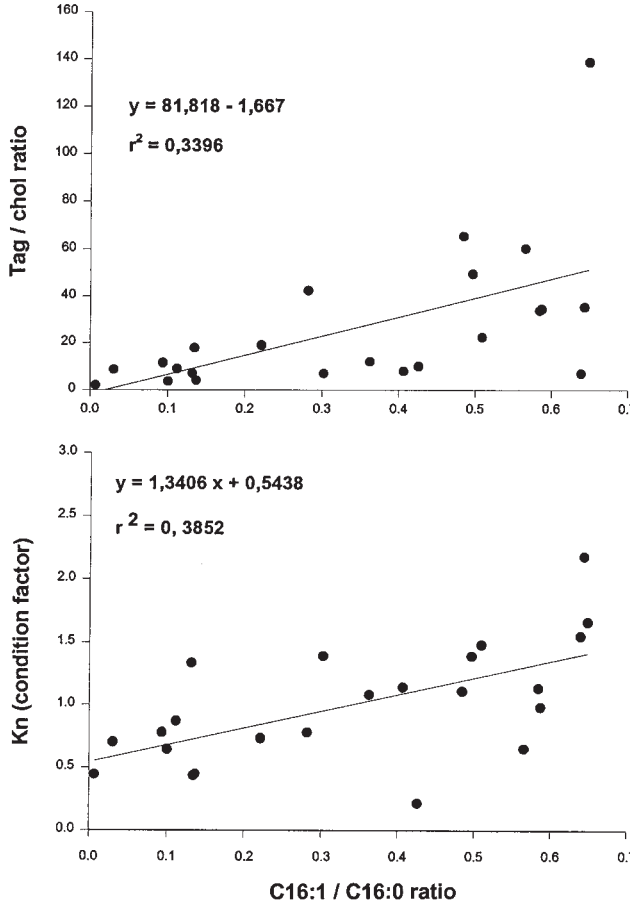


Fig. 7. The ratio between the neutral lipids triacylglycerides (TAG)/the structural lipids cholesterol (CHOL) and the condition factor K_n versus the ratio of the fatty acids C16:1(n-7)/C16:0, indicative of increasing contents of fatty acids originating from diatoms, in juvenile *Liparis* spp.

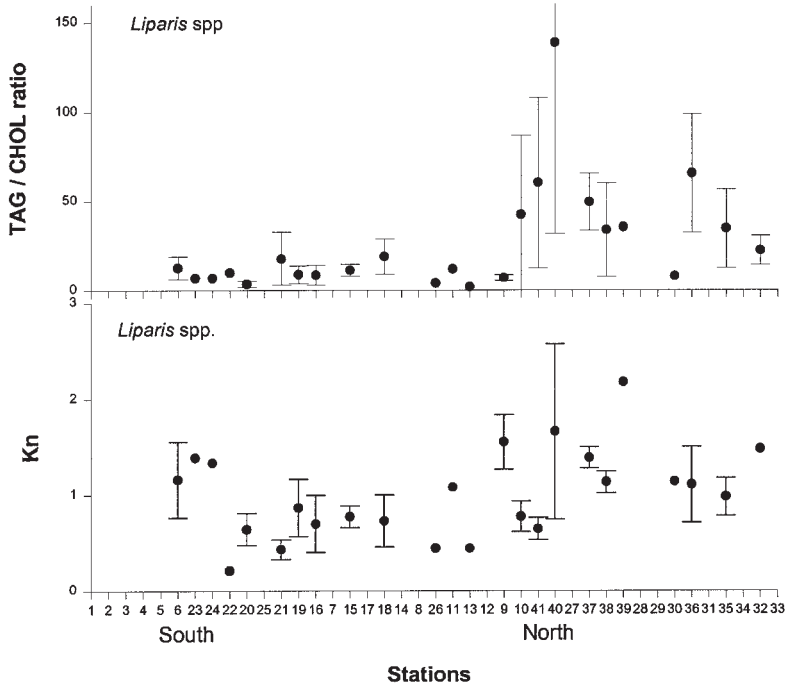


Fig. 8. The ratio between the neutral lipids triacylglycerides (TAG)/the structural lipids cholesterol (CHOL) and the condition factor K_n in *Liparis* spp. caught along the entire transect.

