Seasonal mortality rates of *Oithona similis* (Cyclopoida) in a large Arctic fjord

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Abstract

Instantaneous mortality rates of the common planktonic copepod *Oithona similis* were investigated for the first time in Kola Bay, a region of the Barents Sea that is influenced by freshwater discharge. The rates were estimated in different seasons (December, May, September 2005 and July 2006). A vertical life table approach (VLT) was used to assess mortality. The total abundance of *O. similis* (copepodites IV and V, and adults) was highest in autumn and lowest in winter. The maximum mortality of *O. similis* for the stage pair copepodite IV—copepodite V (0.005 ± 0.001 day⁻¹) occurred in December 2005, while the highest mortality rates for the pairs copepodite VM—adult male (0.453 ± 0.026 day⁻¹) and copepodite VF—adult female (0.228 ± 0.006 day⁻¹) occurred in summer 2006. Simple regression analyses showed that the total abundance of each stage and the mortality rates were positively significantly correlated with water temperature. The mortality rates for the stage pairs copepodite VM—adult male and copepodite VF—adult female were positively significantly correlated with chlorophyll *a* concentration. The abundance and mortality rate of *O. similis* in each season was determined by life cycle factors, and possibly by the dynamics of its food resources and potential predators.

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1. Introduction

Zooplankton are one of the most important components of the marine pelagic ecosystem, where they play a key role in carbon flow processes (Wassmann et al., 2006), consuming primary production and serving as prey for higher trophic levels. Copepods dominate zooplankton communities in Arctic and temperate seas (Raymont, 1983). In the Barents Sea, large copepod species (including *Calanus finmarchicus*, *Calanus glacialis*, *Calanus hyperboreus*, and *Metridia longa*) dominate in terms of the total mesozooplankton biomass (Wassmann et al., 2006), while the small cyclopoid *Oithona similis* Claus 1866 dominates in terms of the total abundance (Dvoretskii, 2007). The former group is the main food source for planktivorous fishes and ichthyoplankton (Pedersen and Fossheim, 2008). *Oithona* spp. are consumed by carnivorous zooplankters as well as early stage larvae of commercial fishes (Raymont, 1983). Thus, *O. similis* is of great significance in the productive food webs of the Barents Sea (Dvoretsky and Dvoretsky, 2009a, 2009c).

Most studies of zooplankton in the Barents Sea have focused on spatial distribution, temporal dynamics, and the life histories of large calanoid species (Dvoretsky, 2007).
2011; Melle and Skjoldal, 1998). Small copepods were often not considered because relatively coarse nets were used for sampling. However, many aspects of the biology of *O. similis* in Arctic waters have been investigated, including its population structure, variability in reproductive parameters, morphological plasticity, and life cycle (Dvoretskii, 2007; Dvoretsky and Dvoretsky, 2009a, 2009b, 2009c; Lischka and Hagen, 2005; Madsen et al., 2008). However, some demographic features of this species are less well known or have not been studied. The mortality rate is a key characteristic reflecting the population dynamics of a species (Aksnes, 1996), and can be used to calculate the production rate of zooplankters (Aksnes et al., 1997), facilitating better understanding of their life histories and habitat choices (Eiane and Ohman, 2004). There are no previous estimates of the mortality of copepods in the Barents Sea, and the mortality rates of marine copepods in polar waters have received little attention. The first estimations of this characteristic involved large common calanoid copepods (Matthews et al., 1978; Ohman and Hirche, 2001), and there have been only three publications where mortality rates of *O. similis* have been reported (Eiane and Ohman, 2004; Hirst and Ward, 2008; Thor et al., 2008).

The main aims of this study were to: (1) calculate the seasonal mortality rate of the most numerous small copepod (*O. similis*) in a large fjord of the Barents Sea; and (2) assess whether there were any correlations between mortality rates and environmental variables.

