Long-term seasonal and spatial patterns in mortality and survival of *Calanus finmarchicus* across the Atlantic Zone Monitoring Programme region, Northwest Atlantic

Stéphane Plourde, Pierre Pepin, and Erica J. H. Head


The vertical life table method was used to estimate stage-specific daily mortality rates and survival from 1999 to 2006 for *Calanus finmarchicus* sampled in the Canadian Atlantic Zone Monitoring Programme, which covers the Newfoundland–Labrador Shelf (NLS), Gulf of St Lawrence (GSL), and Scotian Shelf (SS). Stage-specific mortality rates and survival showed significant regional and seasonal differences, with the largest signal associated with variations in temperature. Density-dependent mortality, associated with the abundance of C6 females, was the main factor influencing mortality in the egg–C1 transition during the period of population growth in spring on the SS, and in summer in the GSL and on the NLS. In autumn, mortality in egg–C1 was positively related to temperature and negatively related to phytoplankton biomass, with particularly high mortality rates on the SS. The integration of our results into stage-specific recruitment rates from egg to C5 revealed that *C. finmarchicus* populations experience their greatest loss (mortality) during the egg–C1 transition. Loss during development to C1 was greater in the GSL than in the other regions during the period of population growth, resulting in lower recruitment success in the GSL. In autumn, *C. finmarchicus* showed low stage-specific daily recruitment rates on the SS at high temperatures, and low phytoplankton biomass compared with those in the GSL and on the NLS. Our findings reinforce the necessity of describing regional and seasonal patterns in mortality and survival to understand factors controlling the population dynamics of *C. finmarchicus*.

**Keywords:** *Calanus finmarchicus*, density-dependence, mortality, Northwest Atlantic, stage-dependence, survival, vertical life table.

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**Introduction**

The copepod *Calanus finmarchicus* is an important component of the zooplankton community inhabiting waters of the Subarctic North Atlantic (Longhurst, 1998; Helaoueet and Beaugrand, 2007). It dominates zooplankton biomass and abundance from winter until late summer in the Labrador Sea, on the continental shelf off Labrador and Newfoundland, in the Gulf of St Lawrence (GSL), on the Scotian Shelf (SS), and in the Gulf of Maine/Georges Bank region (Meise and O’Reilly, 1996; Head et al., 1999, 2003; Pepin et al., 2005). Because of its significant contribution to the zooplankton community, *C. finmarchicus* has been identified as a key species in ecosystems of the North Atlantic and has been the main target of several research programmes (Wiebe et al., 1996; Heath et al., 1999, 2008; Tande and Miller, 2000). It is therefore essential that we acquire basic knowledge of the processes regulating its population dynamics to achieve a good understanding of the overall dynamics of the ecosystems.

The population dynamics of zooplankton are controlled by a combination of bottom-up and top-down processes (Twombly et al., 2007). The role of temperature and food on reproduction, development, and growth (bottom-up) of *C. finmarchicus* in the Northwest Atlantic is well described (Plourde and Runge, 1993; Runge and Plourde, 1996; Campbell and Head, 2000; Campbell et al., 2001). Despite its obvious importance, knowledge of the role of mortality (top-down) in the control of its demography is rather limited, principally because of the difficulty in obtaining reliable mortality estimates. Until recently, the few studies describing the mortality of *C. finmarchicus* were confined to semi-enclosed systems such as fjords or based on relatively short time-series, because of the constraints of the method used (horizontal life table analysis, HLT; Wood, 1994; Ohman and Hirche, 2001; Eiane and Ohman, 2004). The development of the vertical life table (VLT) method has resulted in a robust approach which uses the abundance ratios of successive developmental stages rather than the variability in their absolute abundance over time (as in the HLT; Aksnes and Ohman, 1996). The VLT method allows the measurements of mortality rates on synoptic spatial surveys or during long time-series in more open marine habitats (Aksnes and Ohman, 1996). This approach has been applied to data collected during successive synoptic spatial surveys to describe the seasonal and spatial patterns in stage-specific mortality for *C. finmarchicus* on Georges Bank and in the Irminger Sea (Ohman et al., 2002, 2008; Heath et al., 2008) and for *Calanus pacificus* in the California Current (Ohman and Hsieh, 2008).
The VLT method has also been used with time-series data to describe the seasonal pattern in mortality for *Calanus helgolandicus* in the English Channel and for early stages of *C. finmarchicus* in the lower St Lawrence estuary (Hirst et al., 2007; Plourde et al., 2009). There are few studies, however, that cover a broad geographic range of a species distribution, and even fewer based on many years of observations. To our knowledge, only the Georges Bank example combined the spatial, seasonal, and multiyear data necessary to describe long-term patterns in mortality (Ohman et al., 2002, 2008).

The Atlantic Zone Monitoring Programme (AZMP), implemented by Fisheries and Oceans Canada since 1999, collects physical, chemical, and biological data on phytoplankton and zooplankton communities on the Newfoundland–Labrador Shelf (NLS), in the GSL, and on the SS (Therriault et al., 1998; Pepin et al., 2005). The AZMP monitors environmental variations on interannual and seasonal scales at a network of fixed stations by sampling approximately twice per month, and interannual fluctuations over large spatial scales by occupying a series of oceanographic sections that cover a region ranging from the Labrador Shelf in the north to the lower St Lawrence estuary in the west and to the southwestern SS in the south. The programme represents a unique opportunity to describe both large-scale and long-term average (climatological) patterns in *C. finmarchicus* over an area with a marked heterogeneity in environmental conditions and habitats.

For this study, we used the VLT approach to estimate stage-specific daily mortality for *C. finmarchicus* stages based on data collected routinely as part of the AZMP over an 8-year period (1999–2006). We aimed to describe the long-term average seasonal and spatial patterns in *C. finmarchicus* stage-specific daily mortality rate, survival, and stage-specific recruitment rate. We have tested the null hypothesis of seasonal and spatial homogeneity in stage-specific daily mortality rates in different regions (NLS, GSL, SS) covered by the programme. We also explored the relationships between mortality in the early stages and physical and biological environmental variables. Finally, we contrasted our results with those obtained with a similar approach in the other regions and discuss the conditions and assumptions of the VLT approach with respect to its application to extended datasets.