topography did not reveal major effects from local upwelling, e.g. around fishing banks, thus the investigation area is considered as being a south–north transect. The chlorophyll *a* concentration was within the range previously reported for Disko Bay during mid-July to mid-September (Nielsen and Hansen, 1999). However, the increasing phytoplankton biomass and production off and north of Disko Bay indicate a time delay in the bloom or presumably a second bloom (Andersen, 1981; Nielsen and Hansen, 1999). The succession towards a more heterotrophic food web was not so developed in the northerly plankton community (more diatoms and fewer nanoflagellates) as in the southern one. The southern community was dominated by dinoflagellates and nanoflagellates, which in general are regarded as regular members of the oligotrophic period after blooming. The phytoplankton biomass had a mean value of 18 mg C m^{-3} along the transect. At station 41, the biomass of phytoplankton of 60 mg C m^{-3} was presumably due to outflow from Vaigat where the phytoplankton biomass was a factor of 5–10 times higher than found along the West coast (Jensen *et al.*, 1999). Few reports on phytoplankton biomass exist; however, data from southwest Greenland and Disko Bay confirm the observed standing stocks (Gillbricht, 1968; Nielsen and Hansen, 1995).

The copepod biomass of 5–60 mg C m^{-3} is comparable to results from Disko Bay in 1994 at the same time of year as reported here (Hansen *et al.*, 1999). The

vertical distribution of *Calanus* spp. during their reproductive period is closely related to the algal biomass (e.g. Unstad and Tande, 1991; Nielsen and Hansen, 1995) and therefore the main part of the *Calanus* population is normally found in the upper 50–100 m during the spring bloom (Nielsen and Hansen, 1995) and deeper later in the year (Hansen *et al.*, 1999). During and after a spring bloom off Godhavn, Nielsen and Hansen (1995) found that copepods, dominated by *Calanus* spp., constituted 49–84% of the total zooplankton biomass. In June–July, copepods also made up the main part of the mesozooplankton biomass of which *Calanus* spp. was 60–87% of the total copepod stock (Hansen *et al.*, 1999). Buchanan and Sekerak (1982) found similar values in Lancaster Sound and in Western Baffin Bay (July–October). In the present study, *Calanus* spp. constituted 65% of the mesozooplankton biomass, while *M.longa* only formed a minor proportion. The latter is probably due to the relatively deep distribution (>70 m in the present study) as reported by Hansen *et al.* (1999).

The stage compositions of the *Calanus* spp. revealed a more progressed development in the southern part as compared to the northern part of the transect. Additionally, female *C.finmarchicus* and *C.glacialis* were still present in the surface water in the north. The difference in stage composition was obviously a consequence of the later withdrawal of the sea ice. Furthermore, there seemed to be a difference in the copepodite stage composition of the three *Calanus* species, where the youngest stages were predominant in *C.finmarchicus*, the oldest stages in *C.hyperboreus* and the intermediate stages in *C.glacialis*. Smidt (1979) found a similar stage composition off West Greenland (July–August). The explanation is found in the life cycles of *Calanus* spp. where *C.finmarchicus* presumably have one generation yearly, *C.glacialis* 1–2 generations yearly (Tande, 1991) and *C.hyperboreus* has a multiyear life cycle (Hirche and Niehoff, 1996).

Assuming a predator size-invariant prey length/predator length = 0.05 for maximum prey size preference as suggested for cod larvae and juvenile cod (Munk, 1997), this gives a prey size range of 0.5–1.75 mm for *Liparis* spp. Roughly the same result (~1–4 mm) is obtained if it is assumed that the mouth anatomy, the mouth width versus standard length, was similar for *Liparis* spp. (<2–2.5 mm) in this study as for *L.fabricii* (Hunter *et al.*, 1980; Munk, 1997). Very few empirical data are available on *Liparis* spp. food preferences. However, Grainger *et al.* (1980) reported from gut analysis that *L.fabricii* (mean length 22.8 mm) contained *C.hyperboreus* CIII and females, *M.longa* CV and males, *Pseudocalanus* spp. CV, males and females, and adult *Onchaea borealis*. The stage and thereby body size composition of copepods in the present study revealed that all stations hosted copepods with a relevant prey size for *Liparis* spp. Hence, the >400 μm prey size fraction was relevant for fatty acid analysis.

