Mortality rates of epipelagic copepods in the post-spring bloom period in Disko Bay, western Greenland

Peter Thor[1],*, Torkel Gissel Nielsen[2], Peter Tiselius[1]

[1]University of Gothenburg, Department of Marine Ecology, Kristineberg, 45034 Fiskebäckskil, Sweden
[2]National Environmental Research Institute, Department of Marine Ecology, 399 Frederiksborgvej, 4000 Roskilde, Denmark

ABSTRACT: Mortality rates of the copepods *Calanus hyperboreus*, *C. glacialis*, *C. finmarchicus*, *Pseudocalanus* sp. and *Oithona similis* were investigated during June 2001 in Disko Bay, western Greenland. These 5 species dominated the zooplankton community in the upper 75 m, contributing 89% of the total copepod biomass. Instantaneous mortality rates of copepodites of all 5 species and nauplii of *Pseudocalanus* sp. and *O. similis* were calculated using vertical life tables on abundances and published information on stage duration times. Compared with those covering a range of boreal habitats, the mortality rates were higher, with highest rates occurring in *C. finmarchicus* and *C. glacialis* copepodite stages I to III and *Pseudocalanus* spp. stage III (maximum = 0.18 d^{-1}). Mortality rates remained lower in all stages of *O. similis*. When superimposing mortality rates for all species and stages on copepod size a significant peak at 1.3 mm prosome length was evident. This peak fitted a prey size dependent functional response of predation and the high mortality rates were, therefore, most probably attributable to size-specific predation.

KEY WORDS: Arctic copepods · Mortality rates · *Calanus* · *Pseudocalanus* · *Oithona*

————————— Resale or republication not permitted without written consent of the publisher —————————

INTRODUCTION

Copepods belonging to the genera *Calanus*, *Pseudocalanus* and *Oithona* are among the most abundant epipelagic zooplankton species on Greenland's west coast (Madsen et al. 2001, Head et al. 2003, Thor et al. 2005). These genera form a central node in the structure and function of Arctic epipelagic ecosystems during spring and summer and have accordingly been the focus of most studies of Arctic zooplankton population dynamics. Most of these studies have focused primarily on processes governing population growth such as feeding (Båmstedt et al. 1991, Turner et al. 2001), egg production (Hirche 1989, Hirche et al. 1997, Hansen et al. 1999, Niehoff et al. 2002), egg hatching (Nielsen et al. 2002) or larval stage development (Astthorsson & Gislason 2003). All of these processes are equally important determinants of development of any population; however, the size of populations is determined not only by processes lead-

ing to increases, but also by mortality. Naupliar mortality counteracts egg production during population recruitment; mortality of eggs, nauplii and copepodites controls the size of the present adult generation, whereas mortality of adults interferes with egg production and eventually recruitment to the next generation. It is, therefore, paramount that reliable mortality rates are incorporated into predictive population models if we want to understand variations in Arctic zooplankton communities. Unfortunately, little is known about copepod mortality in the Arctic and to our knowledge only one previously published study exists (Arnkværn et al. 2005).

In the present study we calculated instantaneous mortality rates of all copepodite stages of *Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus*, *Pseudocalanus* sp. and *Oithona similis* and nauplii of *Pseudocalanus* sp. and *O. similis* during June 2001 in Disko Bay, western Greenland, using the vertical life table approach (Aksnes & Ohman 1996).

MATERIALS AND METHODS

Study site and hydrography. Sampling was conducted during daytime at a 250 m deep station off Qeqertarsuaq (Godhavn) in Disko Bay, western Greenland (69° 15' N, 53° 33' W), a site previously used in studies of the epipelagic community in the bay (Fig. 1) (Nielsen & Hansen 1995, Hansen et al. 1999, Levinsen et al. 1999, Madsen et al. 2001).

Vertical profiles (0 to 200 m) of salinity, temperature and chlorophyll *a* (chl *a*) fluorescence were taken at each sampling occasion using a Seabird SBE25-01 CTD probe equipped with a fluorometer. Salinity was calibrated against water samples on a Guildline salinometer. Fluorescence was calibrated against chl *a* concentrations determined spectrophotometrically in water samples taken on each sampling occasion (chl $a = 0.076e^{1.6844 \times F}$, n = 64, r^2 = 0.822).

Copepod sampling. Copepods were collected every third day throughout June 2001 (9 sampling events) and during a day/night study during June 10 (3 sampling events). Five depth intervals were sampled: 0–15, 15–35, 35–50, 50–100 and 100–200 m using a plankton pump (900 l min^{-1}, mouth opening 25 cm) equipped with a 50 µm mesh size net with a non-filtering cod-end. The pump was hoisted slowly through the water column to obtain depth integrated samples. A flow meter (Hydro Bios) at the pump's entrance measured the volume filtered to enable calculation of sample volume when calculating abundances. Average volume pumped per sample was 1.3 m^3 with a min-imum volume of 0.3 m^3. A comparison of samples from the pump with samples from hauls of a WP2 net showed a difference in dry weight biomass of collected copepods of only 2.2% so no adjustments of pumped volume were made. All samples were fixed in 2% buffered formalin and stored for later enumeration and size estimation of zooplankton. For enumeration, the samples were split by a plankton splitter to obtain sample sizes of approximately 500 individuals. *Calanus hyperboreus*, *C. glacialis*, *C. finmarchicus*, *Pseudocalanus* sp. and *Oithona similis* were keyed to species and developmental stage.

Calanus copepodites were identified to species using prosome length criteria according to Table 1. *Pseudocalanus* females were distinguished based on the difference in size and morphology. *P. minutus* has a characteristically slender prosome and a protruding, nearly angular cephalosome (Lischka & Hagen 2005) and is larger (1.35 to 2.14 mm prosome length). Only smaller individuals (1.11 to 1.77 mm prosome length) not matching the morphological features of *P. minutus* were used in the mortality calculations. These could either be *P. acuspes* or *P. elongatus*, but judging from the general distribution of the *Pseudocalanus* genus they would probably be *P. acuspes* (Frost 1989). In the text we refer to these as *Pseudocalanus* sp. *Pseudocalanus* nauplii and copepodites were only identified to genus so abundances of adult females were used to determine the fraction of *P. minutus* copepodites in the samples by assuming equal species distribution of copepodites and adults.

Copepod abundances (individuals [ind.] m^{-2}) used for mortality estimates were calculated by integrating abundances from all samples through the water column taking into account the different sampling depth ranges of the different sampling hauls.