### 2. Materials and methods

Kola Bay is typical of the fjords in the Barents Sea. The bay is influenced by water from the Atlantic Ocean, and the hydrodynamics of the fjord are determined by tidal currents and winds. The inner part of the bay is influenced by freshwater discharge and can be considered an estuarine zone (Matishev, 2009; for details, see Dvoretsky and Dvoretsky, 2009a). Water samples were collected during three surveys in the southern and central parts of Kola Bay (depth range 10–60 m) in spring–autumn 2005–2006, and at a fixed coastal station (depth 8 m) in winter 2005 (Table 1; Fig. 1). Integrated vertical tows were undertaken using a Juday net (mesh size 168 μm, mouth diameter 0.37 m). All samples were preserved by the addition of borax-buffered formalin (final concentration in a sample was 4%). Each sample was divided into 1/2 to 1/8 subsamples with a pipette splitter, depending on the zooplankton abundance. A total of 500–700 individuals of *O. similis* were removed from the subsamples for subsequent analyses. Identification of copepodite stages and adults was performed according to Shuvalov (1980), using a stereomicroscope MBS-10 (32–56 magnification). Because the mesh size was too coarse to quantitatively sample young copepodites (CI–CIII) (Gallienne and Robins, 2001), only the abundances of the older stages having a prosome length >400 μm were considered. The abundance of each stage was calculated per m$^3$.

Hydrographic measurements were conducted concomitantly with the zooplankton sampling. Vertical profiles of temperature and salinity were recorded using a SBE 19 plus SEACAT profiler. Data on the chlorophyll *a* concentration during the study period were obtained from Matishov (2009).

A vertical life table (VLT) approach was used to estimate instantaneous mortality rates across each pair of stages for each sampling event. The main assumption underlying the vertical approach is that daily recruitment to a particular stage should not display either an upward or a downward trend over a period of time corresponding to the duration of two consecutive developmental stages (Aksnes et al., 1997). To test this assumption, the dynamics of stage duration-corrected abundances of *O. similis* copepodite IV and copepodite V were analyzed. No trends were observed for the spring and autumn periods, but the abundance of each copepodite stage (males and females combined) increased during the winter period at stations 1, 4 and 5, and in the summer period at stations 1–7. In all other cases the VLT

### Table 1

<table>
<thead>
<tr>
<th>Season</th>
<th>Period</th>
<th>Sampling platform</th>
<th>Number of stations</th>
<th>Number of samples</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter</td>
<td>22–23 Dec 2005</td>
<td>Daily station</td>
<td>1</td>
<td>10</td>
</tr>
<tr>
<td>Spring</td>
<td>27 May 2005</td>
<td>E/V Belek</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>Summer</td>
<td>14–15 July 2006</td>
<td>Cruise of R/V GSS–440</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>Autumn</td>
<td>12–16 Sep 2005</td>
<td>Cruise of R/V GSS–440</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td></td>
<td><strong>24</strong></td>
<td><strong>36</strong></td>
</tr>
</tbody>
</table>
The instantaneous mortality rate for the pair copepodite IV—copepodite V was calculated (JMP 5.1.1 software) using an iteration procedure (Mullin and Brooks, 1970) according to equation (1):

\[
e^{\beta D_{\text{CV}}} - 1 = \frac{N_{\text{CIV}}}{N_{\text{CV}}}.
\]

where \( \beta \) is the mortality rate, \( N_{\text{CIV}} \) and \( N_{\text{CV}} \) are the abundances (individuals m\(^{-3}\)) of copepodite stages IV and V, respectively, and \( D_{\text{CIV}} \) and \( D_{\text{CV}} \) are the durations of copepodite stages IV and V, respectively.

The development time (D, days) was calculated from equation (2):

\[
D = a(T + a)^{-0.05}
\]

where \( a \) was assumed to be 7.6998 (Nielsen et al., 2002). To obtain the \( a \)-coefficients for CIV and CV, the equation of Sabatini and Kjørboe (1994) (their fig. 7a) was used. The values were derived from stage-specific development times at 15 °C. The CIV and CV stage durations at other temperatures were expressed according to equations (3) and (4), respectively (Hirst and Ward, 2008):

\[
D_{\text{CIV}} = 987 \cdot (T + 7.6998)^{-2.05}\]

\[
D_{\text{CV}} = 1129 \cdot (T + 7.6998)^{-2.05}\]

where \( T \) is the mean water temperature (°C) in the sampled layer.