In order to investigate and trace the origin of food quality in relation to the condition of juvenile snail fish, fatty acid compositions of total lipid from phytoplankton, mesozooplankton and *Liparis* spp. were determined. However, the fatty acid composition of total lipid from natural phytoplankton can vary with the stage of and the species composition in the bloom, as well as with environmental conditions (Kates and Volcani, 1966; Chuecas and Riley, 1969; Harrington *et al.*,

1970; Jeffries, 1970; Piorreck and Pohl, 1984; Ben-Amotz *et al.*, 1985). Thus the dietary lipid of herbivorous calanoid copepods can vary both quantitatively and qualitatively throughout a bloom (Lee *et al.*, 1971; Sargent *et al.*, 1977; Falk-Petersen *et al.*, 1987; Fraser and Sargent, 1989). In the present study, the fatty acid composition of total lipid from natural phytoplankton (0–45 μm size fraction in Table II) revealed a dominance of C18:4(n-3) and C22:6(n-3) along the transect, whereas the ratio C16:1(n-7)/C16:0 was <2, characteristic for Chrysophyceae, Haptophyceae and Dinophyceae. The dominance of species from these phytoplankton classes was further supported by microscopical analysis. The relatively low C20:5(n-3) content in the phytoplankton size fractions indicated low diatom abundance.

From laboratory studies, it has been reported that some species of zooplankton have a preference for diatoms (e.g. Martin, 1970), while others have shown preference for flagellates and dinoflagellates (e.g. Gill and Harris, 1987; Huntley *et al.*, 1987a), and Haptophyceae (Huntley *et al.*, 1987b) are readily consumed by a range of zooplankton grazers. Thus selective feeding by zooplankton may complicate the use of specific fatty acids as biomarkers through the food chain.

In the present study, the marked increase in the ratio C16:1(n-7)/C16:0 (>2) and a relatively low C22:6(n-3) content in mesozooplankton >400 μm in the northerly area probably reflected the mesozooplankton diet originating from a recent decline of a diatom bloom. Tracer fatty acids for diatoms were equally present in mesozooplankton samples from south and north, however. In general, the ratio C16:1(n-7)/C16:0 increased with increasing plankton size fraction as seen by St John and Lund (1996), presumably reflecting the difference in zooplankton metabolization rates of a phytoplankton diet (turnover) with body size. These findings support the idea of a species succession from diatoms to flagellates with an increasing biomass and production north of Disko Bay as a consequence of the later withdrawal of sea ice. In the southern part, there was no evidence of recent uptake of tracer lipids originating from diatoms. On the contrary, in this area, the mesozooplankton had a higher content of the fatty acid C22:6(n-3), which was indicative of dietary lipid of non-diatom origin.

The concept of incorporation of dietary fatty acids into TAG of fish larvae and young fish species is well established (Owen *et al.*, 1972; Gatten *et al.*, 1983; Martin *et al.*, 1984; Fraser *et al.*, 1987). It has been shown that the fatty acid composition of the TAG initially resembles phytoplankton lipid and later on zooplankton lipid, and thus reflects the changing dietary behaviour of the fish as they develop (Gatten *et al.*, 1983). The ratio C16:1(n-7)/C16:0 in juvenile *Liparis* spp. increased in the northern part of the transect. Juvenile fish generally consume the mature wax ester-rich stages of calanoid copepods during summer and autumn. Hence, the increase in this ratio indicated uptake of zooplankton whose dietary lipid had its origin in a diatom diet. The dietary lipid in the juvenile snail fish in the southern part resembled that of the mesozooplankton from the same area whose lipid was based on a non-diatom diet.

Triacylglycerol is used for energy requirements and shows the nutritional condition of larvae and juvenile fish (Håkanson, 1993). Likewise, CHOL is a major cell membrane constituent presenting a good indicator of the amount of

living tissue, and is not catabolized by undernourished fish larvae (Fraser *et al.*, 1987). The condition of the juvenile *Liparis* spp. was expressed by the ratio TAG/CHOL. This ratio increased towards the north. The condition factor K_n also increased from south to north (Figure 8). This fact cannot be explained by inadequate food availability in the south, since the copepod biomass was fairly constant along the entire transect. It is more likely indicative of a relationship between food quality and nutritional condition, where better condition of the juvenile snail fish obviously is related to grazing on zooplankton containing dietary lipid originating in diatoms, i.e. a historical food uptake (Figure 7). Similarly, St John and Lund (1995) found that fish larvae in frontal areas, where diatoms are known to predominate, were generally in a better condition than fish larvae outside frontal areas, characterized by various flagellates. In conclusion, our data demonstrate a direct positive relationship between food uptake originating in a diatom-based food web and the condition of juvenile *Liparis* spp.