Copepod mortality rates. Mortality rates of discrete copepodite stages of *Calanus hyperboreus*, *C. glacialis*, *C. finmarchicus*, *Pseudocalanus* sp. and *Oithona similis* as well as nauplii of *Pseudocalanus* sp. and *O. similis* (average of all stages) were calculated from vertical life tables (Aksnes & Ohman 1996). This method is based on abundances of the different stages at a single sampling event and knowledge on the temporal duration of these stages. It is therefore independent of variations of abundances from one sampling event to the next and, hence, gives instantaneous mortality rates. We based our estimations of stage duration on previous observa-
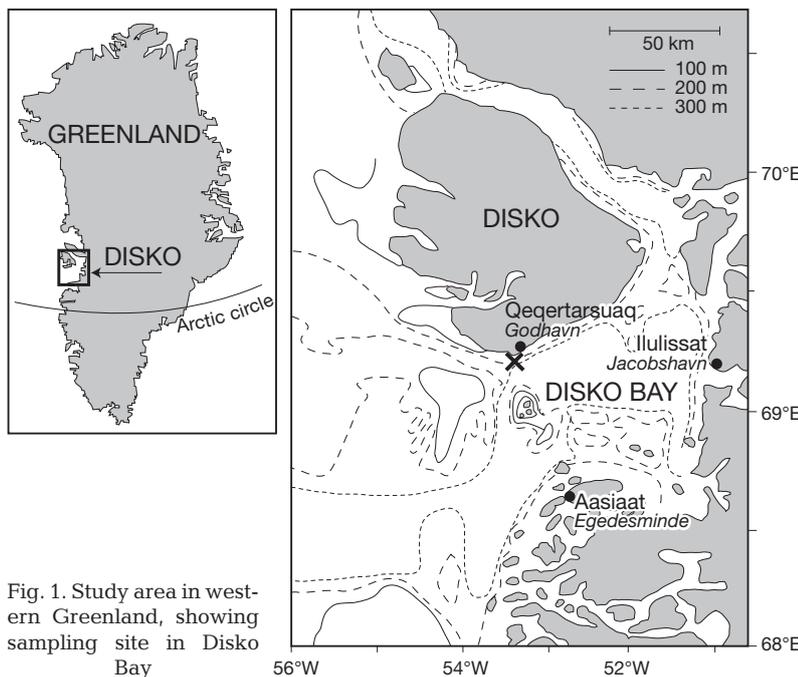

Fig. 1. Study area in western Greenland, showing sampling site in Disko Bay

Table 1. *Calanus* spp. Size ranges (mm) used for speciation of copepodites

Stage	*C. finmarchicus*	*C. glacialis*	*C. hyperboreus*
CI	<0.75	0.75–1.0	>1.0
CII	<1.1	1.1–1.4	>1.4
CIII	<1.6	1.6–2.1	>2.1
CIV	<2.2	2.2–3.0	>3.0
CV	<2.9	2.9–3.9	>3.9
Adult females	<3.2	3.2–4.5	>4.5

tions that stage duration depends strongly on temperature and not so much on food availability (Corkett & McLaren 1978, Vidal 1980, Corkett et al. 1986, Huntley & Lopez 1992, Campbell et al. 2001). Stage duration times for *C. finmarchicus*, *Pseudocalanus* sp. and *O. similis* were estimated using Belehradek's equation, $D = a(T+\alpha)^b$, where D is stage duration time in days and T is temperature (°C). The factor 'a' is a stage specific constant whereas b and α are species-specific constants. All 3 constants were adopted from the literature (Table 2). Mortality rates (m_i) of nauplii (mean of all stages) and copepodite stages I to IV were calculated iteratively from the formula (Aksnes & Ohman 1996):

$$\frac{A_i}{A_{i+1}} = \frac{e^{(m_i D_i)-1}}{1-e^{-m_i D_{i+1}}}$$

where A_i is abundance of the developmental stage i, A_{i+1} is the abundance of the next stage ($i+1$), m_i is instantaneous mortality rate of stage i (d^{-1}), and D followed by subscripts are stage durations of copepodite stages i and $i+1$. Since the stage duration of adults is infinite, mortality rates of copepodite stage V were calculated as:

$$m_5 = \frac{\ln\left(\frac{A_5}{A_{adult}}\right)+1}{D_5}$$

At present, the Belehradek equation is not parameterized for all stages of *Calanus glacialis* and *C. hyperboreus* (Corkett et al. 1986, Arnkværn et al. 2005), and to obtain temperature functions for stage development rate in these species, we calculated the rate of the Belehradek temperature functions based on the similar rates of stage development in *C. finmarchicus* (Arnkværn et al. 2005) as:

$$\varepsilon(T) = \frac{D_x}{D_f}$$

In this equation, D_x is the stage duration of either *Calanus glacialis* or *C. hyperboreus* and D_f is the corresponding stage duration for *C. finmarchicus* (Table 3). Nauplii were only identified to genus, so mortality

Table 2. *Calanus finmarchicus*, *Pseudocalanus* sp. and *Oithona similis*. Stage duration equations used in the calculation of mortality rates. D is stage duration in days, a is a stage specific factor, and T is temperature (°C). $D(T)$ shows stage duration times at the average ambient temperature, which were used to calculate mortality rates

C. finmarchicus: $D = a(T+9.11)^{-2.05}$
(calculated from Campbell et al. 2001)

Stage	a	$D(T)$
CI	966	9.3
CII	1137	11.0
CIII	1428	13.3
CIV	2166	19.0
CV	4083	34.5

Pseudocalanus sp.: $D = a(T+11.45)^{-2.05}$
(Eiane & Ohman 2004)

Stage	a	$D(T)$
N	9224	58.7
CI	2055	12.8
CII	2151	13.4
CIII	1701	10.6
CIV	1542	9.6
CV	2776	17.3

O. similis: $D = a(T+5)^{-2.05}$
(Sabatini & Kiørboe 1994, Eiane & Ohman 2004)

Stage	a	$D(T)$
N	4704	142.8
CI	604	18.3
CII	743	22.6
CIII	790	24.0
CIV	836	25.4
CV	790	24.0

Table 3. *Calanus hyperboreus* and *C. glacialis*. Stage duration used in the calculation of mortality rates. $D(T)$ shows stage duration times at the average ambient temperature, which were used to calculate mortality rates. See text for calculations

	Stage	$D(T)$
C. hyperboreus	CI	13.3
	CII	15.0
	CIII	16.5
	CIV	14.4
	CV	32.5
C. glacialis	CI	11.9
	CII	13.2
	CIII	11.5
	CIV	25.9
	CV	28.9

rates of *Calanus* nauplii were not calculated. The Belehradek equation is not parameterized for *Pseudocalanus acuspes* so we used available stage developmental times for *P. elongatus* for the calculations of mortality rates of *Pseudocalanus* sp.