**Methods**

**Field sampling and laboratory analyses**

Samples were collected as part of the AZMP. In the programme, the aim has been to sample six fixed coastal stations approximately biweekly and 14 oceanographic sections seasonally in three areas: the NLS (four sections), the GSL (six or seven sections), and the SS (three or four sections; Figure 1). We report on data for the period 1999–2006 collected at the fixed sites off St John’s (ST27, 175 m), in the Anticosti Gyre (AG, 340 m) and Gaspé Current (GC, 180 m), and off Halifax (HL2, 150 m), and along all oceanographic sections. The actual sampling frequency at the fixed stations was not always as originally intended, so there were a few gaps of ~30 d at station HL2 (187 samples) and of 30–50 d at ST27 during winter (234 samples). As the frequency of collections was highly variable at AG and GC during the years 2004–2006, only data from 1999 to 2003 were included in our analysis (145 samples). Moreover, data from those two sites were combined because of the similarities in their seasonal cycles. Three surveys

**Figure 1.** Map of the AZMP fixed sites (filled circles) and sampling sites along oceanographic sections. Fixed sites are identified by short abbreviations (ST27, Station 27; AG, Anticosti Gyre; GC, Gaspé Current; SH, Shediac Valley; HL2, Halifax 2; P5, Prince 5). Sections are (1) Seal Island, (2) Bonavista Bay, (3) Flemish Cap, (4) Southeast Grand Banks, (5) Cabot Strait, (6) Bonne Bay, (7) St Lawrence Estuary, (8) Sept-Iles, (9) Anticosti, (10) Îles-de-la-Madeleine, (11) Central GSL, (12) Louisbourg, (13) Halifax, and (14) Browns Bank. Stations sampled during regional surveys are shown as diamonds (NLS), squares (SS), and triangles (GSL). Stations in the Cabot Strait (crosses) were sampled during surveys of the SS and the GSL. Depth intervals are shown using a grey scale.
on the NLS were carried out annually (April/May, July, and November/December) but the northernmost Seal Island section (section 1) was surveyed only in July, and the southeast Grand Banks section (section 4) was sampled only in April/May and November/December (Figure 1). In most years, two surveys of the sections in the GSL (June and November) and on the SS (April/May and October) were completed, with the Cabot Strait section (section 5) often being sampled during both the GSL and SS surveys (i.e. four times per year). All data collected on that section were considered as part of the GSL. No surveys were made in 1999 of the GSL and the NLS, and an additional survey of the GSL was carried out in April 2003. Oceanographic surveys yielded a total of 829 samples from the NLS, 584 from the GSL, of the GSL was carried out in April 2003. Oceanographic surveys yielded a total of 829 samples from the NLS, 584 from the GSL, and 479 from the SS.

At each station, a vertical profile of water-column properties was collected from the surface to the bottom using a rosette-mounted conductivity–temperature–depth (CTD) sensor. The CTD was lowered continuously at a targeted speed of 1 m s\(^{-1}\) to within 5 m of the seabed (or to 1000–2000 m off the continental shelf). Water samples for the determination of chlorophyll \(a\) concentrations were collected using Niskin bottles at a series of fixed depths, whereas the CTD was returning to the surface. Two 100-ml samples were drawn from each bottle and filtered by vacuum filtration onto 25-mm glassfibre filters. After filtration, the filters were put into separate scintillation vials containing 10 ml of 90% acetone and stored at \(-20^\circ\) C. Zooplankton samples were collected using 0.75 m ringnets fitted with a 202-μm mesh net towed vertically from 5 m above the seabed or to a maximum of 1000 m at stations deeper than 1000 m, at 1 m s\(^{-1}\). Once on deck, samples were preserved in 2% formaldehyde for subsequent identification and enumeration.

CTD data were verified and processed using standard quality-control techniques (Emery and Thomson, 1997). Chlorophyll \(a\) was determined from the acetone-extracted samples using one of two methods: (i) the fluorometric procedure of Holm-Hansen et al. (1965); and/or (ii) Welschmeyer’s (1994) modification of (i) to correct for interfering pigments. For zooplankton identification and enumeration, subsamples of the preserved samples were taken such that a minimum of 200 organisms per net were counted and identified to the lowest taxon possible. Additional aliquots were taken until a total of some 75–100 \(C.\) hyperboreus spp. had been identified and staged. The three \(C.\) hyperboreus species found in the regions (\(C.\) finmarchicus, \(C.\) glacialis, \(C.\) hyperboreus) were identified to the level of species and stage. Complete details of field and laboratory protocols are documented in Mitchell et al. (2002).

We averaged temperatures in the upper 25 m and chlorophyll \(a\) in the upper 50 m as representations of the environmental conditions experienced by \(C.\) finmarchicus during development, in particular for the surface-dwelling early stages egg to C3 (Plourde et al., 2001, 2009). Our averaging of the upper 25 m for temperature was taken as representative of the mixed layer and the upper reaches of the thermocline. Chlorophyll \(a\) measurements were averaged over a deeper interval, because short-term variations in the vertical distribution of phytoplankton, caused by growth and sinking, would be more effectively integrated in this way. At first glance, the use of temperature in the upper 25 m could appear simplistic for late development stages C4–C6 that could perform diel vertical migrations (DVM) over a significant depth range. However, DVM is highly variable in response to multiple environmental and physiological parameters, with no clear preferential day/night depths predictable from environmental variables alone (Pearre, 1979, 2003). We therefore chose to use our simple approach to avoid bringing uncertainty into our results by imposing unrealistic day and night vertical distributions.

### Estimates of egg production

Egg production rate (Epr) was estimated with a functional relationship between \(in situ\) Epr and food biomass derived from experiments carried out in the GSL. We predicted Epr in the GSL using an Ivlev (Type II) functional relationship between specific Epr and ambient chlorophyll \(a\) biomass for the region (Plourde and Joly, 2008). \(in situ\) Epr on the NLS and SS was predicted using a Type II relationship between \(in situ\) Epr and chlorophyll \(a\) biomass, based on shipboard measurements in the Labrador Sea (EJHH, unpublished data):

\[
Epr = 62.42(1 - e^{-0.026Chl})\text{.} \tag{1}
\]

Epr was combined with the estimates of the abundance of adult females to calculate population rates of daily egg production (PopEpr), assuming that all females were reproductively active. PopEpr was used as the input data to estimate the mortality of the egg and naupliar stages (see below).

