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PRIMARY RESEARCH PAPER

Seasonal variability in copepod ingestion and egg production on the Faroe shelf

Høgni Debes · Kirstin Eliasen · Eilif Gaard

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Abstract Copepod community ingestion rates of *Calanus finmarchicus*, *Temora longicornis*, *Acartia longiremis* and *Pseudocalanus* spp., and egg production rates of *C. finmarchicus* and *T. longicornis*, were studied in relation to phytoplankton composition, abundance and biomass on the Faroe shelf during a one-year cycle. The phytoplankton community during winter was mainly composed of small flagellates and the copepods of *Pseudocalanus* spp. As the spring bloom progressed, diatoms increased in abundance and dominated the biomass throughout summer. *C. finmarchicus* increased in numbers in early spring, while *T. longicornis* and *A. longiremis* dominated the community during summer and autumn. While no response in ingestion rates was observed for *A. longiremis* and *Pseudocalanus* spp. with increasing diatom biomass, both ingestion rates and egg production of *C. finmarchicus* and *T. longicornis*, generally increased, showing a dependence upon diatoms for production. The daily ingestion for *C. finmarchicus* females was 7% and 22% of body biomass during the pre-bloom and bloom period, respectively, while for *T. longicornis* females it was 33% and 56% and for *A. longiremis* females 22% and 33%, respectively. *C. finmarchicus* accounted for more than 80% of the total copepod ingestion in May, but in mid- and late summer, *T. longicornis* and *A. longiremis* dominated, and represented 80–90% of the total copepod ingestion. The proportion of reproductively mature *C. finmarchicus* increased as the phytoplankton biomass increased. Most of the time there was good agreement between herbivorous ingestion rates and calculated carbon demand for the observed egg production. However, both species showed a peak in egg production prior to the phytoplankton spring-bloom.

Keywords Copepods · Gut fluorescence · Ingestion · Gonad maturity · Egg production · Faroe shelf

Introduction

Copepod reproduction is highly dependent on food availability (e.g. Diel & Tande, 1992; Hirche, 1996; Niehoff et al., 1999; Maps et al., 2005; Pierson et al., 2005) and for most copepod species phytoplankton is the main food item (Irigoien et al., 1998; Meyer-Harms et al., 1999). Seasonal development in primary production and phytoplankton abundance and composition is generally reflected in copepod reproduction and growth (Campbell et al., 2001; Durbin

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et al., 2003; Devreker et al., 2005). In high latitudes, the seasonal difference in phytoplankton production and abundance is high and therefore timing and intensity of primary production highly influences production composition and abundance of the entire copepod community (e.g. Gislason & Astthorsson, 1995; Gaard, 1999).

In pelagic marine environments, copepods are a key link between primary production and higher trophic levels. The timing and the intensity of copepod reproduction is considered to be essential for survival of fish larvae, since they feed largely on copepod eggs or nauplii during their early feeding stage (e.g. McLaren & Avendaño, 1995; Michaud et al., 1996; Gaard & Steingrund, 2001; Voss et al., 2003). As fish grow, they progressively select larger food items, which largely are copepodites (e.g. Thorisson, 1994; Lough et al., 1996; Gaard & Reinert, 2002). Many of the demersal fish species depend highly in their adult life on food items that feed on zooplankton (e.g. sandeel, Norway pout, capelin etc.) and in several areas clear relationships have been observed between plankton, planktivorous fish and demersal fish (Gaard et al., 2002; Astthorsson & Vilhjálmsson, 2002; Temming et al., 2004; Steingrund & Gaard, 2005). Furthermore, several pelagic fish stocks feed on copepods during their entire lifetime, and their individual growth as well as stock production is highly affected by copepod availability (Jacobsen & Hansen, 2000; Holst et al., 2004; Skjoldal et al., 2004).

Understanding the relationship between phytoplankton production and subsequent copepod ingestion, egg production and growth is thus a prerequisite for understanding the dynamics of pelagic ecosystems.

One ecosystem that shows high seasonal and interannual variability in phytoplankton and zooplankton production and abundance is the Faroe shelf ecosystem, situated about midway between Scotland and Iceland (Fig. 1). Despite its small size ($\sim$10,000 km^2), it contains a distinct neritic ecosystem, surrounded by an oceanic environment. The shelf water is relatively well separated from the open ocean by a persistent front that surrounds the shelf, usually between 100 and 130 m bottom depth (Gaard et al., 1998; Larsen et al., 2002). Tidal rectification and other effects drive a current system, which circles the islands in a clockwise direction (Hansen, 1992). Due to strong tidal currents over the shallow parts of the shelf, the water column is mixed from surface to bottom throughout the year and no summer stratification occurs in the shallow areas (Gaard, 1996; Gaard et al., 1998). The average residence time of the shelf water is estimated to be about 2–3 months, but it is highly variable and the monthly flushing rates may vary by about a factor of six (Gaard & Hansen, 2000; Gaard, 2003).

In most years, the primary production starts earlier on the shelf and in the shelf front than in the surrounding oceanic environment (Gaard, 1996, 2000). The timing and the intensity are, however, highly variable between the years. It has been hypothesized that this may be due to variable grazing pressure, mainly by the copepod *Calanus finmarchicus*, which occurs on the shelf in highly variable abundances (Gaard et al., 1998; Gaard, 2003). Recent modelling studies have, however, indicated that variable exchange rates of the shelf water are able to postpone the spring bloom and also to reduce the primary production on the shelf, mainly during prebloom (Eliasen et al., 2005).

The zooplankton community on the Faroe shelf is basically neritic. Copepods dominate the community and neritic copepods (mainly *Temora longicornis* and *Acartia longiremis*) usually occur in high abundances during summer. It is, however, also highly affected by advection of oceanic zooplankton, mainly *C. finmarchicus* (Gaard, 1999, 2003; Debes et al., 2005). This advection is variable between years (Gaard & Hansen, 2000).

Earlier studies have shown clear seasonal (Gaard, 1999; Debes et al., 2005) and interannual (Gaard, 2000; 2003) relationship between phytoplankton abundance, and zooplankton reproduction and community development on the Faroe shelf. Effects from the observed interannual variability in phytoplankton production and abundance on the shelf can be tracked through several trophic levels in the ecosystem and impact feeding conditions for fish and seabirds, growth rates and reproduction of demersal fish on the shelf, stock production and catches (Gaard et al., 2002; Steingrund & Gaard, 2005). Interannual variability in production of higher trophic levels within the ecosystem is clearly caused by variable plankton production. Thus, detailed information on processes at the phyto- and zooplankton levels is important to

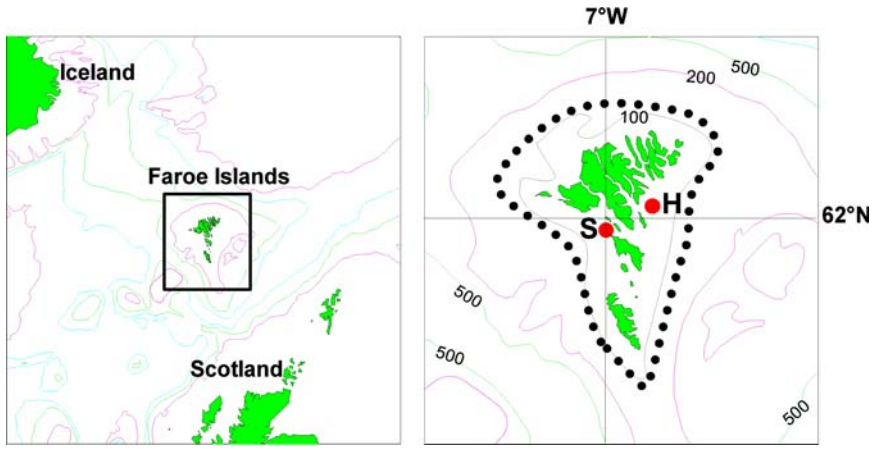

Fig. 1 Location of the Faroe shelf and the sampling stations H and S. The dotted line indicates an approximate location of the shelf front

understand the dynamics and variability in the entire ecosystem.