Acknowledgements

We want to thank the crew and the researchers on R/V 'Pamiut' for helpful assistance during the cruise. We also want to thank T.Lund, M.St John, L.Thymark and E.Buch for comments and discussions during the project, and P.Munk, T.G.Nielsen and H.Ramløv for reviewing the manuscript. The project was supported by Greenland Institute of Natural Resources and by Danish National Research Council project no. 9501038 to B.W.H.

References

Ackman,R.G., Jangaard,P.M., Hoyle,R.J. and Brockerhoff,H. (1964) Origin of marine fatty acids. I. Analyses of the fatty acids produced by the diatom *Skeletonema costatum*. *J. Fish. Res. Board Can.*, **21**, 747–756.

Ackman,R.G., Tocher,C.S. and McLachlan,J. (1968) Marine phytoplankter fatty acids. *J. Fish. Res. Board Can.*, **25**, 1603–1620.

Andersen,O.G.N. (1981) The annual cycle of phytoplankton primary production and hydrography in the Disko Bugt area, West Greenland. *Medd. Grønland. Biosci.*, **6**, 65 pp.

Ben-Amotz,B., Tornabene,T.G. and Thomas,W.H. (1985) Chemical profile of selected species of microalgae with emphasis on lipids. *J. Phycol.*, **21**, 72–81.

Benson,A.A., Lee,R.F. and Nevenzel,J.C. (1972) Wax esters: major marine metabolic energy sources. *Biochem. Soc. Symp.*, **35**, 175–187.

Berggreen,U.C., Hansen,B. and Kiørboe,T. (1988) Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development: implications for the determination of copepod production. *Mar. Biol.*, **99**, 341–352.

Buchanan,R.A. and Sekerak,A.D. (1982) Vertical distribution of zooplankton in Eastern Lancaster sound and Western Baffin Bay, July–October 1978. *Arctic*, **35**, 41–55.

Christie,W.W. (1972) *Lipid Analysis*. Pergamon Press, Oxford.

Christie,W.W. (1989) *Gas Chromatography and Lipids—A Practical Guide*. The Oil Press, Ayr, UK.

Chuecas,L. and Riley,J.P. (1969) Component fatty acids of the total lipids of some marine phytoplankton. *J. Mar. Biol. Assoc. UK*, **49**, 97–116.

Dagg,M. (1977) Some effects of patchy food environments on copepods. *Limnol.Oceanogr.*, **22**, 99–107.

Edler,L. (1979) Recommendations for marine biological studies in the Baltic Sea. *Baltic Mar. Biol. Publ.*, **5**, 1–38.