Mortality rates were calculated at each sampling event and average mortality rates were calculated for the entire sampling period to ensure reliable estimates. Furthermore, mortality rates were only calculated for samples containing more than 16 individuals of the species and stage of interest. Therefore, a lack of data exists for certain stages.

A prerequisite of the vertical life table method is the absence of stage specific cohorts. Cohorts will reveal themselves as progressions in abundances of specific stages and, hence, gradual shifts in calculated mortality rates through time. We therefore applied linear regressions to mortality rates versus time to test for slopes significantly different from zero.

RESULTS

A distinct sub-surface layer of low temperature water between 25 and 50 m was present in the beginning of the sampling period (Fig. 2). As surface temperatures increased through June, this layer became less pronounced towards the end of the period. Between June 10 and 11 the temperature of the surface water (0 to 20 m) increased by approximately 2°C. It seems that a body of water with somewhat higher surface temperature was advected into the area of the sampling station possibly in connection with high winds observed during the previous days. In mid-June the surface water was heated by increased insolation and from June 11 onward a strong stratification of the upper 20 m appeared.

Of the 5 copepod species that dominated the epipelagic zooplankton community *Calanus hyperboreus* contributed 37% of the biomass and *C. glacialis* and *C. finmarchicus* each contributed 24%. *Pseudocalanus* sp. contributed 4% when present and *Oithona similis* 1%. *Pseudocalanus* sp. were only caught in the period before the hydrographic change during June 10. After this only *P. minutus* were caught. *O. similis* contributed 96% and *O. atlantica* 4% of *Oithona* adults; we therefore assumed that *Oithona* nauplii and copepodites belonged entirely to *O. similis*.

All 5 species were found at highest abundances in the upper 100 m and the depth distributions of the different developmental stages did not differ considerably within or among species. For the calculation of the mean temperature at which the copepods developed, we therefore calculated one common centre of mass having a depth of 48 m for all 5 species. The water temperature at this depth increased from 0.1 to 0.7°C during the sampling period and the durations of developmental stages were adjusted accordingly. No diurnal
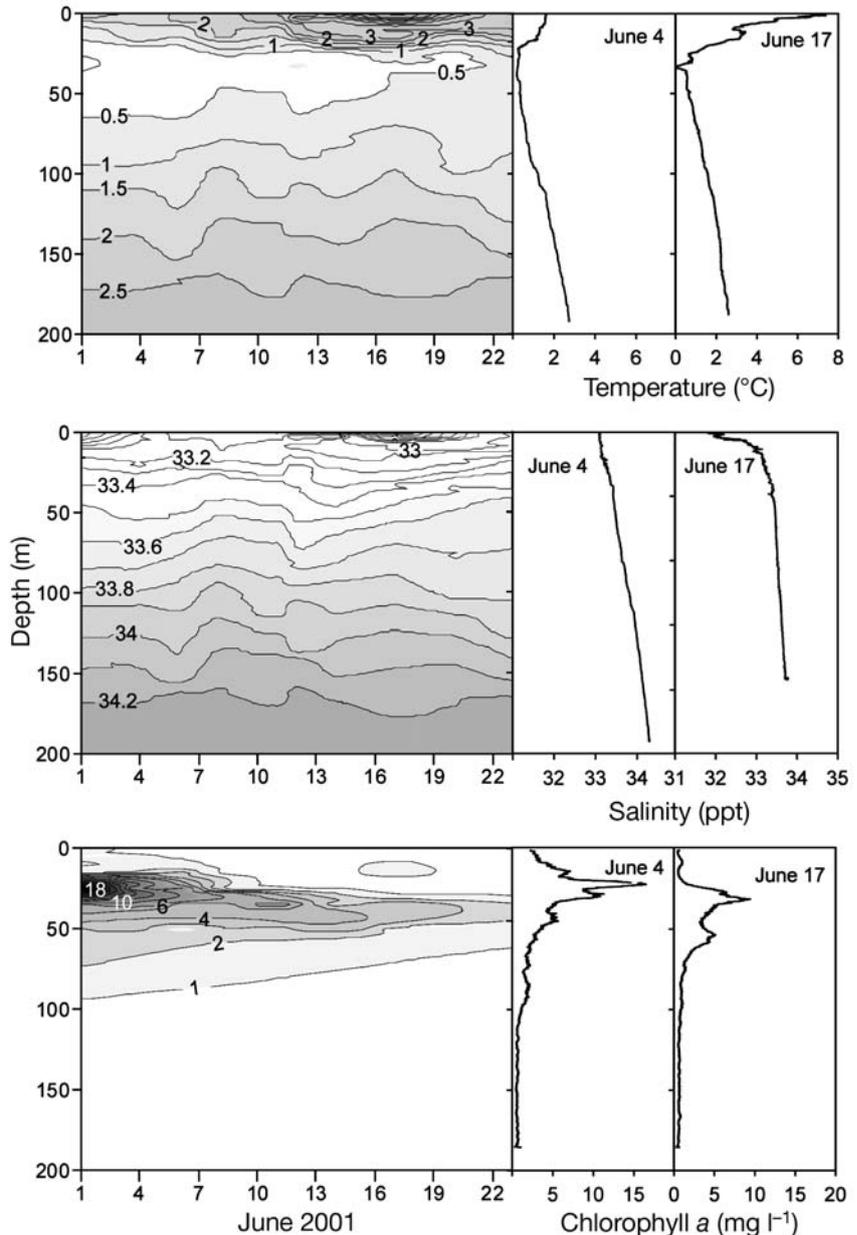

Fig. 2. Temperature, salinity and chl *a* concentration from CTD casts 0 to 200 m during the sampling period. Examples from June 4 and June 17 of vertical profiles representing 2 dominating hydrographical situations are shown on the right. Data are from Thor et al. (2005)

vertical migration was observed (Thor et al. 2005), so the copepods did not experience any daily temperature variations.