Probably two main reasons can be postulated for these unusually clear trophic co-fluctuations in this ecosystem. One reason is that the Faroe shelf is a small and highly uniform system. Thus the productivity at plankton level and its environmental conditions are homogeneous in the entire system. This makes sample procedure and analysis at the plankton level easier to overcome than in most other systems. The other reason is the high degree of variability between years, which can be observed at all trophic levels. The system therefore is very suitable for ecological studies, and information gathered can be useful in other systems as well.

The aim of this article is to describe the phytoplankton–zooplankton relationships at the process level. Copepod ingestion and reproduction rates on the shelf were studied during a one-year cycle and related to phytoplankton abundance and species composition.

Materials and methods

Study sites and sampling

Sampling was carried out at a fixed station (62°03 N, 6°37 W) on the central Faroe shelf (marked H on Fig. 1). The bottom depth was 55 m. Samples were collected during daytime on 16 cruises with RV *Magnus Heinason* every 1–2 weeks during the season from late March until mid-November 2004. On each cruise, measurements were made of: CTD profiles, chlorophyll *a* and copepod abundance and composition. Furthermore, egg production rates and gut fluorescence were measured on key copepod species.

Frequent measurements of temperature and chlorophyll *a* were also carried out at a land-based station (marked S on Fig. 1). This station received seawater from 18 m bottom depth at a highly turbulent locality.

Hydrography and chlorophyll *a*

Vertical temperature profiles at station H were obtained on each cruise using a Seabird 9 plus CTD. In addition, seawater temperature at 18 m depth was monitored daily at station S (Fig. 1).

Chlorophyll *a* samples were collected at 5, 20 and 50 m depths and measured spectrophotometrically according to Parsons et al. (1984). Chlorophyll *a* was furthermore measured on a weekly basis on samples from the coastal station S during the period from April until September.

Phytoplankton

Samples for phytoplankton species identification and enumeration were collected at a depth of 20 m and preserved with Lugol solution (final concentration 1%). The algae were identified and counted using an inverted microscope after overnight settlement in 10 ml sample chambers. Each phytoplankton cell was measured and converted to carbon content based on simple geometrical shapes according to the Baltic

Marine Biologists (1979) and using a carbon conversion factor of 0.13 for flagellates (Smetacek, 1975) and 0.11 for all other phytoplankton (Strathmann, 1967).

Copepod abundance and biomass

Copepods were sampled with oblique hauls down to approximately 50 m depth using a Bongo net (diameter: 0.6 m) with mesh sizes of 100 and 200 μm, respectively. The volumes filtered by the nets were measured with digital Hydro Bios flow meters mounted at the net openings. The samples were preserved in 4% formaldehyde. In the laboratory, subsamples of 200–300 copepods in both 100 and 200 μm were identified and counted. Copepod nauplii were identified and counted from the 100 μm subsamples only. The prosome length was measured on each copepod (total length for nauplii). Copepod biomass was calculated using constant length–weight regressions for all stages within each species: *C. finmarchicus* (Hay et al., 1991); *Pseudocalanus* spp., *T. longicornis* and *Centropages typicus* (Klein-Breteler et al., 1982); *A. longiremis* (Berggreen et al., 1988); *Oithona similis* (Sabatini & Kiørboe, 1994). For *Microcalanus* sp. and the category "other copepods", which together only accounted for a minor fraction of the total copepod biomass throughout the season, we used the same equation as for *O. similis*.

The nauplii biomass was also estimated using constant length–weight regressions for all nauplii stages within each species: *C. finmarchicus* (Hay et al., 1991); *Pseudocalanus* spp., *T. longicornis* (Klein-Breteler et al., 1982); *A. longiremis* and other nauplii using the equation for *A. clausi* (Klein-Breteler et al., 1982).

Egg production

Egg production measurements were carried out on two copepod species: *C. finmarchicus* and *T. longicornis*. The measurements started on March 25 and ended on June 10 and 30 for *T. longicornis and C. finmarchicus*, respectively.

Samples for egg production were collected on vertical hauls from a depth of 50 m with a 200 μm mesh size WP−2 net equipped with a 1 l non-filtering cod-end. Immediately after sampling, healthy females were sorted into 0.5 l plastic containers filled with 60 μm-filtered seawater (one female per container) and incubated at in situ temperature and dim light for 24 h. Each container was equipped with a "false-bottom" consisting of 300 μm mesh size net, to minimize egg cannibalism. Replicates of between 20 and 30 females were incubated on each cruise, except for *T. longicornis* on March 25, April 20 and May 10, when less than 6 females were used.

The prosome length of each female was measured with an ocular micrometer, and carbon content was estimated using length-weight regressions from the literature (see above). Average egg production rate was converted to specific egg production assuming a carbon content of 0.231 μg C egg^{-1} for *C. finmarchicus* (Ohman & Runge, 1994) and 0.0883 μg C egg^{-1} for *T. longicornis* (Dam & Lopes, 2003).

Gonad maturity of *C. finmarchicus*

Gonad maturity of *C. finmarchicus* females was determined according to the method described by Niehoff & Hirche (1996). The females were graded into four different maturity stages GS1–GS4, where GS1–GS3 represents immature females and GS4 characterizes females that are mature and ready to spawn.

Gut fluorescence

Gut-fluorescence measurements were made on four copepod species: *C. finmarchicus*, *T. longicornis*, *A. longiremis* and *Pseudocalanus* spp. Immediately after sampling, the content of the cod-end was gently filtered through a small 30 μm mesh size net, put into a plastic bag and frozen quickly using freezing spray (−50°C). The samples were kept dark and frozen (−20°C) until further measurements (usually 2–4 weeks, max 3 months).

The measurements were carried out according to Båmstedt et al. (2000). At the laboratory, the samples were gently rinsed into a container using filtered seawater (Whatmann GF/F filters) and kept dark and ice-cooled during the rest of the procedure (15–30 min). Copepods were sorted under dim light into test tubes containing 5 ml 90% acetone and

extracted over night in refrigerator. The numbers of individuals in each test tube varied with copepod size; for large copepods like *C. finmarchicus* females and CV, 5–7 individuals and 6–7 replicates were made, while for smaller copepods like CII-CIII, *Pseudocalanus* spp. and *A. longiremis*, 20–40 individuals and 2 replicates were used. The chlorophyll content was measured on a Turner Model 10 fluorometer before and after acidification with 3–4 droplets of concentrated hydrochloric acid.

Gut contents (G) were calculated according to the following equations:

$$\text{Chlorophyll}\, a = C(F_o - F_a)/n$$

$$\text{Phaeopigment} = C(R \times F_a - F_o)/n$$

where C is the fluorometer calibration constant, F_o and F_a are the fluorescence reading before and after acidification, R is the acidification ratio and n is the number of individuals per cuvette sample.

The gut content (chlorophyll equivalents per individual) was then calculated as

$$G = (\text{chlorophyll}\, a + 1.51 \times \text{phaeopigment})$$

When calculating carbon content from chlorophyll, a constant conversion factor of 40 from chlorophyll to carbon was used (Riemann et al., 1989).