### Estimating mortality rate, survival, and daily recruitment

We used the VLT approach to calculate the instantaneous daily mortality rate. Development times \((D)\) were estimated with temperature averaged in the upper 25 m of the water column. We did not consider food limitation in the determination of development time because it appears to have a limited influence on estimated mortality rates (Ohman et al., 2004; Hirst et al., 2007).

We were faced with choosing between the studies of Corkett et al. (1986) and Campbell et al. (2001) to predict stage-specific development times based on the Belehrádek (1935) equation. The impact of selecting the developmental parameters estimated from either study on mortality estimates will depend on the stage and the temperature at which observations were gathered. Overall development times from egg to adulthood for both observation sets are generally comparable (Figure 2), with the most important deviations \(<4^\circ\) C, when the analysis of Corkett et al. (1986) predicts shorter generation time than would be forecast from the parameters of Campbell et al. (2001). This deviation is not entirely unexpected given that \(4^\circ\) C represents the lower limit of the latter’s experiments. Development times, and consequently mortality rates, for two stages, egg to C1 and C3 to C4, will be little affected by the choice of parameter source. The parameters of Corkett et al. (1986) estimate much longer stage durations for C1–C2 and C2–C3, causing the estimates of mortality rate to be reduced relative to those obtained with the values from Campbell et al. (2001). The reverse occurs for the two older developmental stages (C4–C5 and C5–C6), because in both instances, development rates predicted by Corkett et al. (1986) are considerably faster than those of Campbell et al. (2001). Overall, the impact might appear minor at first glance, but the non-linearity of temperature-dependent development leads to the most rapid rate of change in predicted stage durations at temperatures below the lower limit of the Campbell et al. (2001) observations. As a significant proportion of our observations from oceanographic surveys (37%) and fixed stations (44%) were collected at...
temperatures < 4°C, we feel it more appropriate to apply the parameters of Corkett et al. (1986) in our analysis.

Mortality rate ($m$) averaged across egg–C1 ($m_{\text{egg-C1}}$) was estimated from Equation (4) of Ohman et al. (2002):

$$\frac{A_{C1}}{\text{PopEpr}} = \exp^{-m_{\text{egg}}D_{\text{egg}}} \frac{[1 - \exp^{-m_{C1}D_{C1}}]}{m},$$

(2)

where $A_{C1}$ is the abundance of C1 (number m$^{-2}$) and $D_{\text{egg}}$ and $D_{C1}$ the development times of the aggregate stages egg–N6 and C1, respectively.

Mortality rates ($m$) for copepodite stage pairs were derived through an iterative solution of Equation (2) of Ohman et al. (2002):

$$\frac{A_i}{A_{i+1}} = \exp^{m_{D_i} - 1} \frac{1 - \exp^{-m_{D_{i+1}}}}{m},$$

(3)

and the joint C5–C6 mortality was estimated from their Equation (3):

$$m = \frac{\ln[A_{C5}/A_{C6} + 1]}{D_{C5}},$$

(4)

where $A_i$ and $A_{i+1}$ are the abundance (number m$^{-2}$) and $D_i$ and $D_{i+1}$ the development times of each stage pair.

The proportion surviving through each pair ($i, i+1$) was calculated based on Equations (6) and (7) of Hirst et al. (2007):

$$S_{i,i+1} = \exp(-m_{i,i+1} \times D_{i,i+1}).$$

(5)

Using daily PopEpr to initiate cohort development and assuming steady state, we applied survival across all stage pairs to estimate the instantaneous daily survival in each stage (or stage-specific recruitment rate in number m$^{-2}$ d$^{-1}$) from egg to C5. We did not include stage C6 in the estimate of daily recruitment rate because abundance of C6f was already used in the estimate of the egg recruitment rate (PopEpr).

**Application of the VLT method**

The VLT method assumes that the population is in steady state during a period equivalent to the duration of the stages used in the calculations (Aksnes and Ohman, 1996). Examination of the stage structure of *C. finmarchicus* averaged for the period 1999–2006 during the different surveys provided insights on potential biases inherent in the AZMP sampling programme (Figure 3).

![Figure 2. Comparison of the stage-specific development times (D) predicted using the Belehrádek equation $D = a(t - \alpha)^b$, where $a$ and $\alpha$ are the estimated constants and $b$ is set to $-2.05$, based on the parameters estimated by Corkett et al. (1986) relative to those of Campbell et al. (2001).](https://academic.oup.com/icesjms/article-abstract/66/9/1942/725089)

![Figure 3. Averaged stage abundance of *C. finmarchicus* in the GSL, on the NLS, and on the SS on spatial surveys conducted in (a) spring, (b) summer, and (c) autumn from 1999 to 2006. Lack of data from the SS in summer is denoted by "no data".](https://academic.oup.com/icesjms/article-abstract/66/9/1942/725089)
The population stage structure in spring both in the GSL (one survey) and on the NLS showed a clear dominance of stage C1 and either stages C5–C6 (GSL) or C6 (NLS), indicating that populations were at the onset of reproduction and cohort development (Figure 3a). Consequently, we did not include the spring data collected in the GSL or on the NLS in our results because they were in violation of the assumptions and conditions of application of the VLT method. The situation was markedly different on the SS in spring (Figure 3a) and in the GSL and on the NLS during summer (the SS is not sampled in summer; Figure 3b), when populations were sampled during their growth period, so providing a valid and comparable basis for the application of the VLT method. Stage structure was similar among all regions in autumn, with clear dominance of C4–C5 suggesting that the population was dominated by the overwintering stock and was already in diapause (Johnson et al., 2008; Figure 3c). We therefore considered the autumn data as comparable among regions, although results involving overwintering stages have to be considered carefully (see the Discussion section). Data were analysed based on two seasonal groups (growth period and autumn) and three regions (NLS, GSL, and SS).