The stage distribution was not uniform in any of the 5 copepod species and we observed relatively higher abundances of distinct developmental stages (Fig. 3). Nevertheless, we observed erroneous progressions of calculated mortality rates only in *Calanus hyperboreus* CIII and CV, *C. glacialis* CI, and *Pseudocalanus* sp. CIII (linear regression of mortality rates versus time: p < 0.05).

Overall mortality rates among all 5 species varied between 0 and 0.18 d^{-1} (Fig. 4). Mortality rates were highest in *Calanus finmarchicus* and *C. glacialis* copepodite stages I to III and *Pseudocalanus* sp. CIII and CIV copepodites. They remained comparatively low in all stages of *Oithona similis*, and were highest for CI copepodites. Superimposing mortality rates of all stages and species on prosome lengths revealed a clear peak in mortality rates at 1.3 mm prosome length, which fitted a prey size dependent functional response of predation [Regression: $m = (372/L)e^{-1298/L}$, $r^2 = 0.64$, where m is instantaneous mortality rate (d^{-1}) and L is prosome length (μm), $F_{1,173} = 304$, p < 0.001] (Fig. 5). Outside this peak mortality rates were below 0.08 d^{-1} for all species and stages.

Until June 10 *Pseudocalanus* sp. contributed between 66 and 100% and *P. minutus* between 0 and 44% of the adult population of *Pseudocalanus*. We assume this also applied to the copepodites. The relatively large contribution of *P. minutus* could bias the mortality rate estimates, but a sensitivity test showed this to be a minor problem. In this test the abundances of adjacent developmental stages were allowed to vary between the possible extremes and the resulting mortality rates were calculated. This introduced changes in calculated mortality rates below 30%. Since the Belehradek equation is not parameterized for *P. minutus* mortality rates could not be calculated for this species.

DISCUSSION

Phytoplankton production is high in June on the west coast of Greenland (Nielsen & Hansen 1995) and in 2001 we observed maximum phytoplankton concentrations corresponding to 20 μg chl *a* l^{-1}. The high phytoplankton concentrations fuelled significant egg production rates of *Calanus finmarchicus* and *C. glacialis* (Thor et al. 2005) and under these conditions mortality due to starvation was not likely. Still, we found comparatively high mortality rates in Disko Bay during this period.

Interestingly, mortality rates showed a significant peak at copepod prosome lengths around 1.3 mm, which fitted a prey size dependent functional response
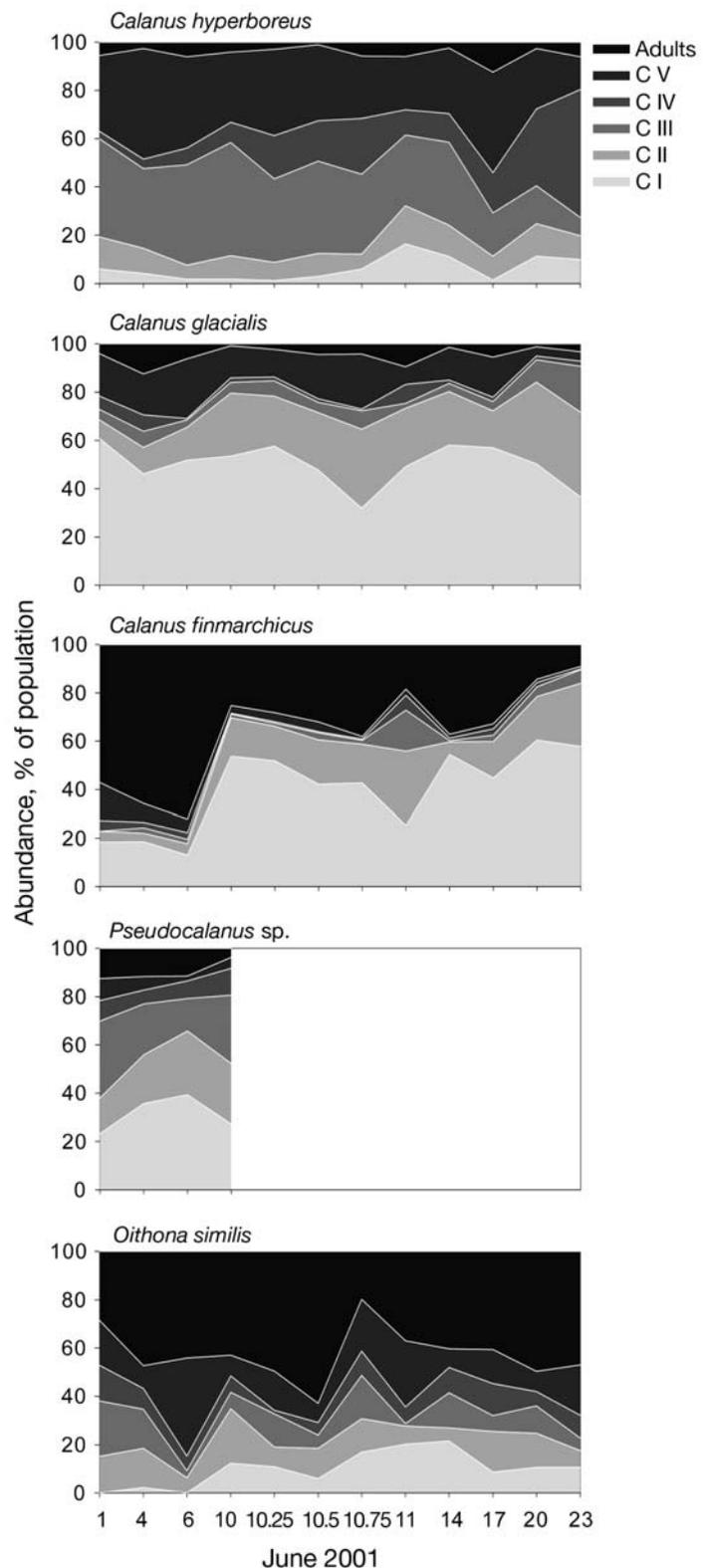