Gut clearance

Samples for gut clearance rate measurements of *C. finmarchicus* stage CV and females were collected on the Faroe shelf in April 2005. The samples were collected as described for gut fluorescence. The content of the cod-end was transferred directly into a container with 25 l of seawater that had been filtered through Whatmann GF/F filters, and incubated at in situ temperature. Subsamples were taken from the container after 5, 10, 15 and 30 min and treated for gut fluorescence measurements as described above.

Gut clearance rates were calculated assuming an exponential decrease in gut content with time (Dam & Peterson, 1988), and were described by the equation

$$G_t = G_0 e^{-kt}$$

where G_0 = initial level of gut contents, G_t = level at time t and k = instantaneous gut clearance rate.

The gut clearance rates were temperature adjusted to seasonal in situ temperature using a $Q_{10} = 2.21$ (Dam & Peterson, 1988).

Ingestion

Copepod ingestion rates (I) were estimated according to the equation

$$I = G \times k$$

where G = level of gut content (ng chlorophyll equivalents) and k = instantaneous gut clearance rate (min^{-1}). Ingestion rates were converted to carbon (see above). No pigment destruction was incorporated in the calculations.

In order to estimate the total ingestion rate of the copepod community, as well as the grazing impact on the phytoplankton biomass, lack of data was treated as follows: On occasions with no gut content measurements, daily ingestion rates were calculated using specific ingestion rates derived from the same specific copepod species, during the same productive period (pre-bloom, bloom, post-bloom, late summer or winter). To estimate daily consumption for the group "other copepods", we used the specific ingestion rates derived from *Pseudocalanus* spp. females. For calculation of daily ingestion rates of *C. finmarchicus* stage CI, we applied the specific ingestion rates derived from *C. finmarchicus* stage CII and CIII.

Since no measurements were made on nauplii, ingestion rates from the literature were used in estimating total copepod grazing. Ingestion rates of *C. finmarchicus* nauplii (NIII–NVI) were calculated using an average ingestion rate for NIII–NVI from Rey et al. (2001) and stages NIV–NVI from Irigoien et al. (2003). The ingestion rates of all other nauplii (NIII–NVI) were calculated using an average of the calculated specific ingestion rate for *C. finmarchicus* nauplii NIII–NVI.

Results

Temperature and phytoplankton

During the research period, the temperature increased steadily from 6.8°C in late March to a maximum of

11.0°C in late August and then decreased again to about 9°C in November. No temperature differences were observed with depth at any time during the research period, showing that no summer thermocline was established.

Five periods of phytoplankton biomass were distinguished at station H on the Faroe shelf during 2004 (Fig. 2, upper panel). During pre-bloom (March 25 to May 10), the phytoplankton biomass was generally low, especially during March and April (<0.5 mg chl *a* m^{-3}), but increased slightly to about 1 mg chl *a* m^{-3} in early May. Small flagellates dominated the phytoplankton community during this period (Fig. 2, lower panel).

The biomass increased further during the spring bloom period (May 11 to July 12) and reached a maximum of 9 mg chl *a* m^{-3} in late June. The phytoplankton community changed during this period from small diatoms (mainly small solitary cells of *Chaetoceros* spp., <10 μm) in late May to a dominance of the two diatom species *Rhizosolenia styliformis* and *Guinardia delicatula* during the rest of the period. *R. styliformis* is very large with cell lengths of about 200 μm and colonies frequently reach sizes of >1 mm. *G. delicatula* is, on the other hand, an average-sized diatom with colonies of about 300–400 μm.

The bloom collapsed in early July and the phytoplankton biomass decreased rapidly to less than 1 mg chl *a* m^{-3} during the post-bloom period (July 13 to August 9). During this period the phytoplankton community was totally dominated by small flagellates.

In late August, the biomass increased again, giving rise to two secondary peaks of about 3 mg chl *a* m^{-3} during the late summer bloom period (August 10 to September 9). Both solitary and colony forming diatoms (mainly *Chaetoceros* spp.) dominated during this period. By October, the phytoplankton biomass had decreased to winter values (<0.5 mg chl *a* m^{-3}).

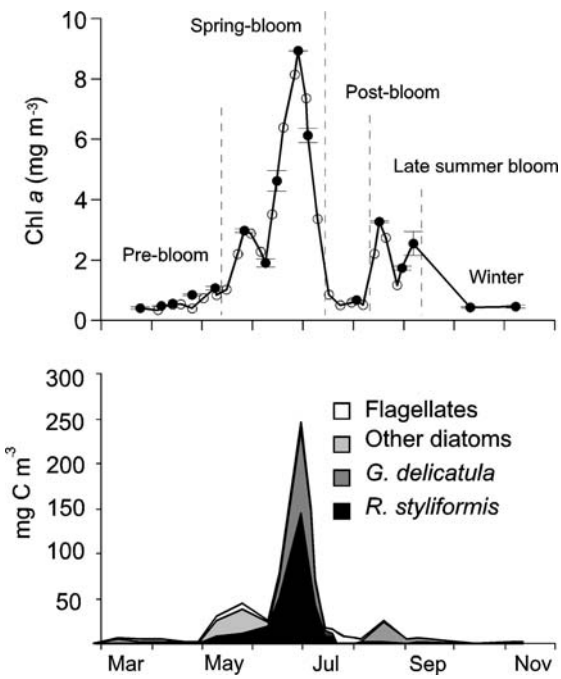

Fig. 2 Upper panel: Mean chlorophyll *a* concentrations at station S (open circles) and at 5, 20 and 50 m depth at station H (solid circles). Vertical bars represent standard error between the three depths at station H. Lower panel: Phytoplankton species composition shown as mg C m^{-3} at station H. Vertical dashed lines delineate the five periods of bloom formation/dispersion

Copepod species composition and abundance

While the abundance data of the smaller copepod species is based on the 100 μm mesh sized bongo samples, the data on *C. finmarchicus* abundance is based on both the 100 μm and the 200 μm samples. A randomisation test showed that the 100 μm net was significantly better ($p < 0.006$) at sampling the smaller copepodite stages CI–CIII compared to the 200 μm net, while there was no difference between the two nets for the larger copepodite stages CIV-adult. The results for CI–CIII of *C. finmarchicus*, are thus based on the 100 μm net samples, while the results for the other stages are based on the standard 200 μm net samples.

The copepod species composition varied considerably during the season (Fig. 3). During early spring the copepod community was dominated by *Pseudocalanus* spp. Spot checks during the season showed that this was *P. elongatus*. Thus, we assume that the majority of the genus belonged to this species, although other species may have co-occurred. The species is, however, addressed as *Pseudocalanus* spp. As the phytoplankton spring bloom progressed, the abundance of neritic copepod species, especially *T. longicornis* and *A. longiremis* increased, and dominated the community during mid- and late

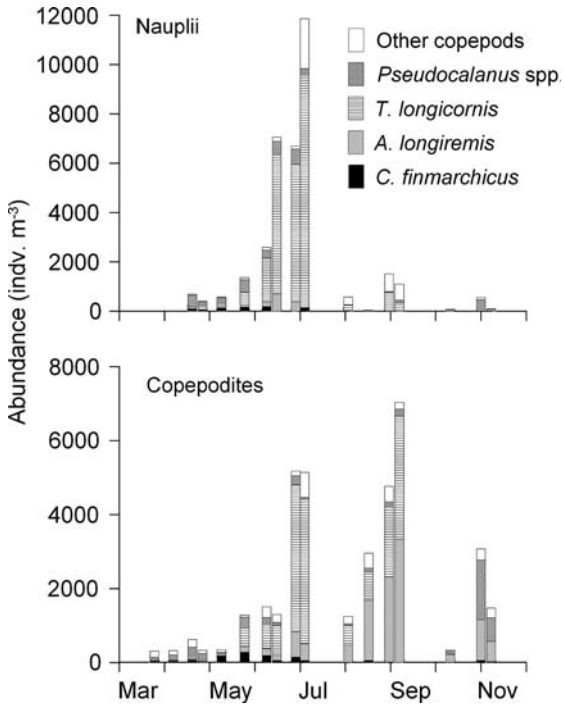

Fig. 3 Abundance and species composition of nauplii and copepodites at station H

summer. The oceanic copepod *C. finmarchicus* was only abundant during spring and until mid-summer.