The PopEpr usually shows important seasonal variations (Plourde et al., 2001), representing an additional source of potential bias when estimating mortality with the VLT method when applied to time-series data. We tested this assumption following Hirst et al. (2007) by examining loge transformed PopEpr during the period 1999–2006 to identify periods with consistent temporal trends in population reproduction at the fixed stations. We compared the daily rate of change in PopEpr (slopes of linear regressions between PopEpr and day of year) with the mean mortality in egg–C1 during each period. The former metric represented daily variations in egg input, and the latter the daily variation in standing stock of egg–C1. Daily rate of change in PopEpr was typically one order of magnitude lower (not shown) than \( m_{\text{eq-C1}} \) (0.01 vs. 0.18 d\(^{-1}\)). We therefore concluded that temporal changes in PopEpr would not significantly bias our mortality estimates.

The VLT method is also appropriate for estimating mortality in stage pairs that experience the same effect of transport (Aksnes and Ohman, 1996; Ohman et al., 2004). Although our estimates of mortality in egg–C1, C1–2, and C2–3 should not suffer from a violation of this assumption, because most of these early stages are located in the upper layer, one could expect a likely bias in the estimate between stage pairs such as in C3–C4 when transition from no DVM to active DVM generally occurs (Tande, 1988; Basedow et al., 2008). However, because DVM is highly variable in response to multiple environmental drivers such as hunger, animal condition, food availability, and predation risk (Pearre, 1979, 2003), we chose to include all data because of the large temporal and spatial scales considered in our study.

### Analysis

We excluded mortality estimates less than \( -3 \) or greater than \( +3 \) from our analysis because they are likely to indicate substantial violations of the assumptions and conditions of the application of the VLT method (Heath et al., 2008).

Monthly averages of environmental variables, *C. finmarchicus* reproduction, and stage-specific mortality rates were used to describe the seasonal patterns of variation at the fixed sites sampled in the three regions. The absence of some stages during portions of the time-series at the fixed sites resulted in a scarcity of mortality estimates during some parts of the year. However, monthly averages of mortality were generally derived based on 4–32 estimates for each month, a number that corresponds to the recommendation that 6–10 replicates are needed to obtain stable mortality estimates (Aksnes and Ohman, 1996). All positive and negative mortality estimates were included in our time-series analysis for the fixed sites because a comprehensive interpretation of negative mortality values could be achieved through our general knowledge of regional circulation and of *C. finmarchicus* population dynamics and timing of the overwintering period at the sites (Johnson et al., 2008).

Data from each station visited during the oceanographic surveys showed high occurrences of “discontinuous” stage structure, yielding a large proportion of missing mortality estimates (Table 1; Heath et al., 2008). Given the need for 6–10 replicates to achieve reliable mortality estimates with the VLT method (Aksnes and Ohman, 1996), we chose to average the stage structure, temperature, and chlorophyll \( a \) data for each section to derive daily mortality rates from the broad-scale surveys. Owing to their proximity, data collected on the seven transects in the GSL were grouped into four regions according to the general

### Table 1. Effect of averaging section data on the mortality estimates.

<table>
<thead>
<tr>
<th>Region</th>
<th>Type of estimate</th>
<th>All data</th>
<th>Transect averages</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Egg–C1</td>
<td>C1–C2</td>
</tr>
<tr>
<td>NLS</td>
<td>No estimate</td>
<td>0.44</td>
<td>0.39</td>
</tr>
<tr>
<td></td>
<td>Negative</td>
<td>0.11</td>
<td>0.20</td>
</tr>
<tr>
<td></td>
<td>Positive</td>
<td>0.46</td>
<td>0.41</td>
</tr>
<tr>
<td></td>
<td>( n )</td>
<td>829</td>
<td>829</td>
</tr>
<tr>
<td>GSL</td>
<td>No estimate</td>
<td>0.28</td>
<td>0.45</td>
</tr>
<tr>
<td></td>
<td>Negative</td>
<td>0.00</td>
<td>0.21</td>
</tr>
<tr>
<td></td>
<td>Positive</td>
<td>0.72</td>
<td>0.34</td>
</tr>
<tr>
<td></td>
<td>( n )</td>
<td>584</td>
<td>584</td>
</tr>
<tr>
<td>SS</td>
<td>No estimate</td>
<td>0.48</td>
<td>0.43</td>
</tr>
<tr>
<td></td>
<td>Negative</td>
<td>0.09</td>
<td>0.20</td>
</tr>
<tr>
<td></td>
<td>Positive</td>
<td>0.43</td>
<td>0.37</td>
</tr>
<tr>
<td></td>
<td>( n )</td>
<td>479</td>
<td>479</td>
</tr>
</tbody>
</table>

Values are the proportions of \( n \). No estimate indicates the proportion of cases for which no estimate of mortality was obtained.
hydrography in the region: sections 7 and 8 (northwest GSL), section 9 and the western half of section 10 (western GSL), section 5 and the eastern half of transect 10 (southeast GSL), and sections 6 and 11 (northeast GSL; Figure 1). This approach reduced considerably the proportion of missing estimates, with the drawback of reducing the number of observations (Table 1). However, the use of averages of stage abundance stabilized our data, and we firmly believe that this resulted in more-robust mortality estimates in a manner similar to the use of replicates (Aksnes and Ohman, 1996). On average, daily mortality rates were estimated using the mean stage abundance calculated from 8–21 stations on sections on the NLS, 5–10 stations on sections in the GSL, and 4–8 stations on sections on the SS. Only positive mortality estimates were included in our contrast among regions because we assumed that negative estimates obtained from averaged transect data would indicate violation of the assumptions of the VLT method. Of the 179 potential estimates of mortality on the synoptic spatial cruises, our approach resulted in 158, 104, 88, 83, 89, and 149 estimates of mortality in egg–C1, C1–C2, C2–C3, C3–C4, C4–C5, and C5–C6, respectively.

Non-parametric statistical tests (Kruskal–Wallis for contrast among more than two groups; Mann–Whitney for contrast among two groups) were used to contrast mortality estimates among months and fixed stations with the time-series data, and among the three regions and periods (population growth period and autumn) from our oceanographic surveys. We used non-linear regression models to describe the relationships between mortality estimates in all stage pairs and temperature from each oceanographic section, and linear multiple regression to describe the relationships between mortality at early stages (egg–C1) and temperature, phytoplankton biomass, and C6 female (C6f) abundance. The data were separated into the population growth period and autumn to determine whether different processes could be affecting the pattern of variation in mortality, and because the conditions in the various regions were likely to be confounded by other environmental variables.