Falk-Petersen,S., Sargent,J.R. and Tande,K. (1987) Lipid compostion of zooplankton in relation to the Sub-arctic food web. *Polar Biol.*, **8**, 115–120.
Fewster,M.E., Burns,B.J. and Mead,J.F. (1969) Quantitative densitometric thin-layer chromatography of lipids using copper acetate reagent. *J. Chromatogr.*, **43**, 120–126.
Fraser,A.J. and Sargent,J.R. (1989) Formation and transfer of fatty acids in an enclosed marine food chain comprising phytoplankton, zooplankton and herring (*Clupea harengus* L.) larvae. *Mar. Chem.*, **27**, 1–18.
Fraser,A.J., Sargent,J.R., Gamble,J.C. and MacLachlan,P. (1987) Lipid class and fatty acid composition as indicators of the nutritional condition of larval Atlantic herring. *Am. Fish. Soc. Symp.*, **2**, 129–143.
Gatten,R.R., Sargent,J.R. and Gamble,J.C. (1983) Diet-induced changes in fatty acid composition of herring larvae reared in enclosed ecosystems. *J. Mar. Biol. Assoc. UK*, **63**, 575–584.
Gill,C.W. and Harris,R.P. (1987) Behavioural responses of the copepods *Calanus helgolandicus* and *Temora longicornis* to dinoflagellate diets. *J. Mar. Biol. Assoc. UK*, **67**, 785–801.
Gillbricht,M. (1968) *The Phytoplankton During NORWESTLANT 1–3*. ICNAF, Spec. Publ., Int. Comm. Northw. Atlant. Fish, No. 7, NORWESTLANT 1–3, Part I–II, pp. 73–84.
Grainger,E.H., Mohammed,A.A. and Robinson,K. (1980) A marine biological study of Brevoort Harbour and nearby waters of Estern Baffin Island. Zooplankton biology. *Can. Man. Rep. Fish. Aquat. Sci.*, **1557**, 51–74.
Håkanson,J.L. (1984) The long and short term feeding condition in field-caught *Calanus pacificus*, as determined from the lipid content. *Limnol. Oceanogr.*, **29**, 794–804.
Håkanson,J.L. (1989) Condition of larval anchovy (*Engraulis mordax*) in the Southern California Bight, as measured through lipid analysis. *Mar. Biol.*, **102**, 153–159.
Håkanson,J.L. (1993) Nutritional condition and growth rate of anchovy larvae (*Engraulis mordax*) in the California Current: two contrasting years. *Mar. Biol.*, **115**, 309–316.
Hansen,B., Verity,P., Falkenhaugh,T., Tande,K.S. and Norbin,F. (1994) On the trophic fate of *Phaeocystis pouchetii* (Harriot). V. Trophic relationships between *Phaeocystis* and zooplankton: an assessment of methods and size dependence. *J. Plankton Res.*, **16**, 487–511.
Hansen,B.W., Nielsen,T.G. and Levinsen,H. (1999) Plankton community structure and carbon cycling on the western coast of Greenland during the stratified summer situation. III. Mesozooplankton. *Aquat. Microb. Ecol.*, **16**, 233–249.
Harrington,G.W., Beach,D.H., Dunham,J.E. and Holz,G. (1970) The polyunsaturated fatty acids of marine dinoflagellates. *J. Protozool.*, **17**, 213–219.
Hirche,H.J. and Mumm,N. (1992) Distribution of dominant copepods in the Nansen Basin, Arctic Ocean, in summer. *Deep-Sea Res.*, **39**, 485–505.
Hirche,H.J. and Niehoff,B. (1996) Reproduction of the Arctic copepod *Calanus hyperboreus* in the Greenland Sea—field and laboratory observations. *Polar Biol.*, **16**, 209–219.
Hunter,J.G., Jones,M.B. and Rich L.M. (1980) A marine biological study of Brevoort Harbour and nearby waters of Estern Baffin Island. Fishes. *Can. Man. Rep. Fish. Aquat. Sci.*, **1557**, 97–130.
Huntley,M.E., Ciminiello,P. and Lopez,M.D.G. (1987a) Importance of food quality in determining development and survival of *Calanus pacificus* (Copepoda: Calanoida). *Mar. Biol.*, **95**, 103–113.
Huntley,M.E., Tande,K. and Eilertsen,H.C. (1987b) On the trophic fate of *Phaeocystis pouchetii* (Hariot). II. Grazing rates of *Calanus hyperboreus* (Krøyer) on diatoms and different size categories of *Phaeocystis pouchetii*. *J. Exp. Mar. Biol. Ecol.*, **110**, 197–212.
Jeffries,H.P. (1970) Seasonal composition of temperate plankton communities: fatty acids. *Limnol. Oceanogr.*, **15**, 419–426.
Jensen,H.M., Pedersen,L., Burmeister,A.D. and Hansen,B.W. (1999) Pelagic primary production during summer along 65 to 72°N off West Greenland. *Polar Biol.*, **21**, 269–278.
Kates,M. and Volcani,B.E. (1966) Lipid components of diatoms. *Biochim. Biophys. Acta*, **116**, 264–278.
Klein Breteler,W.C.M., Fransz,H.G. and Gonzales,S.R. (1982) Growth and development of four calanoid copepod species under experimental and natural condition. *Neth. J. Sea Res.*, **16**, 195–207.
Le Cren,E.D. (1951) The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). *J. Anim. Ecol.*, **20**, 201–219.
Lee,R.F., Nevenzel,J.C. and Paffenhöfer,G.-A. (1971) Importance of wax esters and other lipids in the marine food chain: phytoplankton and copepods. *Mar. Biol.*, **9**, 99–108.
Martin,F.D., Wright,D.A. and Means,J.C. (1984) Fatty acids and starvation in larval striped bass (*Morone saxatilis*). *Comp. Biochem. Physiol. B*, **77**, 785–790.
Martin,J.H. (1970) Phytoplankton-zooplankton relationships in Narragansett Bay. IV. The seasonal importance of grazing. *Limnol. Oceanogr.*, **15**, 413–418.