The category "other species" includes mainly *O. similis*, but also variable amounts of *Centropages hamatus*, *Microcalanus* sp., *Paracalanus* spp., *Metridia lucens* and some young stages of unidentified copepods.

Gut pigment content

During pre-bloom, the gut pigment content was generally low for the large individuals (Fig. 4). At the onset of the phytoplankton spring bloom in early May, the gut pigment content in the late stages of *C. finmarchicus* and *T. longicornis* females increased markedly, and reached maximum values in late May. In June and July the gut pigment content decreased even though the phytoplankton biomass continued to increase. No increase in gut pigment content was observed for these two species coinciding with the phytoplankton bloom in late August/early September.

The difference in gut pigment content between the bloom and the pre-bloom phases was less pronounced in the small-sized copepods (*A. longiremis* and *Pseudocalanus* spp.) compared to the larger copepods (late stages of *C. finmarchicus* and *T. longicornis* females) (Fig. 4). The gut pigment content increased with increasing body size, from the small copepods *Pseudocalanus* spp., *A. longiremis* as well as early stages of *C. finmarchicus*, to the somewhat larger *T. longicornis* and later stages of *C. finmarchicus*. However, relative to body size, the gut content was highest in the smallest copepods and vice versa.

Gut clearance rates and ingestion rates

The results of the gut clearance rate measurements for females and CV copepodites of *C. finmarchicus* are shown in Fig. 5. The constants were 0.0326 and 0.0313 min^{-1}, respectively. There was no significant difference between the two gut clearance rate constants (likelihood ratio test $p = 0.39$). An average was used for CIV and younger stages of *C. finmarchicus*, as well as for all the other copepod species throughout the research period.

The ingestion rate patterns of the single species and stages (Fig. 6) were quite similar to the gut content pattern (Fig. 4) and did not change much due to increasing gut clearance rates induced by seasonal temperature changes.

When *C. finmarchicus* were abundant during spring and early summer, they accounted for the majority of the total copepod grazing (Table 1). The proportion of *C. finmarchicus* grazing was 20–30% in early spring and increased to about 80% in early bloom (including nauplii). Due to reduced abundance of *C. finmarchicus*, the fraction gradually decreased during June, and from July they were of minor importance. The grazing proportion of *T. longicornis* increased rapidly in late June and peaked in early July and again in early September with 80% of the total copepod grazing. *A. longiremis* was never as important a grazing contributor as the two former species. It increased in mid-summer and peaked in mid-August and early September with about 20% of the total copepod grazing. Thus, *T. longicornis* and *A. longiremis* accounted for the majority of the total copepod ingestion (and thus production) in mid- and late summer. The other species occurring on the shelf were always of minor importance, except for *Pseudocalanus* spp. during winter and early spring.

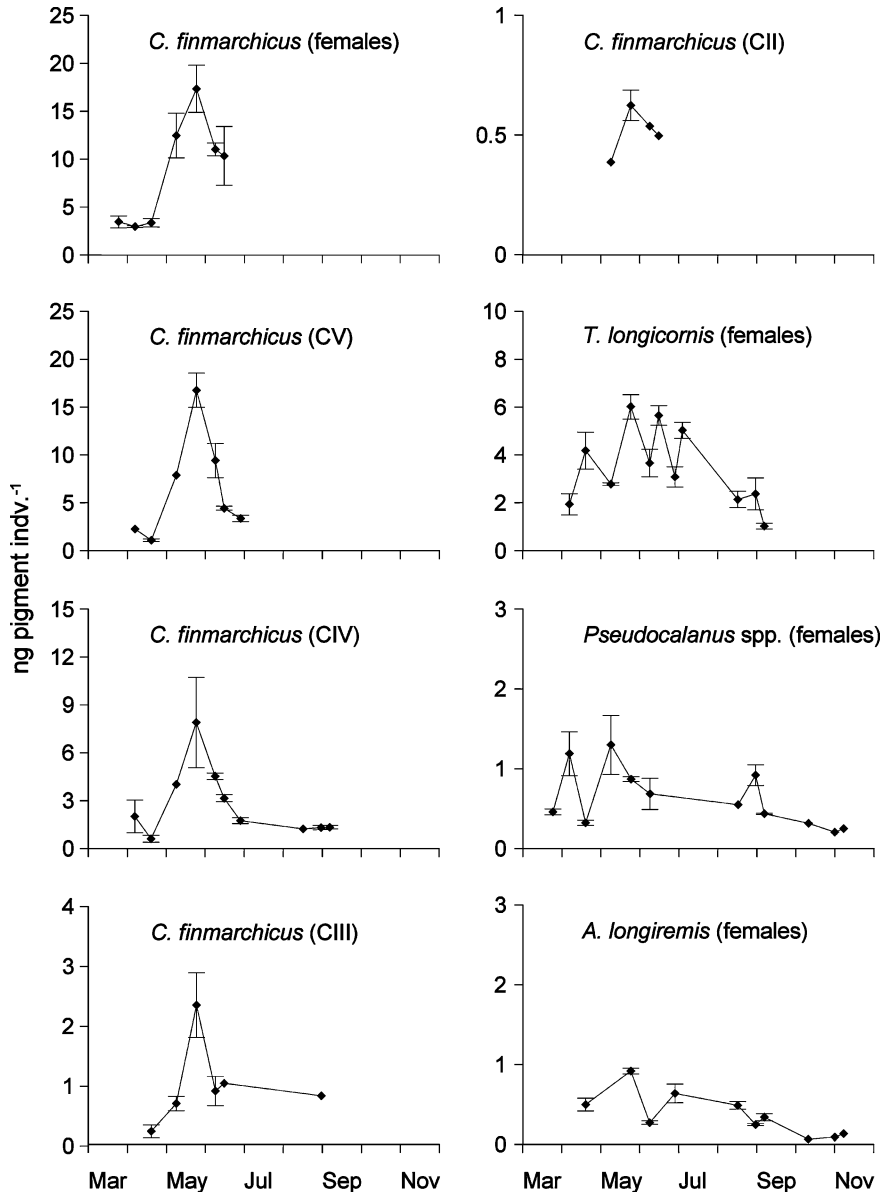

Fig. 4 Time course of gut pigment contents (ng pigments indv.$^{-1}$) at station H. Vertical bars represent standard error

In total, *T. longicornis* was the main copepod grazer with almost 50% of the total copepod ingestion. *C. finmarchicus* was second with about 30%, and *A. longiremis* was third with about 10–12%. Thus, these three species represented around 90% of the total phytoplankton ingestion (and presumably also production) from March to November 2004.

The average, weight-specific ingestion rates for females were higher for the small-sized copepod species as well as for *T. longicornis*, compared to *C. finmarchicus* during the entire season (Table 2). Especially *T. longicornis* females showed high weight-specific ingestion rates, with an average 33% and 56% body carbon per day during pre-bloom and bloom, respectively, compared to 7% and 22%, respectively, for *C. finmarchicus* females.