Fig. 3. Fractional mean abundances of all copepodite (CI to CV) and adult stages of copepods from 0 to 50 m during the sampling period. The day/night sampling period is denoted by decimals during June 10
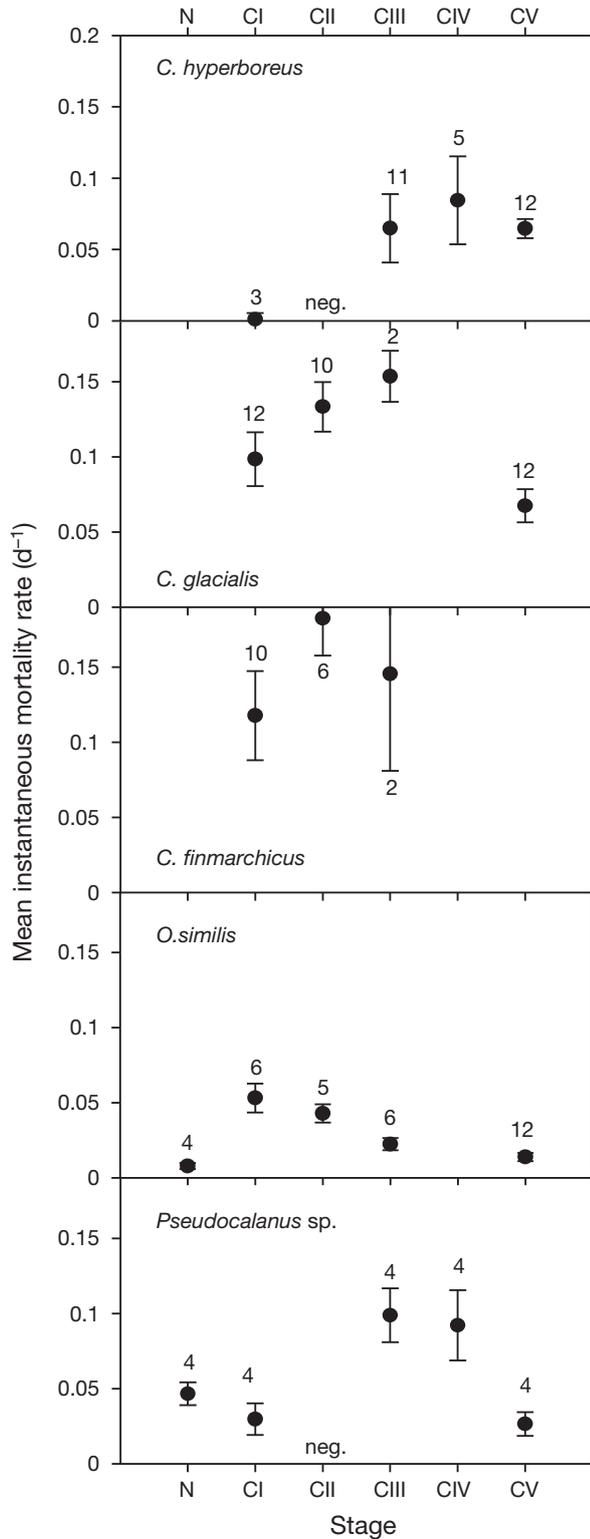
Fig. 4. Instantaneous mortality rates of *Calanus hyperboreus*, *C. glacialis*, *C. finmarchicus*, *Pseudocalanus* sp. and *Oithona similis*. Values are means ± SD; numbers at symbols denote number of samples used (samples with >16 individuals per sample) and neg. denotes negative values (see discussion in text). N = nauplii, CI–CV = copepodite stages I through V
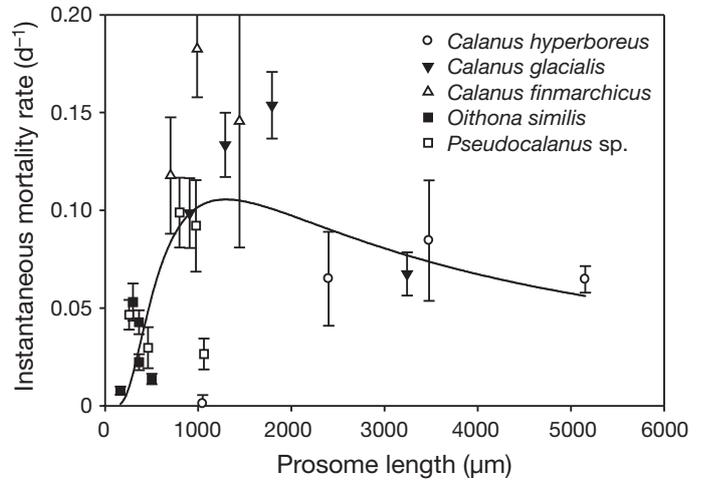

Fig. 5. Mean instantaneous mortality rates of all species and stages versus prosome lengths. Regression is $m = (372/L)e^{-1298/L}$, $r^2 = 0.64$, where m is instantaneous mortality rate (d^{-1}) and L is prosome length (µm)

of predation. In the 3 *Calanus* species the mortality rates were high in the CI to CIII stages, with maximum rates of 0.18 d^{-1}. This is higher than for *C. finmarchicus* copepodites at lower latitudes in the Atlantic Ocean (Ohman et al. 2004) and also higher than for copepodites of *C. hyperboreus*, *C. glacialis* and *C. finmarchicus* from another Arctic fjord on Svalbard, Norway (Arnkværn et al. 2005). Similarly, mortality rates of *Pseudocalanus* sp. and *Oithona similis* were higher than in copepods from these genera in the North Sea (Eiane & Ohman 2004). In general it seems that the Disko Bay environment is conducive to high mortality rates in epipelagic copepods. *Pseudocalanus* sp. showed a similar peaked mortality, with a maximum at stage CIII to CIV. These stages are similar in size to *C. glacialis*, *C. finmarchicus* CII and *C. hyperboreus* CI, so the mortalities of *Pseudocalanus* sp. fitted the same size related pattern as for the *Calanus* species. Accordingly, the vulnerability to attack by predators such as the carnivorous copepod *Euchaeta elongata*, shows an identical size dependency (Greene & Landry 1985). Previous predictions suggest that predation may account for most of the total mortality in pelagic copepods (Hirst & Kiørboe 2002) and the peaked mortalities in the present study do indeed suggest that the high mortality rates may have been inflicted mainly by predation (Greene & Landry 1985, Caparroy et al. 2000). Regardless of the predictions of Greene & Landry (1985) and Hirst & Kiørboe (2002), observations with high mortalities only in nauplii have until now dominated studies of pelagic copepods (Ohman 1986, Eiane et al. 2002, Eiane & Ohman 2004, Ohman et al. 2004) and peaked mortalities have only been observed on 2

different occasions previously. As in Disko Bay, mortality rates of *C. finmarchicus* peaked in early copepodites on Georges Bank, northwest Atlantic Ocean (Ohman et al. 2004), whereas *P. newmani* showed a bimodal pattern with peaks at N to CI and CV in Puget Sound, northeast Pacific Ocean (Ohman & Wood 1996). In these studies it was argued that peaks at CI in *C. finmarchicus* and CV in *P. newmani* arose from increased susceptibility of larger size stages to attack from predators such as large carnivorous copepods.