**Results**

**Seasonal variations in mortality rates at the fixed stations**

The seasonal patterns of surface layer temperature, phytoplankton biomass, and *Calanus finmarchicus* C6f abundance and PopEpr showed marked differences among the AZMP subregions (Figure 4). The surface layer (0–25 m) was consistently warmer at HL2 than at ST27 and the AG/GC site, whereas the latter was colder than ST27 during summer and autumn (Figure 4a). On the continental shelves, the spring phytoplankton bloom was slightly earlier at HL2 than at ST27 in April, whereas the onset of the bloom at AG/GC was 1 month later (May), although there, in contrast to the other stations, phytoplankton biomass remained elevated until August (Figure 4b). Maximum abundance of C6f was during the peak in phytoplankton biomass at HL2 and ST27, whereas it slightly preceded the spring bloom at AG/GC in May; as with chlorophyll biomass, however, C6f abundance in this region remained high until July (Figure 4c), later than at the other sites. The PopEpr followed the seasonal pattern of abundance of C6f at all three sites (Figure 4d).

In general, stage-specific daily mortality rates showed significant variations among months and fixed stations (sites; Kruskal–Wallis, K–W hereafter, *p* < 0.001; Figure 5). The only exception was the C2–C3 estimates of mortality, which did not differ among sites (Figure 5c). The seasonality in mortality rates was generally less pronounced at AG/GC than at HL2 and ST27. Egg–C1 mortality rates were significantly different among months and stations (K–W, *p* < 0.001) with maximum values ranging 0.21 d⁻¹ in October at ST27, 0.23 d⁻¹ at AG/GC in May, and 0.69 d⁻¹ at HL2 in September (Figure 5a). Seasonally, mortality rates of egg–C1 were higher at AG/GC than at the other sites in May and June, lowest at ST27 during summer, and
highest at HL2 in autumn. Mortality rates of later developmental stages (C3–C5) also showed important seasonal and regional variations (Figure 5d and e). Mortality of C3–C4 peaked in July at ST27 (0.32 d⁻¹), but was generally higher at AG/GC throughout the year (Figure 5d). C4–C5 mortality was relatively high at ST27 in late summer, whereas rates were generally similar and low at the two other locations. A marked feature of the seasonality in mortality in these stages was the occurrence of sustained negative estimates of mortality on the SS in late summer and autumn, a pattern also observed to a lesser extent in C3–C4 on the NLS (Figure 5d and e). Average mortality rates in the stage pair C5–C6 were always >0 d⁻¹. Mortality in C5–C6 was generally greatest at HL2, and there were notable increases starting in June (HL2) or August (AG/GC, ST27) with maximal values occurring in September/October at HL2 and ST27 (Figure 5f). In contrast, the mortality rate at AG/GC remained relatively low (~0.1 d⁻¹) and constant in autumn (Figure 5f). Overall, mortality in C5–C6 was significantly lower at AG/GC than at HL2 and ST27 (K-W, p < 0.0001).

Regional variations in mortality rates on the seasonal surveys
The temperature of the surface layer (0–25 m) was significantly lower during the growth period on the SS than in the GSL and on the NLS (K-W, p < 0.0001), because the growth period was during the spring survey on the SS, but during the summer surveys in the other two regions (Figure 6a). In contrast, temperatures were much higher on the SS than in the other two regions in autumn. Chlorophyll a biomass indicated that the growth period of C. finmarchicus was generally during the spring phytoplankton bloom on the SS, whereas in the GSL and on the NLS, it took place under post-bloom conditions (Figure 6b). In all three regions, chlorophyll a biomass and PopEpr were generally greater during the growth period than in autumn (K-W, p < 0.001; Figure 6c).

Stage-specific daily mortality rates exhibited important variations among the regions, with different spatial patterns during the periods of population growth and autumn (Figure 7). Overall, mortality (all data pooled) was significantly greater in autumn than during the growth period, largely because of the
elevated values on the SS (Mann–Whitney, M–W hereafter, \( p < 0.0001 \)). On a regional basis, mortality was, in general, lower on the SS than in the other regions during the period of population growth, but greater in autumn (K–W, \( p < 0.001 \)). Daily mortality rates of egg–C1 were significantly different among regions during both periods (K–W, \( p < 0.0001 \)), with greater values in the GSL (0.13 d\(^{-1}\)) than in the other regions (0.08 d\(^{-1}\) on the NLS, 0.05 d\(^{-1}\) on the SS) during the growth period, and 2–3 times greater on the SS (0.56 d\(^{-1}\)) than in the other regions (K–W, \( p < 0.001 \)) during the growth period (Figure 7). Mortality in C5–C6 was also greater on the SS (2%) than in the GSL and on the SS in autumn (K–W, \( p < 0.0001 \); Figure 8b).