Gonad maturity of *C. finmarchicus*

During early spring most of the *C. finmarchicus* females were immature, but the proportion of mature

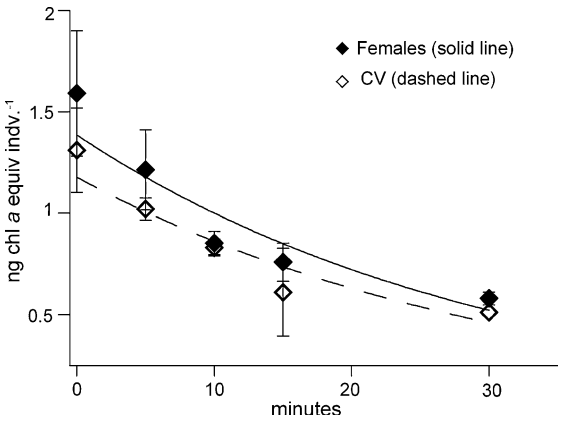

Fig. 5 Gut clearance rate for *C. finmarchicus* females and copepodite stage five (CV) at 7°C. Vertical bars represent standard error

females increased during pre-bloom (Fig. 7). In early May, as the phytoplankton spring bloom started, most of the females were mature, but towards the end of the bloom, the proportion of immature females increased slightly again.

Egg production of key copepod species

The daily egg production rates of *C. finmarchicus* and *T. longicornis* are shown in Fig. 8. Fecundity of both species was low in early spring, but in late April a pre-bloom peak of 9 and 44.6 eggs female^{-1} day^{-1}, respectively, was observed. Both species showed reduced fecundity again in early May, but increased to $\sim$20 and $\sim$45 eggs female^{-1} day^{-1} respectively, as the phytoplankton spring-bloom progressed later in May and June. The daily egg production rates were generally 2–3 times higher for *T. longicornis* than for *C. finmarchicus*.

Discussion

Ingestion rates

The results presented here of copepod ingestion rates are within the range of other reported values, also using the gut pigment content method (e.g. Ohman & Runge, 1994; Durbin et al., 1995, 1997; Irigoien et al., 1998). The method has its advantage in providing data on ingestion rates directly from the field and measuring of copepods of different body sizes. This is important since several authors have reported size dependent ingestion rates for copepods (e.g. Bautista & Harris, 1992; Barquero et al., 1998; Halvorsen et al., 2001; Bode et al., 2003). This relationship was also evident in this study where ingestion rates of late copepodite stages of the large copepod *C. finmarchicus* were much higher than for small copepod species like *Pseudocalanus* spp. and *A. longiremis*.

During pre-bloom, when phytoplankton biomass was low, ingestion rates were low for *C. finmarchicus*, while they were relatively high for the small-sized copepod species like *A. longiremis* and *Pseudocalanus* spp as well as *T. longicornis*. This might indicate a better ability for these species to capture their prey during this period. The phytoplankton community during pre-bloom was mainly composed of small flagellates (5–8 μm). Several researchers have found that prey motility can influence the feeding behaviour of copepods (Saiz, 1994; Saiz & Kiørboe, 1995; Kiørboe et al., 1996; Jakobsen, 2001). In addition, Saiz & Kiørboe (1995) and Kiørboe et al. (1996) reported that *Acartia tonsa* was able to switch from suspension feeding to an ambush feeding behaviour at low phytoplankton concentrations. Thus, during the pre-bloom period in our study, the small-sized copepods might have been better able to capture the prey than the larger copepods like *C. finmarchicus*. However, investigations by Meyer-Harms et al. (1999) showed that *C. finmarchicus* was able to positively select dinoflagellates (8–12 μm) during periods of low phytoplankton biomass, and suggested that it might be due to the prey-switching theory described above. Therefore, our results, showing a relatively higher ingestion rate for the small-sized copepods, might be due to a combined effect of prey motility and low phytoplankton biomass as well as prey size, since the phytoplankton during pre-bloom generally were in the lower end of the prey-size spectrum for the larger copepod *C. finmarchicus*.

The pattern in gut pigment contents – and thus ingestion rates – observed mainly for *C. finmarchicus* during the spring-bloom period, with a marked increase in May followed by a decrease in June, to a large extent reflects changes in the phytoplankton species composition, in addition to a general increase in phytoplankton biomass. During the onset of the spring bloom in May, the phytoplankton species

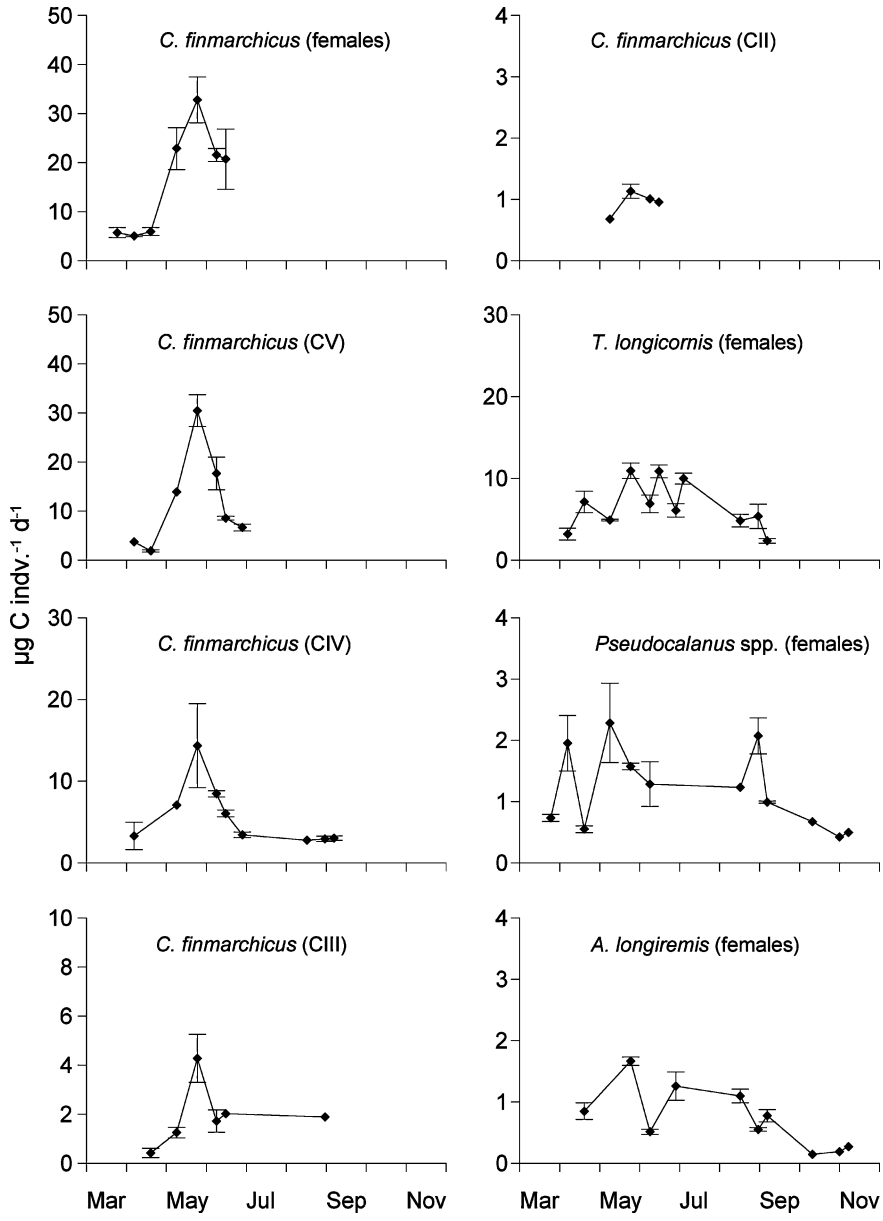

Fig. 6 Time course of ingestion rates (µg C indv.$^{-1}$ d^{-1}) at station H. Vertical bars represent standard error