Variations in mortality among different species and stages of different sizes may arise either from divergent patterns of predator avoidance among prey species, or simply from the ability of predators to detect and catch prey most efficiently within a certain size range. The predation impact of mechanosensoric predators, like copepods and chaetognaths, depends on the hydromechanical signal from swimming prey. Likewise, visual predators such as fish, fish larvae and amphipods detect prey by their movements and when swimming speed increases so does the susceptibility to attack by predators (Saito & Kiørboe 2001). On the other hand, the ability to escape predation increases with size (Kiørboe et al. 1999) so the peaked mortality rates can be explained by shifting ratios of attack susceptibility and escape ability with copepod size, leading to a peaked prey size dependent functional response (Caparroy et al. 2000). The ascending left leg of this functional response can thereby be explained by increasing attack susceptibility with size. This explains the low mortality rates of *Oithona similis*. Due to their small size and quiescent swimming behaviour, these copepodites may not elicit attack responses and, thus, avoid predation altogether (Saito & Kiørboe 2001). On the other hand, the descending right leg of the functional response can be explained by increasing escape success by the larger individuals such as the later stage *Calanus hyperboreus* and *C. glacialis* (Caparroy et al. 2000).

Despite the significant peak, there was considerable scatter in mortality rates of copepods at 1 to 2 mm prosome lengths. *Pseudocalanus* sp. CV showed much lower mortality rates than all other similar sized copepods. Attack susceptibility is not entirely related to size, but also to specific swimming behaviour (Visser 2007). *Pseudocalanus* employ a slow moving or stationary feeding mode (Tiselius & Jonsson 1990) and may induce weaker attack responses than similar-sized copepods of other species. However, *Calanus* also exhibit slow movements during grazing (Turner et al. 1993) so the discrepancy between these 2 genera remains obscure.

Several invertebrate predators were present during the study period. Adults and copepodites of the large carnivorous copepod *Pareuchaeta norvegica* were present with an average abundance of 1600 ind. m^{-2}. Given their predominant size range in Disko Bay, *P. norvegica* preys on copepods between 0.8 and 1.4 mm and could be an important predator on early stage *Calanus* copepodites and late stage *Pseudocalanus* sp. copepodites. However, *P. norvegica* is a mesopelagic species and during the daytime samplings we found this species at highest densities deeper than 100 m. While studies at lower latitudes have shown considerable diurnal vertical migration by *P. norvegica* (Tiselius 1988), we did not observe any migration of most copepod species, including *P. norvegica*, in Disko Bay (Thor et al. 2005). This may be the normal behaviour of *P. norvegica* at high latitudes where it remains deep despite the larger prey potential in the epipelagic zone (Fleddum et al. 2001), and *P. norvegica* would not exert any significant predation on epipelagic copepods in Disko Bay. Chaetognaths are known to be important predators on copepod populations (Sullivan & Meise 1996) and showed average abundances of 570 ind. m^{-2} in Disko Bay, which is higher than, for instance, in the Norwegian Sea during the same season (Falkenhaug 1991). Chaetognaths were not identified to species, but earlier studies on Greenland west coast zooplankton showed that *Sagitta elegans* was the most abundant species (Smidt 1979). Arctic *S. elegans* range in size from 15 to 40 mm (Falkenhaug 1991) and given this size range, they could prey on copepods between 0.8 and 3.0 mm prosome length. Indeed, gut analyses have proved that *S. elegans* do prey on copepodites of *Pseudocalanus* spp. and *C. finmarchicus* (Ohman 1986, Tönnesson & Tiselius 2005). Several species of carnivorous amphipods, of which *Parathemisto abyssorum* is the most abundant, are present in western Greenland waters throughout the year (Smidt 1979). During the sampling period amphipods showed average abundances at 360 ind. m^{-2}. Like chaetognaths, amphipods showed considerable vertical migration and these potential predators increased in abundance to ~1000 ind. m^{-2} during night in the upper 50 m.

A distinct peak in mortality rate could also arise from predation by planktivorous fish and fish larvae. We did not sample fish or fish larvae, but earlier studies showed high abundances of larvae of several planktivorous fish species in the Disko Bay area (Munk et al. 2003). The prey size spectra for these fish larvae show a peak at 0.7 mm prosome length (Munk et al. 2003), whereas older fish would prefer larger prey. We therefore cautiously predict that fish larvae may exert an additional predation impact on epipelagic copepods in the bay.

Regardless of the predator, the size related mortalities of copepods in Disko Bay fit a prey size dependent functional response of predation, which implies high predation impact on the copepod community during

this early Arctic growth season. Mortality rates in the range found in the present study may have profound effects on the entire epipelagic copepod community structure. Paradoxically, if mortality rates of the magnitude found here in June prevailed through the summer season the copepod community would be unable to contribute to the overwintering stock. In this event, the epipelagic copepod community in Disko Bay would have to rely entirely on import of zooplankton from the outer shelf area. But even if the high mortality rates were confined to the early growth season the resulting diminished abundances will reverberate through the growth season with important implications for later population sizes. This is especially true for *Pseudocalanus* sp. and *Oithona similis*. While these species show peaks of reproduction during June at high latitudes their abundances are also at the annual lowest during this period (Lischka & Hagen 2005). High individual mortality during this particular period therefore will not only affect the abundances of the present generation, but also will be additionally detrimental to recruitment to the next generation and ultimately affect the overwintering stock. Clark et al. (2003) found that predatory regulation of copepod populations early in the growth season will actively generate inter-annual differences in the structure of the entire epipelagic copepod community throughout the following summer in the North Sea. Our results suggest that this kind of top-down control of the zooplankton community may also exist on the west coast of Greenland.