Relationship between mortality in early stages (egg–C1) and the environment

The mortality rates of all stages sampled during all oceanographic surveys were significantly related to average temperature over all sections (Table 2). The general aspect of the relationship between daily mortality in all stage pairs and temperature is illustrated in Figure 10a. The relationships explained 7–70% of the variation in mortality rates at each stage. The strength of the relationship was greatest for egg–C1 and weakest for C1–C2. For most of the copepodite stages, the coefficient of determination of temperature-dependence was similar (0.171–0.177), except C1–C2, for which temperature-dependence was weakest (0.074). Temperature-dependence was strongest for the youngest (egg–C1) and oldest developmental stages (C5–C6) during the period of population growth, and in autumn where the coefficients of determination were \( > 0.66 \), more than three times the average for other copepodite stages. The coefficients of temperature-dependence were similar for most stages (0.074–0.110), with the exceptions of egg–C1, C2–C3, and C5–C6 during the growth period (0.159–0.253; Table 2).
To further investigate the causes of variation in egg–C1 mortality rates, we applied separate multiple regression models to the data from the growth and autumn periods because the conditions in the various regions were confounded by other environmental variables. During the period of population growth, neither temperature \( (p = 0.167) \) nor chlorophyll \( a \) concentration \( (p = 0.374) \) had a statistically significant effect on egg–C1 mortality rates, whereas the abundance of adult females had a significant positive impact on mortality rates \( (p = 0.003) \). The overall model was \( \ln(m) = -0.238 + 0.071 \ln(\text{Temperature}) - 0.024 \ln(\text{Chlorophyll}) + 0.094 \ln(C6f) \) \( (F_{3,68} = 4.08, r^2 = 0.15, p = 0.01) \), where the standard errors of the coefficients were 0.138, 0.051, 0.027, and 0.031, respectively. Mortality rates during this period of development were generally <0.3 d\(^{-1}\). In contrast, mortality rates in autumn were significantly positively influenced by temperature \( (p < 0.0001) \) and negatively by phytoplankton abundance \( (p < 0.001) \), but showed no significant relationship with the abundance of adult females \( (p = 0.595) \). The overall model was \( \ln(m) = -0.103 + 0.920 \ln(\text{Temperature}) - 0.355 \ln(\text{Chlorophyll}) + 0.033 \ln(C6f) \) \( (F_{3,69} = 38.13, r^2 = 0.624, p < 0.001) \), where the standard errors of the coefficients are 0.275, 0.101, 0.102, and 0.061, respectively. High temperatures and low levels of phytoplankton biomass were found principally on the SS, so the two variables are somewhat confounded. There is considerable scatter when contrasting the predicted and observed values (Figure 10b and c), but the models are intended to represent general trends rather than serve as predictive models.
relationships. Too many unmeasured factors could be influencing local patterns in mortality. We can conclude, however, that egg–C1 mortality rates \(0.4 \text{ d}^{-1}\) were mainly associated with temperatures \(>13^\circ\text{C}\) and with chlorophyll \(a\) concentrations \(<50 \text{ mg m}^{-2}\).

**Discussion**

Our study showed significant variations in stage-specific mortality in *C. finmarchicus*, both seasonally and regionally, over a large area that extends from the southern Labrador Shelf in the north to the GSL in the west and the SS in the south. This is the first comprehensive report of long-term averaged stage-specific mortality in *C. finmarchicus* derived from long-term monitoring, and it includes a broad range of ambient temperature and phytoplankton biomass conditions (Figure 4). Any comparison of estimated mortality rates among regions in the North Atlantic should be made with caution, by considering the method applied to the data (VLT or HLT) and the prevailing temperatures. Our results from oceanographic surveys collected during a period of population growth were derived over a narrow range of temperatures (3–6°C), comparable with conditions under which mortality estimates were obtained for populations on Georges Bank and in the

![Box plot showing the proportion surviving through each stage pair in *C. finmarchicus* in the GSL (dark grey), on the NLS (light grey), and on the SS (black) during (a) the population growth period, and (b) in autumn of 1999–2006. Boxes show the median and 25th–75th percentiles, grey circles denote the upper and lower 10th percentiles, and error bars show either the lower 10th–25th or the upper 75th–90th percentiles.](https://academic.oup.com/icesjms/article-abstract/66/9/1942/725089)
Irminger Sea based on the VLT method (Ohman et al., 2002; Heath et al., 2008). Mortality of the early copepodite stages appeared to be substantially greater on the Canadian continental shelves and in the GSL than on Georges Bank or in the Irminger Sea. Mortality of C1–C2 (0.10–0.13 d$^{-1}$), C2–C3 (0.09 d$^{-1}$), and C3–C4 (0.09–0.11 d$^{-1}$) in the GSL and on the NLS tended to be slightly above those on Georges Bank (<0.10 d$^{-1}$), a region also located

![Figure 9](https://example.com/figure9.png)

**Figure 9.** Stage-specific daily recruitment rate during the cohort development of *C. finmarchicus* in the GSL (dark grey), on the NLS (light grey), and on the SS (black) during (a) the population growth period, and (b) in autumn of 1999–2006. Values represent the mean ± s.e.

**Table 2.** Stage-specific $r^2$, significance, and coefficients of the relationship between estimated daily mortality rates and environmental temperature from the regional oceanographic surveys.

<table>
<thead>
<tr>
<th>Stage</th>
<th>$r^2$</th>
<th>p-value</th>
<th>$a$</th>
<th>$b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg–C1</td>
<td>0.700</td>
<td>&lt;0.001</td>
<td>0.033</td>
<td>0.214</td>
</tr>
<tr>
<td>C1–C2</td>
<td>0.074</td>
<td>0.003</td>
<td>0.074</td>
<td>0.074</td>
</tr>
<tr>
<td>C2–C3</td>
<td>0.172</td>
<td>&lt;0.001</td>
<td>0.033</td>
<td>0.159</td>
</tr>
<tr>
<td>C3–C4</td>
<td>0.177</td>
<td>&lt;0.001</td>
<td>0.048</td>
<td>0.110</td>
</tr>
<tr>
<td>C4–C5</td>
<td>0.171</td>
<td>&lt;0.001</td>
<td>0.050</td>
<td>0.100</td>
</tr>
<tr>
<td>C5–C6 growth</td>
<td>0.659</td>
<td>&lt;0.001</td>
<td>0.015</td>
<td>0.253</td>
</tr>
<tr>
<td>C5–C6 autumn</td>
<td>0.802</td>
<td>&lt;0.001</td>
<td>0.137</td>
<td>0.105</td>
</tr>
</tbody>
</table>

Data were fitted by iterative non-linear least-squares to the equation $m = ae^{bT}$, where $m$ is the estimated mortality rate and $T$ the 0–25 m average temperature.

![Figure 10](https://example.com/figure10.png)

**Figure 10.** (a) Relationship between daily mortality rate in all stage pairs of *C. finmarchicus* and temperature, and observed and predicted values of mortality egg–C1 determined from a multiple linear regression model with temperature, chlorophyll $a$ biomass, and abundance of C6 during (b) the population growth period, and (c) in autumn. Multiple regression statistics are provided in text. The lines in (b) and (c) show the output from a linear regression model (see text for statistics and parameters), with 95% confidence intervals around the slope denoted by broken lines.
Mortality and survival of Calanus finmarchicus in the Northwest Atlantic