composition changed from small flagellates to different diatoms (mainly *Chaetoceros* spp. 10–40 µm). Later in June, it changed again to a dominance by the diatom species *R. styliformis*, and later also *G. delicatula*. The former is a very large diatom species that forms colonies frequently reaching >1 mm in length and is therefore most likely not ideal as food for copepods ranging in size from about 0.5 to 3–4 mm. The decrease in gut pigment content in June coincided with this shift in the phytoplankton species composition. Several researchers have shown ingestion by different copepod species to be correlated with phytoplankton species composition, both with regard to nutritive quality (Cowles et al., 1988; Runge & Plourde, 1996) and size of the algae (Frost, 1972; Bautista & Harris, 1992). Thus, the copepod ingestion rates could be affected by changes in the phytoplankton species composition on the shelf.

Estimated ingestion rates of *C. finmarchicus* and *T. longicornis*, which were derived by applying

Table 1 Average daily grazing rates of the four key copepod species on the Faroe shelf during 2004 (the values include all copepodite stages and nauplii NIII–NVI), phytoplankton biomass in mg C per m^{-3}, and grazing impact by the entire copepod community on the phytoplankton standing stock

Date	*C. finmarchicus* mg C m^{-3} d^{-1}	*T. longicornis*	*Pseudocalanus*	*A. longiremis*	Other copepods	Phytoplankton biomass (mg C m^{-3})	Grazing impact (%)
Mar 25	0.044 (34%)	0.021 (16%)	0.059 (45%)	0.003 (2%)	0.009 (7%)	16	0.8
Apr 7	0.037 (18%)	0.034 (16%)	0.123 (59%)	0.003 (1%)	0.013 (6%)	19	1.1
Apr 20	0.125 (31%)	0.068 (17%)	0.171 (43%)	0.017 (4%)	0.016 (6%)	21	1.9
Apr 27	0.051 (16%)	0.112 (36%)	0.122 (39%)	0.023 (7%)	0.006 (2%)	16	2.0
May 10	1.236 (90%)	0.007 (0.5%)	0.107 (8%)	0.007 (0.5%)	0.009 (0.7%)	43	3.2
May 26	2.500 (74%)	0.645 (19%)	0.177 (5%)	0.058 (2%)	–	119	2.9
Jun10	1.552 (69%)	0.519 (23%)	0.092 (4%)	0.06 (3%)	0.024 (1%)	76	3.3
Jun 17	0.235 (26%)	0.423 (46%)	0.08 (9%)	0.113 (12%)	0.064 (7%)	185	0.5
Jun 30	0.204 (8%)	1.844 (73%)	0.147 (6%)	0.232 (9%)	0.113 (4%)	357	0.7
Jul 6	0.057 (3%)	1.745 (80%)	0.05 (2%)	0.223 (10%)	0.105 (5%)	245	0.9
Aug 19	0.054 (3%)	1.077 (65%)	0.022 (1%)	0.389 (24%)	0.110 (7%)	131	1.3
Sep 2	0.023 (1%)	1.624 (79%)	0.027 (1%)	0.273 (13%)	0.102 (5%)	69	2.9
Sep 9	–	0.920 (61%)	0.081 (5%)	0.371 (25%)	0.140 (9%)	102	1.5
Oct 14	0.002 (3%)	0.007 (12%)	0.041 (68%)	0.004 (7%)	0.002 (3%)	17	0.3
Nov 4	0.016 (8%)	–	0.156 (74%)	0.032 (15%)	0.001 (0.4%)	–	–
Nov 11	0.009 (5%)	–	0.166 (87%)	0.009 (5%)	0.002 (1%)	18	1.0

Numbers in brackets indicate percentage of total copepod community grazing

Table 2 Mean body carbon content (*B*) (±standard error) of the four, key copepod species (females) during the pre-bloom and bloom period, and average daily ingestion (*I*) expressed as percentage of mean body carbon during the same periods

Species	Pre-bloom		Bloom	
	B (μg C $indv.^{-1}$)	I (% of B)	B (μg C $indv.^{-1}$)	I (% of B)
C. finmarchicus	82 ± 3 (n = 24)	7	115 ± 3 (n = 69)	22
T. longicornis	26 ± 1 (n = 19)	33	37 ± 2 (n = 27)	56
P. elongatus	7.9 ± 0.4 (n = 38)	16	9 ± 2 (n = 4)	19
A. longiremis	4.5 ± 0.4 (n = 7)	22	5.5 ± 0.1 (n = 19)	33

Number of replicates shown in brackets

filtration rates from the literature, follow our measurements of ingestion rates quite well. Assuming an average filtration rate for *C. finmarchicus* females on diatoms of 133 ml per day (Meyer-Harms et al., 1999), gives an ingestion rate that is only slightly lower than our measurements based on the gut pigment content. Reported filtration rates of *T. longicornis* are highly variable, but, assuming an average filtration rate of ~150 ml per day for *T. longicornis* (Van Duren et al., 2003), yield an ingestion rate that is slightly higher than our measurements.

Maximum weight-specific ingestion rates were observed early during the spring-bloom period for all four species investigated, coinciding with a dominance of relatively small diatoms in the phytoplankton community. For *C. finmarchicus* it equalled 22% of body carbon. This is slightly lower than values reported from the North Sea (50%) (Gamble, 1978) and at Weathership M (30%) (Irigoien et al., 1998b). Since our measurements were made on a weekly or fortnightly basis, it may have been higher in between samplings. For *T. longicornis*, the maximum daily weight-specific ingestion of

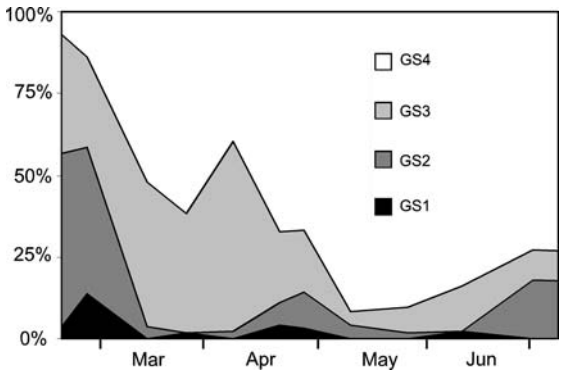

Fig. 7 Time course of the gonad maturity index of *C. finmarchicus* females. GS4 represents reproductively mature females

phytoplankton equalled 56% of body carbon. This is in the same range as several other reported results (e.g. Dam, 1986; Klein-Breteler et al., 1990; Dam & Lopes, 2003), but lower than the 146% and 170% of body carbon reported by Harris & Paffenhöfer (1976) and Klein-Breteler et al. (1990), respectively. Our measurements of weight-specific ingestion rates might have underestimated the actual specific ingestion rates since the method used only measures the amount of pigment ingested and thus does not include potential heterotrophic prey items. *T. longicornis* is known to ingest heterotrophic prey just as readily as phytoplankton (Dam & Lopes, 2003). However, research made by Debes et al. (2005) showed the biomass of protozooplankton to be negligible during the bloom, compared to autotrophic phytoplankton. Besides of the lack of heterotrophic prey, an underestimation could also be caused by the use of the constant carbon/chlorophyll *a* ratio. This ratio has been shown to vary considerably during the season as well as between different nutrient regimes (Riemann et al., 1989).