The instantaneous mortality rates for the stage pairs copepodite VM—adult male and CVF—adult female were estimated according to equation (5) (Aksnes and Ohman, 1996):

\[
\beta = \frac{\ln \left( \frac{N_{\text{CV}}}{N_{\text{CIV}}} + 1 \right)}{D_{\text{CV}}}
\]

where \( N_{\text{CVI}} \) is the total abundance of either males or females of \( O. \) similis (individuals m\(^{-3}\)). It was assumed
that adults do not die of old age (Shuvalov, 1980), but instead are subject to a constant rate of mortality, and that the mortality rate is constant within each stage. According to Shuvalov (1980), the genders of stage V *O. similis* copepodites are not distinguishable; sexual differences become apparent only after they molt to the adult stage. Therefore, the actual sex ratio for CV remains uncertain, and a balanced sex ratio (1:1) (Hirst and Ward, 2008) was assumed, where the number of CV <sub>males</sub> = the number of CV <sub>females</sub> = 0.5*total number of CV.

All mean values are presented with the standard error (±SE). The seasonal differences in hydrological parameters, abundance, and mean mortality rates of *O. similis* were tested using the non-parametric Kruskal–Wallis tests (one-way ANOVA on ranks) because the present data were non-homogenous (Levene’s test, α = 0.05), even following log-transformation. Simple linear regression analyses were applied to reveal relationships between physical variables (mean temperature, salinity, and chlorophyll a concentration in the sampling layer) and the total abundance of late stage *O. similis* (CIV–CVI) and the mortality rates for the stage pairs copepodite IV–copepodite V and copepodite V–adults.

### 3. Results

The mean values of temperature and salinity for the integrated water column (0 m–bottom) are presented in Table 2. In winter 2005 the mean temperature varied from 1.9 to 2.0 °C. The highest values were recorded in summer 2006 (8.7–10.0 °C). In autumn 2005 the temperature ranged from 7.1 to 7.6 °C. The minimum salinity values occurred in summer (27.21–29.21 psu), and the maximum values occurred in winter (31.24–32.96 psu). In the surface layer of the inner part of Kola Bay during winter the concentration of chlorophyll a varied from 0.01 to 0.04 mg m<sup>–3</sup>. In summer (July 2006) the chlorophyll a concentration (1.70–2.77 mg m<sup>–3</sup>) was considerably higher than in spring (2005; 0.13–0.38 mg m<sup>–3</sup>). During autumn the concentration of chlorophyll a decreased considerably, to 0.09–0.28 mg m<sup>–3</sup> (Matishov, 2009) (Table 2). Thus, the four periods considered in calculations of mortality rates differed in terms of environmental variables (Kruskal–Wallis test, *p* < 0.001).

During winter 2005 the total abundance of *O. similis* varied from 60 to 216 ind. m<sup>–3</sup>, while in spring it ranged from 76 to 165 ind. m<sup>–3</sup> (Table 2). The total abundance of copepodites IV–VI was highest in summer (range 591–1028 ind. m<sup>–3</sup>), while the highest number of *O. similis* occurred in autumn (range 490–7175 ind. m<sup>–3</sup>; Table 2). Analysis based on the Kruskal–Wallis tests showed that there were significant differences in the number of *O. similis* stages among all seasons (*p* < 0.001 for all cases).

During the study the instantaneous mortality rate for the *O. similis* stage pair copepodite IV–copepodite V varied from 0.001 to 0.007 day<sup>–1</sup> (Table 2). The minimum mortality rate for this stage pair occurred in autumn, while the maximum was found in winter. One-way ANOVA on ranks revealed that there were significant differences among seasons for this parameter (*p* < 0.001).

The instantaneous mortality rate for the stage pair copepodite VM–females varied from 0.031 to 0.240 day<sup>–1</sup> (Table 2), and there was a peak of mortality in summer. Significant differences in this parameter were found among the seasons investigated (*p* < 0.001).