on the continental shelf, but markedly greater than the mortality in the deep oceanic Irminger Sea (<0.05 d⁻¹; Ohman et al., 2002; Heath et al., 2008). Mortality rates on the SS during the growth period were within the range of values measured on Georges Bank, but temperatures on the SS were somewhat lower (3°C) than on Georges Bank (5°C). Mortality of late development stage pairs C4–C5 and C5–C6 in the AZMP region during the population growth period appeared to fall within the same range (c.a. 0.05–0.1 d⁻¹) as those observed on Georges Bank, the sole location for which mortality in late stages using the VLT has been reported (Ohman et al., 2004). Mortality rates of egg–C1 are more difficult to compare because no such stage pair has been used with the VLT method in previous studies. However, mortality rates in the GSL during the growth period (0.13 d⁻¹) were in the upper range of the mortality rates averaged over naupliar stages estimated using the HLT method in two Norwegian fjords (Ohman et al., 2004). Finally, mortality rates throughout our study area appeared to be substantially greater than those obtained through the application of the HLT method to data from station M in the Norwegian Sea (deep oceanic site) or to data from the northern North Sea (continental shelf) in spring under conditions with roughly similar temperatures (Eiane and Ohman, 2004; Ohman et al., 2004). Overall, mortality rates experienced by C. finmarchicus in the AZMP region appeared to be somewhat higher than estimates from several other regions, but a detailed quantitative meta-analytical comparison using mortality estimates from several sources is needed for better comparison of C. finmarchicus life histories in different habitats and regions.

Mortality rates were significantly correlated with the local average temperature for all stages of development, in terms of both the seasonal and regional patterns (Table 2, Figure 10a). Temperature is a key factor controlling metabolic processes of marine copepods (Hunley and Lopez, 1992; Hirst and Bunker, 2003; Bunker and Hirst, 2004), as well as other components of the ecosystem. Its general effect on mortality in Calanus spp. has been described before (Ohman et al., 2002; Hirst et al., 2007; Plourde et al., 2009), but results from our large-scale study allowed a more complete description of the functional relationship because of the wide range of temperatures encountered throughout the complete annual cycle and across large spatial scales. Clearly, there was very high mortality at the upper end of the temperature range (−1 to 16°C) encountered in our study, much greater than the temperature range (6–10.6°C) considered optimal for surface-dwelling C. finmarchicus in the North Atlantic (Heloueat and Beaugrand, 2007). Therefore, those high temperatures, which were mostly restricted to the SS in autumn, resulted in poor survival and recruitment of surface-dwelling stages from egg to C3 (Figure 9b). However, the high variability (generally low r²) inherent in many of these relationships, as well as the general effect of temperature on metabolism, suggests that temperature acts to scale the inherent mortality rate across seasonal or spatial scales, with other environmental factors serving as the key drivers that determine local or short-term patterns of variation in mortality.

Elevated mortality in the egg–C1 stage was also associated with conditions of low ambient phytoplankton biomass (see the Results above). Low phytoplankton biomass could be detrimental to survival from egg to C1 through two distinct effects: (i) cannibalism or predation on eggs and early non-feeding naupliar stages, and (ii) starvation in later naupliar stages and C1. Cannibalism by late development stages of C. finmarchicus and predation by other filter-feeding copepods, including conspecific Calanus spp. on eggs and early naupliar stages, are known, although solid quantitative knowledge of feeding behaviour is still generally lacking (Sell et al., 2001; Bonnet et al., 2004; Ohman et al., 2008). Calanus spp. (and other filter-feeding organisms) have been shown either to exhibit prey-switching (Landry, 1981) or are probably inherently omnivorous (Basedow and Tande, 2006). Both feeding modes could result in greater ingestion of eggs and early nauplii at low concentrations of phytoplankton, either because predators switch to animal prey (active prey-switching) or because eggs and early nauplii represent a large proportion of the particles being filtered (passive omnivory). Food-limited growth and survival could also influence our estimates of mortality for egg–C1. Food concentrations limiting to nauplii growth and development (1.75 mg Chl a m⁻³ using a Chl a:C ratio of 40 as in Campbell et al., 2001; Heath et al., 2008) or necessary for Calanus nauplii survival (0.6 mg Chl a m⁻³; Lopez, 1996; Irigoien et al., 2003) were common throughout our study region (Figures 4b and 6b). On average, integrated phytoplankton biomass was <1 mg Chl a m⁻³ (or <50 mg m⁻² in the 0–50-m layer) during the post-bloom period at ST27 and H12 and over the whole AZMP region in autumn, and <1.5 mg Chl a m⁻³ in the GSL and on the NLS in June and July (during the growth period). As growth in later development stages is limited at even higher food concentrations (Campbell et al., 2001), food limitation was likely an important factor of control for mortality patterns in the AZMP region. Feeding on microzooplankton (omnivory) by different development stages of C. finmarchicus appears significant, especially during periods of low phytoplankton biomass (Ohman and Runge, 1994; Irigoien et al., 1998, 2003; Castellani et al., 2008), which could compensate for low algal availability. However, the fact that high rates of mortality (i.e. low survival) or suboptimal Epr values have generally been associated with periods of low algal biomass indicates that C. finmarchicus is probably food-limited during such periods (Ohman and Runge, 1994; Niehoff et al., 1999; Hirche et al., 2001; Mayor et al., 2006; Heath et al., 2008). Therefore, low food availability is likely to have played a key role in the determination of the mortality patterns in our study.

We obtained rather weak evidence of density-dependent mortality for egg–C1 from the large-scale oceanographic surveys during the growth period, which is no surprise considering our data. First, zooplankton were sampled over a wide range of temperatures and chlorophyll concentrations, both variables being of primary importance in the scaling of mortality rates (Hirst and Kiorboe, 2002; Heath et al., 2008). Second, density-dependence is likely mediated through cannibalism by later development stages on conspecific eggs and early nauplii, a signal that might have been weakened by the inclusion of all naupliar and C1 stages in the estimate (Ohman and Hirche, 2001; Ohman et al., 2002; Plourde et al., 2009). Third, most of the data came from oceanographic surveys conducted in summer (GSL and NLS) or autumn (all regions), after the seasonal maximum in C6f abundance (Figure 4c). Finally, our sampling did not allow discrimination between overwintering and active C4–C5 stages (see below), precluding their inclusion in our regression model in the way they were considered by Ohman and Hirche (2001) and Heath et al. (2008). Those stages could represent a significant proportion of the active feeding C. finmarchicus population before the onset of diapause in late summer and early autumn, a period of elevated mortality.
during the egg–C1 transition throughout the region (Figure 5a; Johnson et al., 2008).