There are many assumptions to be met when using the vertical life tables approach. The method relies heavily on knowledge about the duration of specific developmental stages and as such is sensitive to changes in the developmental rate of the copepods. In general temperature alone is thought to explain more than 90 % of the variation in growth rates of marine copepods (Huntley & Lopez 1992). Accordingly, the Belehradek equation describes the stage duration time exclusively as a function of temperature. But growth of any heterotroph is, of course, additionally influenced by a range of environmental factors. Vidal (1980) and Hart (1990) previously argued that food availability and quality may be equally important for stage developmental rates. Based on experimental data Vidal (1980) suggested that not only temperature but also food concentrations may influence stage development of *Calanus pacificus* and *Pseudocalanus* sp. in nature. But the data from Vidal's (1980) study clearly showed that temperature has an overall effect on all developmental stages while the food concentration effects were restricted to the later developmental stages and to food concentrations below 150 µg C l^{-1}. In Disko Bay phytoplankton concentrations were almost always higher than 3 µg chl *a* l^{-1} (~150 µg C l^{-1}) during the

post-spring bloom period in 2001. Mesocosm studies have showed that while food availability may induce changes in body mass growth, the rate of stage development remains unaffected in *C. finmarchicus* on the Norwegian west coast (Hygum et al. 2000). Admittedly, laboratory feeding experiments on *P. elongatus* have shown differences in stage developmental rate with varying food quality, but these differences only occurred when feeding on monocultures of microalgae of exceptionally bad quality (Koski et al. 1998), a scenario not likely to occur in nature.

The mortality calculation may also be hampered by the ontogeny of *Calanus* spp. and *Pseudocalanus* sp. In contrast to *Oithona similis* these genera only develop one generation per year at high latitudes (Madsen et al. 2001, Lischka & Hagen 2005) and their hibernation may set in at different developmental stages. While this is believed to occur in stage CV in *C. hyperboreus*, it may stop as early as in stage CIII or CIV in *C. glacialis*, *C. finmarchicus* and *Pseudocalanus* sp. (see Table 60 in Mauchline 1998). The calculated stage duration times of these later stages are, therefore, relatively ambiguous, which calls for caution when incorporating the reported mortality rates of these stages into predictions about population development. However, while longer stage duration times would diminish mortality rates considerably in the larger stages, the peak in mortality rates at 1.3 mm prosome length would still prevail. Additionally, diminished mortality rates in the later stages would help to explain the paradox mentioned previously that the high mortality rates would impede the population's ability to contribute to the overwintering stock. Only the early copepodite stages would experience high mortality rates while those evolving into the later stages would have an increased chance of survival. The use of stage duration times for *P. elongatus* for the calculation of mortality rates of *Pseudocalanus* sp., which most likely were *P. acuspes*, is ambiguous. *P. elongatus* is found primarily at lower latitudes (Frost 1989) and as such would experience longer stage duration times than *P. acuspes* in Disko Bay. Therefore, the possible shorter stage duration time would increase the calculated mortality rates for *Pseudocalanus* sp.

A prerequisite of the vertical life table method is an absence of stage specific cohorts. We did observe non-uniform stage distributions in all 5 copepod species with relatively higher abundances of distinct stages. This could arise from the presence of cohorts, thus hampering the vertical life tables. We observe progressing mortality rates — a result of cohorts evolving through the sampling period — in *Calanus hyperboreus* CIII and CV, *C. glacialis* CI, and *Pseudocalanus* sp. CIII, which could, at least in part, explain the low and negative mortality rates in *C. hyperboreus* CI and

CII and *Pseudocalanus* sp. CII. Egg production rates were constantly high for *C. finmarchicus* and *C. glacialis* during the entire study period (Thor et al. 2005) and there is no reason why egg production rates should have been different during the preceding spring bloom period. Thus, new production of nauplii and, hence, later stages would be taking place continuously, which would obliterate development of cohorts in these 2 species during the study period.

LITERATURE CITED

Aksnes DL, Ohman MD (1996) A vertical life table approach to zooplankton mortality estimation. Limnol Oceanogr 41: 1461–1469

Arnkværn G, Daase M, Eiane K (2005) Dynamics of coexisting *Calanus finmarchicus*, *Calanus glacialis* and *Calanus hyperboreus* populations in a high-Arctic fjord. Polar Biol 28:528–538

Astthorsson OS, Gislason A (2003) Seasonal variations in abundance, development and vertical distribution of *Calanus finmarchicus*, *C. hyperboreus* and *C. glacialis* in the East Icelandic Current. J Plankton Res 25:843–854

Båmstedt U, Eilertsen HC, Tande KS, Slagstad D, Skjoldal HR (1991) Copepod grazing and its potential impact on the phytoplankton development in the Barents Sea. Polar Res 10:339–353

Campbell RG, Wagner MM, Teegarden GJ, Boudreau CA, Durbin EG (2001) Growth and development rates of the copepod *Calanus finmarchicus* reared in the laboratory. Mar Ecol Prog Ser 221:161–183

Caparroy P, Thygesen UH, Visser AW (2000) Modelling the attack success of planktonic predators: patterns and mechanisms of prey size selectivity. J Plankton Res 22: 1871–1900

Clark RA, Frid CLJ, Nicholas KR (2003) Long-term, predation-based control of a central-west North Sea zooplankton community. ICES J Mar Sci 60:187–197

Corkett CJ, McLaren IA (1978) Biology of *Pseudocalanus.* Adv Mar Biol 15:1–231

Corkett CJ, McLaren IA, Sevigny JM (1986) The rearing of the marine calanoid copepods *Calanus finmarchicus* (Gunnerus), *C. glacialis* Jaschnov, and *C. hyperboreus* Kroyer with comment on the equiproportional rule. Syllogeus 58:539–546

Eiane K, Ohman MD (2004) Stage-specific mortality of *Calanus finmarchicus*, *Pseudocalanus elongatus* and *Oithona similis* on Fladen Ground, North Sea, during a

spring bloom. Mar Ecol Prog Ser 268:183–193

Eiane K, Aksnes DL, Ohman MD, Wood S, Martinussen MD (2002) Stage specific mortality of *Calanus* spp. under different predation regimes. Limnol Oceanogr 47:636–645

Falkenhaug T (1991) Prey composition and feeding rate of *Sagitta elegans* var. *arctica* (Chaetognatha) in the Barents Sea in early summer. Polar Res 10:487–506