The highest mortality rate for the stage pair copepodite VF–males occurred in summer 2006, while the lowest occurred in spring 2005 (Table 2). One-way
ANOVA on ranks indicated that the four seasons differed significantly from each other ($p < 0.001$).

Table 3 shows the results of analyses relating the dependent population variables of *O. similis* to environmental variables. Simple regression analyses showed that the total abundance of each stage and mortality rates were significantly positively correlated with water temperature. This factor explained 32.8–73.6% of the total variation. Mortality rates in the stage pairs copepodite VM–adult male and copepodite VF–adult female were positively significantly correlated with chlorophyll $a$ concentration, which explained 28.8–38.0% of the total variation; the same pattern was found for abundances of adult stages (Table 3).

### 4. Discussion

In this study the mortality rate of *O. similis* in the Barents Sea was investigated for the first time. To estimate the sex-specific mortality rates in the pre-adult stage a 1:1 male:female ratio was assumed, as no data on the actual sex ratio at CV are available. Thus, the estimates are preliminary only. However, it has recently been reported that the proportion of male *Acartia clausi*, *Pseudodiaptomus marinus*, *C. finmarchicus*, *P. acutus*, *P. xiphias*, and *P. elongatus* is not significantly different from 0.5 (Hirst et al., 2010), and consequently the 1:1 sex ratio used in this study for estimating mortality of *O. similis* (especially, late copepodes) is a reasonable assumption.

The mean mortality rate for the *O. similis* pair copepodite V–females in the North Sea in spring 1976 was $0.003 \pm 0.031$ day$^{-1}$ (Eiane and Ohman, 2004), which is considerably lower than the rate determined in the present study. Thor et al. (2008) reported that the mortality rate for the pair copepodite V–adults reached 0.014 day$^{-1}$ in Disco Bay (western Greenland waters) in June 2001, which is significantly less than the rates found in the present study. In Kola Bay the mortality rates in *O. similis* were higher for adult stages, but for CIV and CV were lower than reported for Antarctic waters (Scotia Sea, spring 2006), where the mean mortality rates for the pairs copepodite IV–copepodite V, copepodite V–females, and copepodite V–males were 0.008, 0.018, and 0.110 day$^{-1}$, respectively (Hirst and Ward, 2008). The differences in *O. similis* mortality rates among Arctic (Disco Bay: Thor et al., 2008; Kola Bay: this study), Antarctic (Scotia Sea: Hirst and Ward, 2008), and temperate (North Sea: Eiane and Ohman, 2004) waters may be related to inter-annual differences in the structure of the pelagic communities present (from microplankton to ichthyoplankton), and differences in the hydrological conditions.

The clear decrease in abundance of *O. similis* in Kola Bay in late summer reported by Dworetzky and Dworetzky (2009a) suggested that mortality rates in this period are high, and the results of the present study support this suggestion. Several hypotheses can be proposed regarding factors controlling this pattern. It is evident that biotic factors affect mortality rates in marine copepods (Hirst and Kjørboe, 2002). An increase in mortality during summer may be associated with the feeding ecology of this species. *O. similis* is a typical omnivorous copepod that primarily consumes microzooplankton, although phytoplankton is known to be significant in the diet of *Oithona* species generally (Castellani et al., 2008). Previous studies (Druzkhov et al., 1997) indicate that the protozooplankton biomass in the coastal Barents Sea has a peak in late July–early August. There is a marked decrease in the abundance of ciliates that commences in mid-September, and this coincides with a decrease in the abundance *O. similis*. It is a common observation that increases in the abundance of a species...
are accompanied by an increase in mortality rates (Raymont, 1983). Therefore, high phytoplankton biomass may result in an increase in the abundance of protozooplankton, which are a food source for omnivorous copepods; this could lead to an increase in the abundance of *O. similis*. As a result, the mortality rate of *O. similis* increases during periods of high abundance because of intra-species competition and parasitism (Raymont, 1983).