Munk,P. (1992) Foraging behaviour and prey size spectra of larval herring *Clupea harengus*. *Mar. Ecol. Prog. Ser.*, **80**, 149–158.
Munk,P. (1997) Prey size spectra and prey availability of larval and small juvenile cod (*Gadus morhua*). *J. Fish. Biol.*, **51**, 340–351.
Nielsen,T.G. and Hansen,B. (1995) Plankton community structure and carbon cycling on the western coast of Greenland during and after the sedimentation of a diatom bloom. *Mar. Ecol. Prog. Ser.*, **125**, 239–257.
Nielsen,T.G. and Hansen,B.W. (1999) Plankton community structure and carbon cycling on the western coast of Greenland during the stratified summer situation. I. Hydrography, phytoplankton and bacterioplankton. *Aquat. Microb. Ecol.*, **16**, 205–216.
Omori,M. (1969) Weight and chemical composition of some important oceanic zooplankton in the North Pacific Ocean. *Mar. Biol.*, **3**, 4–10.
Owen,J.M. (1973) An analogue device for correcting densitometric measurements of coloured spots on chromatograms for the effect of light scattering. *J. Chromatogr.*, **79**, 165–171.
Owen,J.M., Adron,J.W., Sargent,J.R. and Cowey,C.B. (1972) Studies on the nutrition of marine flatfish. The effect of dietary fatty acids on the tissue fatty acids of the plaice *Pleuronectes platessa*. *Mar. Biol.*, **13**, 160–166.
Piorreck,M. and Pohl,P. (1984) Formation of biomass, total protein, chlorophylls, lipids and fatty acids in green and blue-green algae during one growth phase. *Phytochemistry*, **23**, 217–223.
Pohl,P. and Zurheide,F. (1979) Fatty acids and lipids of marine algae and the control of their biosynthesis by environmental factors. In Hoppe,A.H., Levring,T. and Tanaka,Y. (eds), *Marine Algae in Pharmaceutical Science*. Walter de Gruyter & Co., Berlin, pp. 473–523.
Sabatini,M. and Kiørboe,T. (1994) Egg production, growth and development of the cyclopoid copepod *Oithona similis*. *J. Plankton Res.*, **16**, 1329–1351.
Sargent,J.R. (1976) The structure, function and metabolism of lipids in marine organisms. In Malins,D.C. and Sargent,J.R. (eds), *Biochemical and Biophysical Perspectives in Marine Biology*. Academic Press, London, pp. 150–212.
Sargent,J.R. (1978) Marine wax esters. *Sci. Prog. Oxf.,* **65**, 437–458.
Sargent,J.R. and Henderson,R.J. (1986) Lipids. In Corner,E.D.S. and O'Hara,S.C.M. (eds), *The Biological Chemistry of Marine Copepods.* Clarendon Press, Oxford, pp. 59–164.
Sargent,J.R., Gatten,R.R., Corner,E.D.S. and Kilvington,C.C. (1977) On the nutrition and metabolism of zooplankton. XI Lipids in *Calanus helgolandicus* grazing *Biddulphia sinensis*. *J. Mar. Biol. Assoc. UK*, **57**, 525–533.
Sargent,J.R., Parkers,R.J., Mueller-Harvey,I. and Henderson,R.J. (1987) Lipid biomarkers in marine ecology. In Sleigh,M.A. and Horwood,E. (eds), *Microbes in the Sea.* Chichester, UK, pp. 119–138.
St John,M.A. and Lund,T. (1996) Lipid biomarkers: linking the utilization of frontal plankton biomass to enhanced condition of juvenile North Sea cod. *Mar. Ecol. Prog. Ser.*, **131**, 75–85.
Smidt,E.L.B. (1979) Annual cycles of primary production and of zooplankton at Southwest Greenland. *Meddr. Grønland Biosci.*, **1**, 1–52.
Tande,K.S. (1991) *Calanus* in the North Norwegian fjords and in the Barents sea. *Polar Res.*, **10**, 389–407.
Unstad,K.H. and Tande,K.S. (1991) Depth distribution of *Calanus finmarchicus* and *Calanus glacialis* in relation to environmental conditions in the Barents Sea. *Polar Res.*, **10**, 409–420.

Received on August 10, 1998; accepted on April 13, 1999