Grazing impact

The potential grazing impact by the copepod community on the phytoplankton biomass of the Faroe shelf was low throughout the season in 2004 (Table 1). The daily grazing pressure was about 3% of the phytoplankton biomass during the early phase of the spring bloom period and during the secondary bloom in late August, and less than 1% during the rest of the season. This is in accordance with previously reported results, which rarely exceed 10% of the phytoplankton biomass (e.g. Bautista & Harris, 1992; Barquero et al., 1998; Bode, 2003; Li et al., 2003; Saunders et al., 2003).

The highest grazing impact occurred when the abundance of *C. finmarchicus* and *T. longicornis* was high, and reflects the relatively large size of the former, and the high abundance and weight-specific ingestion rates of the latter species. Hence, especially *C. finmarchicus* and *T. longicornis* were the main copepod grazers, and thus the main link in the classical food chain between primary production and higher trophic levels on the Faroe shelf in 2004. The copepod species composition on the Faroe shelf may, however, vary considerably between years, with interannually highly variable amounts of *C. finmarchicus* (originally advected onto the shelf from the surrounding oceanic environment) and neritic species (Gaard, 1999, 2003; Gaard & Hansen, 2000). Therefore, the relative grazing importance of the species may vary considerably between years.

Nauplii seem to account for a relatively large fraction of the grazing impact on the phytoplankton biomass. However, the estimated grazing rates of nauplii might be biased due to the use of average ingestion rates from the literature, as well as the use of relatively large mesh size (100 μm) in the Bongo net (see below).

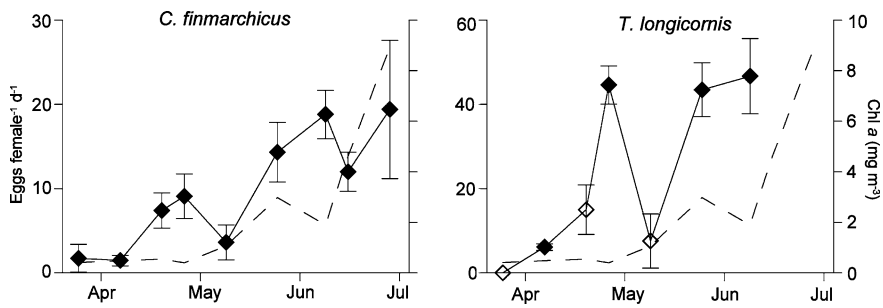

Fig. 8 Fecundity (eggs female^{-1} d^{-1}) of *C. finmarchicus* and *T. longicornis* females. Vertical bars represent standard error. Dashed line represents the phytoplankton biomass (mg chl *a* m^{-3}). Open diamonds represent measurements based on less than 6 females

Factors affecting the estimated grazing rates

Although our estimates of grazing rates and the impact on the phytoplankton standing stock are in agreement with the range of other reported values, there are several factors that might affect the estimates, and in most cases might have contributed to an underestimation of the actual grazing impact.

One critical factor is the gut clearance rate. Previous results have shown the gut clearance rate to increase with temperature (Dam & Peterson, 1988; Irigoien, 1998). The average gut clearance rates (0.032 min^{-1}) estimated for *C. finmarchicus* females and stage CV in this study are within the range of other reported values for the same species (Tande & Båmstedt, 1985) or other species of the same body size (Dagg & Wyman, 1983; Bautista & Harris, 1992; Bode et al., 2003). Applying the equation in Dam & Peterson (1988), where temperature determines the gut clearance rate, yields a rate of 0.027 min^{-1}, which is only slightly lower than the rate determined in our study.

Several researchers have reported gut clearance rate to increase with body size (Bautista & Harris, 1992; Barquero et al., 1998; Bode et al., 2003). However, other researchers have reported it to be independent of body size (Morales et al., 1990; Li et al., 2003), which, to a certain degree, justifies our application of estimated gut clearance rate for adult *C. finmarchicus*, to the rest of the copepod community.

Gut content – and thus ingestion – has been reported to vary with time of sampling during the day, with night time values up to several times higher than during daytime (Morales et al., 1991; Barquero et al., 1998; Li et al., 2003). The samples in our study were all taken during the day, and the actual ingestion rates might therefore have been underestimated. Although diel feeding rhythms vary between different localities and do not always occur (Head & Harris, 1987; Morales et al., 1991), this should be kept in mind when estimating ingestion rates in the field.

Another factor that potentially contributes to an underestimation of the ingestion rates is pigment degradation during gut passage. There is great uncertainty about the degree of pigment destruction in copepods, and reported values are highly variable ranging from 0 to 95% (Båmstedt et al., 2000 and references therein). Recalculation of the grazing impact with an average pigment degradation of 33% (Dam & Peterson, 1988) only increases maximum grazing impact to 4.9%. This is still within the range of results reported by other researchers (see above), and is most likely not able to control phytoplankton growth in most cases.

The use of a constant C:chl *a* relationship throughout the season may also cause erroneous ingestion rate calculations. Although the C:chl *a* relationship varies with the season and the phytoplankton species composition, we used a value of 40 throughout the season. Using a higher value of $\sim$50, which is commonly accepted (Meyer-Harms et al., 1999; Li et al., 2003; Saunders et al., 2003; Gislason, 2005) would increase the ingestion rates by 20%. The grazing impact on the phytoplankton standing stock, however, would be unaffected since the conversion factor would increase the phytoplankton biomass correspondingly.

We did not make any attempt to size fractionate the phytoplankton community in this study, when estimating the grazing impact. Several studies have shown that copepods prefer to feed on particles larger than 5–10 μm (Berggreen et al., 1988; Dam & Peterson, 1991; Bautista & Harris, 1992). Research made by Meyer-Harms et al. (1999) in the Norwegian Sea showed a positive selection for dinoflagellates (8–12 μm) and diatoms (length: $\sim$40 μm) by *C. finmarchicus*, and suggested that this observed behaviour was due to algal sizes. Li et al. (2003) reported from the Bohai Sea that when only taking the large phytoplankton cells into account, a considerable proportion would be grazed by the copepod community. Thus, the actual grazing impact on large phytoplankton cells might be higher.

Finally, the copepod biomass might be overestimated. The copepod community during the productive season was dominated by early copepodite stages (Debes & Eliasen, 2006). Since larger copepodites contain more biomass relatively to length than small copepodites, our use of a constant length-weight regression for all stages within each species, might have resulted in an overestimation of the total copepod biomass. This will ultimately have contributed to an overestimation of the grazing impact on the phytoplankton standing stock. Nauplii biomass, on the other hand, is most likely underestimated due to biased sampling by using a mesh size of 100 μm. Results of mesh selection of copepods and nauplii

made by Nichols & Thompson (1991) indicate that especially nauplii from the small neritic copepods might be underestimated in this study. The importance of the small-size fraction of the total copepod community is being increasingly recognized (e.g. Morales et al., 1991; Barquero et al., 1998), but to what extent this might have contributed to a potential underestimation of the total grazing impact is not possible to determine from our data.

Egg production

Egg production rates of *C. finmarchicus* were clearly related to the chl *a* concentrations. This relationship has been reported earlier on the Faroe shelf (Gaard, 2000; Debes et al., 2005), as well as at other localities (Hirche et al., 1991; 1997; Irigoien et al., 1998; Niehoff et al., 1999; Gislason, 2005).