In addition, an increase in phytoplankton biomass could indirectly affect *O. similis* mortality because an increase in the concentration of microalgae should lead to an increase in herbivorous zooplankters, which could stimulate an increase in the abundance of predators of copepods, including *O. similis*. Collection of potential predators of *O. similis* was beyond the scope of the present study, but previously published data (Dvoretsky and Yurko, 2009) for the period 2000–2006 indicate that the carnivorous copepod *Metridia* spp., the chaetognath *Parasagitta elegans*, hydromedusae, and ctenophores reached maximum abundances in July–September (as estimated from zooplankton samples collected using a Juday net of 168 μm mesh size). In other seasons the concentrations of potential predators of *O. similis* were 3–20 times lower (Dvoretsky and Yurko, 2009).

The increased mortality rates of *O. similis* adults in late summer may be related to the life cycle of the species in Kola Bay. The summer generation of *O. similis* appears in late June–early August (Dvoretsky and Dvoretsky, 2009a); it develops under high summer temperatures and has a short life cycle (2–3 months). Similarly, Shuvalov (1980) observed that the summer generation of *O. similis* in the coastal White Sea was characterized by rapid development and a short life span. In Kongsfjorden (Svalbard waters) *O. similis* has two generations per year (Lischka and Hagen, 2005). It is likely that the decreasing abundance of *O. similis* in late summer (Dvoretsky and Dvoretsky, 2009a) and the high mortality in July 2006 were associated with death of the summer generation.

The elevated mortality rates of *O. similis* in Kola Bay relative to other regions can also be explained by the hydrographic conditions in this area, particularly the salinity regime. Kola Bay is characterized by reduced salinity in the southern part (Matishov, 2009). *O. similis* is a true marine species, and its distribution may be limited by low salinity. This is consistent with the observation that in the central Baltic Sea *O. similis* tends to remain in the permanent halocline layer, and avoids waters of reduced salinity (Hansen et al., 2004). Similar findings of decreasing survival rates at lower salinities have been reported for other marine planktonic copepods (Jeffries, 1962; Lance, 1963). However, the regression analysis results in the present study did not support the hypothesis that salinity effects reduce *O. similis* survival rates. This may be explained by the location of the sampling stations. These are in the central and southern parts of Kola Bay where the mean salinity (ca. 30 psu) is considerably higher than in the inner part of the bay, where salinity can be <17–18 psu because of inflow from the Kola River (Matishov, 2009).

Another important factor affecting mortality in marine copepods is water temperature. It has been found that mortality rates in broadcast-spawning copepods increase as temperature increases (Hirst and Kiørboe, 2002). A similar relationship was found between mortality rate and water temperature in *O. similis* for all stage pairs investigated.

5. Conclusion

This study showed that the total abundance of *O. similis* in Kola Bay was highest in autumn and lowest in winter. The maximum mortality for the stage pair copepodite IV–copepodite V occurred in December 2005, while the highest mortality rates for the pairs copepodite VM–adult male and copepodite VF–adult female occurred in July 2006. These values are higher than the mortality estimates obtained in temperate, Arctic, and Antarctic waters. The total abundance of each stage and the mortality rates of *O. similis* in Kola Bay were positively significantly correlated with water temperature. The mortality rates of the stage pairs copepodite VM–adult male and copepodite VF–adult female were positively significantly correlated with chlorophyll *a* concentration. The abundance and mortality rates of *O. similis* in different seasons were determined by life cycle factors, and possibly by the dynamics of its food resources and potential predators. The seasons used in the analysis were not sequential, occurring over two years. However, the years 2003–2007 were a warm period with similar temperature regimes and food conditions, and consequently it is likely that the data provide an adequate representation of the seasonal cycle of *O. similis* mortality in Kola Bay.

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References


Castellani, C., Irigoien, X., Mayor, D.J., Harris, R.P., Wilson, D., Hirst, A.G., Bonnet, D., Conway, V.P., Kiørboe, T., 2010. Does and


Dvoretsky, V.G., Dvoretsky, A.G., 2009c. Spatial variations in


Lischka, S., Hagen, W., 2005. Life histories of the copepod Pseudocalanus minutus, P. acuspes (Calanoida) and Oithona similis (Cyclopoidea) in the Arctic Kongfjorden (Svalbard). Polar Biol. 28, 910–921.