Fleddum A, Kaartvedt S, Ellertsen B (2001) Distribution and feeding of the carnivorous copepod *Paraeuchaeta norvegica* in habitats of shallow prey assemblages and midnight sun. Mar Biol 139:719–726

Frost BW (1989) A taxonomy of the marine calanoid copepod genus *Pseudocalanus.* Can J Zool 67:525–551

Greene CH, Landry MR (1985) Patterns of prey selection in the cruising calanoid predator *Euchaeta elongata.* Ecology 66:1408–1416

Hansen BW, Nielsen TG, 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

Hart RC (1990) Copepod post-embryonic durations: pattern, conformity, and predictability. The realities of isochronal and equiproportional development, and trends in the copepodid–naupliar duration ratio. Hydrobiologia 206: 175–206

Head EJH, Harris LR, Yashayaev I (2003) Distributions of *Calanus* spp. and other mesozooplankton in the Labrador Sea in relation to hydrography in spring and summer (1995–2000). Prog Oceanogr 59:1–30

Hirche HJ (1989) Egg production of the Arctic copepod *Calanus glacialis*: laboratory experiments. Mar Biol 103: 311–318

Hirche HJ, Meyer U, Niehoff B (1997) Egg production of *Calanus finmarchicus*: effect of temperature, food and season. Mar Biol 127:609–620

Hirst AG, Kiørboe T (2002) Mortality of marine planktonic copepods: global rates and patterns. Mar Ecol Prog Ser 230:195–209

Huntley ME, Lopez MDG (1992) Temperature-dependent production of marine copepods — a global synthesis. Am Nat 140:201–242

Hygum BH, Rey C, Hansen BW, Tande K (2000) Importance of food quantity to structural growth rate and neutral lipid reserves accumulated in *Calanus finmarchicus.* Mar Biol 136:1057–1073

Kiørboe T, Saiz E, Visser A (1999) Hydrodynamic signal perception in the copepod *Acartia tonsa.* Mar Ecol Prog Ser 179:97–111

Koski M, Klein Breteler WCM, Schogt N (1998) Effect of food quality on rate of growth and development of the pelagic copepod *Pseudocalanus elongatus* (Copepoda, Calanoida). Mar Ecol Prog Ser 170:169–187

Levinsen H, Nielsen TG, Hansen BW (1999) Plankton community structure and carbon cycling on the western coast of Greenland during the stratified summer situation. II. Heterotrophic dinoflagellates and ciliates. Aquat Microb Ecol 16:217–232

Lischka S, Hagen W (2005) Life histories of the copepods *Pseudocalanus minutus*, *P. acuspes* (Calanoida) and *Oithona similis* (Cyclopoida) in the Arctic Kongsfjorden (Svalbard). Polar Biol 28:910–921

Madsen SD, Nielsen TG, Hansen BW (2001) Annual population development and production by *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* in Disko Bay, western Greenland. Mar Biol 139:75–93

Mauchline J (1998) The biology of calanoid copepods. Academic Press, San Diego, CA

Munk P, Hansen BW, Nielsen TG, Thomsen HA (2003) Changes in plankton and fish larvae communities across hydrographic fronts off West Greenland. J Plankton Res 25:815–830

Niehoff B, Madsen SD, Hansen BW, Nielsen TG (2002) Reproductive cycles of three dominant *Calanus* species in Disko Bay, West Greenland. Mar Biol 140:567–576

Nielsen TG, 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 TG, Møller EF, Satapoomin S, Ringuette M, Hopcroft RR (2002) Egg hatching rate of the cyclopoid copepod *Oithona similis* in arctic and temperate waters. Mar Ecol Prog Ser 236:301–306

Ohman MD (1986) Predator-limited population growth of the copepod *Pseudocalanus* sp. J Plankton Res 8:673–713

Ohman MD, Wood SN (1996) Mortality estimation for planktonic copepods: *Pseudocalanus newmani* in a temperate fjord. Limnol Oceanogr 41:126–135

Ohman MD, Eiane K, Durbin EG, Runge JA, Hirche HJ (2004) A comparative study of *Calanus finmarchicus* mortality patterns at five different localities in the North Atlantic. ICES J Mar Sci 61:687–697

Sabatini M, Kiørboe T (1994) Egg production, growth and development of the cyclopoid copepod *Oithona similis.* J Plankton Res 16:1329–1351

Saito H, Kiørboe T (2001) Feeding rates in the chaetognath *Sagitta elegans*: effects of prey size, prey swimming behaviour and small-scale turbulence. J Plankton Res 23:1385–1398

Smidt ELB (1979) Annual cycles of primary production and of zooplankton at SW Greenland. Greenland Biosci 1:1–52

Sullivan BK, Meise CJ (1996) Invertebrate predators of zooplankton on Georges Bank, 1977–1987. Deep-Sea Res II 43:1503–1519

Thor P, Nielsen TG, Tiselius P, Juul-Pedersen T and others (2005) Post spring bloom community structure of pelagic copepods in the Disko Bay, Western Greenland. J Plankton Res 27:341–356

Tiselius P (1988) Effects of diurnal feeding rhythms, species composition and vertical migration on the grazing impact of calanoid copepods in the Skagerrak and Kattegat (Scandinavia). Ophelia 28:215–230

Tiselius P, Jonsson PR (1990) Foraging behavior of six calanoid copepods: observations and hydrodynamic analysis. Mar Ecol Prog Ser 66:23–33

Tönnesson K, Tiselius P (2005) Diet of the chaetognaths *Sagitta setosa* and *S. elegans* in relation to prey abundance and vertical distribution. Mar Ecol Prog Ser 289: 177–190

Turner JT, Tester PA, Strickler JR (1993) Zooplankton feeding ecology: a cinematographic study of animal-to-animal variability in the feeding behavior of *Calanus finmarchicus.* Limnol Oceanogr 38:255–264

Turner JT, Levinsen H, Nielsen TG, Hansen BW (2001) Zooplankton feeding ecology: grazing on phytoplankton and predation on protozoans by copepod and barnacle nauplii in Disko Bay, West Greenland. Mar Ecol Prog Ser 221: 209–219

Vidal J (1980) Physioecology of zooplankton. II. Effects of phytoplankton concentration, temperature, and body size on the development and moulting rates of *Calanus pacificus* and *Pseudocalanus* sp. Mar Biol 56:135–146

Visser AW (2007) Motility of zooplankton: fitness, foraging and predation. J Plankton Res 29:447–461