Egg production rates of *C. finmarchicus* populations are closely related to the proportion of reproductively mature females (Campbell & Head, 2000; Gaard & Nattestad, 2002; Gislason, 2005). The fecundity was low during the early pre-bloom period although about 50% of the females were mature. The chl *a* concentration during this period was low ($\sim$0.5 mg m^{-3}). Assuming that ingestion rates of mature and immature females were equal and further assuming a gross growth efficiency of 33% (Hansen et al., 1997), ingestion rates of the mature females were still in excess of carbon demand for the egg production during this period (Table 3). Although the excess of carbon is low and might not even be sufficient for respiration, this might indicate that a larger fraction of the ingested food was allocated to final gonad maturation of the females during this period. Although it is widely accepted that gonad formation and maturation may be fuelled by internal lipid reserves, several researchers have suggested that actual ingestion is needed for final gonad maturation in several copepod species, including *C. finmarchicus* (Plourde & Runge, 1993; Niehoff & Hirche, 1996; Rey et al., 1999). Irigoien et al. (1998) hypothesized that this might partly explain the relationship often observed between ingestion and/or phytoplankton biomass and egg production rates during pre-bloom. In addition to an increase in the egg production rate, our results also show that the majority of the *C. finmarchicus* females reached maturity coinciding with the initiation of the phytoplankton spring bloom in May, supporting the hypothesis described above.

The fecundity of *C. finmarchicus* during the spring bloom on the Faroe shelf was low, compared to results from other localities (e.g. Niehoff et al., 1999; Gislason, 2005), even though the ingestion was clearly in excess of carbon demand for egg production for most of the period (Table 3). All previous studies of *C. finmarchicus* fecundity made on the central Faroe shelf have reported relatively low egg production rates during the phytoplankton spring bloom (Gaard, 2000; Debes et al., 2005). Gaard (2000) found mainly immature females on the central shelf in early spring and hypothesized that the relatively low egg production might be due to the females being "spent", i.e. the eggs having been released. However, an increase in egg production, as well as the maturity index of *C. finmarchicus* females during the productive season in 2004, does not support this hypothesis, since the majority of the females reached maturity at the onset of the phytoplankton spring bloom, and on average 85% of all females were reproductively mature during the bloom.

The fecundity of *T. longicornis* was relatively abundant during pre-bloom and seemed not to be coupled to the chl *a* concentration to the same degree as for *C. finmarchicus* females. *T. longicornis* is a species with high metabolic requirements, and high turnover of biomass, but has, at the same time, low energy reserves (lipids) (Mayzaud et al., 1992). It is therefore not able to rely on stored energy during periods of low food supply, and might therefore be expected to respond quickly to changes in food quantity or quality. However, with the exception of the first measurements, we did not observe any marked change in either phytoplankton biomass or species composition during the period of egg production measurements.

Dam & Lopes (2003) showed that *T. longicornis* ingested protozooplankton just as readily as autotrophic phytoplankton, and observed no significant difference in egg production when fed either prey type. We did not make any attempt to measure protozooplankton abundance or biomass during the present study. However, research made by Debes et al. (2005) in the same area in 1999 showed that the biomass of protozooplankton was similar to phytoplankton biomass during pre-bloom, but negligible

Table 3 Average ingestion rates (± standard error) of *C. finmarchicus* and *T. longicornis* females, and estimated carbon demand from egg production, assuming a 33% gross growth efficiency

Date	*C. finmarchicus* (μg C female^{-1} d^{-1})		*T. longicornis* (μg C female^{-1} d^{-1})	
	Ingestion	Carbon demand	Ingestion	Carbon demand
March 25	5.8 ± 1.1	1.2 ± 1.2	–	–
April 7	5.0 ± 0.2	1.0 ± 0.4	3.2 ± 0.7	1.6 ± 0.2
April 20	6.0 ± 0.8	5.2 ± 1.5	7.1 ± 1.3	4.0 ± 1.6
April 27	–	6.4 ± 1.9	–	11.9 ± 1.2
May 10	22.9 ± 4.3	2.5 ± 1.5	4.9 ± 0.1	2.0 ± 1.7
May 26	32.8 ± 4.7	10.0 ± 2.5	10.9 ± 0.9	11.6 ± 1.7
June 10	22.6 ± 1.3	13.1 ± 2.0	6.9 ± 1.1	12.5 ± 2.4
June 17	20.6 ± 6.1	8.4 ± 1.6	10.9 ± 0.8	–
June 30	16.3 ± 3.5	13.8 ± 5.7	6.1 ± 0.8	–

during the bloom. Protozooplankton might, therefore, have been a potential important food source for *T. longicornis* during the pre-bloom period.

Reported values of maximum egg production rates (MEP) for *T. longicornis* are highly variable. High MEP of 75.5 and 60 eggs female^{-1} d^{-1} were recorded in the eastern English Channel and in the Wadden Sea, respectively (Devreker et al., 2005; Fransz et al., 1992). The chl *a* concentration during these investigations was high (15 and > 35 mg m^{-3}, respectively). Somewhat lower MEP was observed in the Oosterscheld estuary (25 eggs female^{-1} d^{-1}), in coastal waters off Plymouth (21 eggs female^{-1} d^{-1}) and in the southern Gulf of St. Lawrence (22.2 eggs female^{-1} d^{-1}) (van Rijswijk et al., 1989; Bautista et al., 1994; Maps et al., 2005). The chl *a* concentration during these investigations was variable ranging from ~1 mg m^{-3} in the southern Gulf of St. Lawrence to 10–35 mg m^{-3} in the Oosterscheld estuary.

The MEP of *T. longicornis* during the spring bloom in the present study was 46.7 eggs female^{-1} d^{-1}. This is rather high compared to the other results listed above, considering that the chl *a* concentration was only 2–3 mg m^{-3}. Moreover, chl *a* concentration is an indirect measure of phytoplankton biomass. It also does not distinguish between algae size and nutritive quality. Indeed, some authors have pointed out the lack of coupling between the non-size-fractionated concentration of chl *a* and the egg production rate of *T. longicornis* (Dam & Peterson, 1991; Arendt et al., 2005), while others have pointed out the importance of food quality for copepod egg production (Paffenhöfer & van Sant, 1985; Devreker et al., 2005). Some algal species e.g. *Phaeocystis* sp. have been recognized as low-value food, while diatoms generally are considered to be of high nutritive quality (Hansen & van Boekel, 1991; Turner et al., 2002; Dam & Lopes, 2003; Devreker et al., 2005). The early phase of the phytoplankton spring bloom in the present study was to a large extent dominated by small diatoms (mainly different species of colony-forming *Chaetoceros* spp.). The relatively high egg production rates observed for *T. longicornis* during this period in our study might therefore be related to algal composition rather than the chl *a* concentration.

Assuming a gross growth efficiency of 33% (Hansen et al., 1997), there was a good agreement between herbivorous ingestion and carbon demand for the observed production (Table 3). However, on June 10 the estimated herbivorous ingestion was clearly lower than the calculated carbon requirements. The phytoplankton species composition changed during this time to a dominance of very large chain-forming diatoms. Previous results have suggested that feeding history is important for copepod egg production (e.g. Nival et al., 1990; Hirche et al., 1997; Båmstedt et al., 1999; Rey et al., 1999). Reproductive response to phytoplankton changes is not instantaneous. The high egg production rate, even when the phytoplankton species composition had changed from diatoms of favourable size to large chain-forming species, could thus potentially be due to the feeding history of *T. longicornis* females.

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