Our estimates of mortality rate at the fixed stations may have been influenced by the advection of surface-dwelling stages particularly at the onset of reproduction in spring, when temperatures were low. This could well have been the case for egg–C1 in the GSL during the first months of population growth in April and May, as illustrated by there being higher mortality rates at the AG/GC site than at the other two stations (Figure 5a). Development from egg to C1 would have taken ~50~80 d at the ambient temperatures of 0~3°C in the GSL in April and May (Figure 4a), a period characterized by strong residual downstream surface current and low surface water residence time in the lower St Lawrence Estuary (LSLE) and Northwest Gulf (NWG; Campbell et al., 2001; Sauzier et al., 2003). Moreover, the AG/GC site is located at the upstream western end of the Laurentian Channel, the overwintering habitat of C. finmarchicus in the GSL (Plourde et al., 2001, 2002). These physical characteristics serve to delay the onset of C. finmarchicus reproduction in the LSLE (Plourde et al., 2001; Johnson et al., 2008) and may result in limited upstream transport of C. finmarchicus into the region during April and May, and a greater potential for downstream advection of the surface-dwelling stages in spring. Only later in the year would local processes control population dynamics at AG/GC as a result of longer residence times, more rapid development, and increased reproduction across the LSLE~NWG region. A similar assessment of the effect of advective losses on mortality estimates at ST27 and HL2 is more difficult. Although both ST27 and HL2 are located in the inshore branch of currents flowing north to south along the continental shelves, seasonal variations in transport may be less pronounced than in the GSL because of the lesser influence of freshwater outflow in the regions of these stations relative to AG/GC. Our knowledge of the seasonal pathways for the transport of females emerging from diapause in the Labrador Sea (affecting ST27) and the Laurentian Channel, Scotian slope waters, and Emerald Basin (which can all affect HL2) are still uncertain. Furthermore, Pepin and Head (2009) noted that significant numbers of adult females and C5s were present in the surface waters of the NLS throughout the year. Overall, however, we expect that the major emergence sites of C. finmarchicus sources for both ST27 and HL2 are remote and that transport of animals from their overwintering areas to these coastal stations could result in a differential influx rate for different stations. This could lead to negative estimates of mortality, depending on the magnitude of the immigration relative to that of biological processes (i.e., production and true mortality).

For the oceanographic surveys of each region, in contrast to the time-series sites, we do not believe that advection should have had a major impact on our determination of long-term stage-specific daily mortality. The NLS, GSL, and SS are well connected by the regional surface circulation on the continental shelf (Loder et al., 1998). The NLS is an upstream source of water for the GSL and SS, and waters from the GSL influence the inner SS. The survey sections were designed to cross the major oceanographic features, so providing a comprehensive assessment of conditions and ensuring coverage of potential source and sink populations that could affect the dynamics of the continental shelf. Our estimates of mortality rates were based on averaging the data from each section on the NLS and SS and over stations within regions of the GSL, so that our approach provided an integrated view of the source and sink elements for the areas represented by each section. At the temperatures that prevail from spring to autumn, development times from egg to C5 typically range from 40 to 80 d, with the development time between adjacent stages seldom being more than 4~10 d, except egg–C1, the consequences of which are discussed below. With prevailing currents ranging from 0.1 to 0.5 m s~1, the abundances of adjacent stages on a given section are more likely a reflection of their shared history rather than their relationship with animals sampled from adjacent sections, which are generally several hundred kilometres away. We therefore argue that the nature of our sample averaging and the distance between adjacent sections or regions are such that the population characteristics observed for each section, or region (GSL), represent a reasonable reflection of a local aggregation of C. finmarchicus approximating an equilibrium state.

The long development of the egg–C1 stage could result in a bias in our application of the VLT method for our time-series data from the fixed sites. The VLT method assumes constancy of rates in each stage pair during a period equivalent to their developmental time (Aksnes and Ohman, 1996). Our assessment of daily rate of change in PopEpr at the fixed stations showed that the overall daily rate of mortality at the egg–C1 transition (0.18 d~1) was typically one order of magnitude greater than the rate of change of PopEpr (0.01 d~1), indicating that the latter had a low effect on mortality estimates (see Methods; Hirst et al., 2007; Plourde et al., 2009). However, an examination of the seasonal pattern in PopEpr and abundance of C1 at the fixed stations helped to identify where there might be potential biases (Figure 11). The peak in abundance of C1 was at the end of 3~4 months of high and constant PopEpr at AG/GC and HL2, whereas it was more than 2 months later at ST27 during a period of low PopEpr. This lag corresponds roughly to the mean development time from egg to C1 of 55 d at the ambient temperatures found from March to June, indicating that these C1s likely originate from eggs laid towards the end of the period of high PopEpr at ST27 (Figure 11; Corkett et al., 1986). Therefore, environmental conditions and reproduction of C. finmarchicus at ST27 showed an apparent decoupling between PopEpr and C1 abundance, leading to near zero or negative estimates of mortality, a situation not encountered at AG/GC or HL2 (Figure 5a). Conversely, long development times from egg to C1 during periods of high PopEpr in winter and spring could result in overestimation of mortality at all stations (Figure 11). However, such biases should not mask the strong seasonal patterns that appear to be driven mainly by variations in temperature (Figures 4a and 5a). The pattern of mortality at ST27 raises the concern that there could be similar biases in estimates of mortality for egg–C1 for the summer oceanographic surveys on the NLS, but not for the surveys in the other areas which took place during periods of relatively constant population reproduction (Figure 4d). However, Pepin et al. (2008) noted that the abundance of calanoid nauplii on the Newfoundland Shelf was relatively constant during both April and July surveys, indicating that the potential for bias at ST27 may not be present throughout the region. The constancy in PopEpr during 1~2 months before most regional surveys confirms that the required “stability” of rates during a period equivalent to the developmental duration of stages considered in the estimates was mostly met (Aksnes and Ohman, 1996). Finally, the fact that negative values were not included in our analyses and that data from surveys represented a spatial integration over a wide region should counteract any potential biases associated with the use of the egg–C1 stage.
The presence of overwintering stages (arrested development) certainly affected our estimates of mortality in later stage pairs. *Calanus finmarchicus* overwinters predominantly as C5, but C4 can also contribute to the overwintering stock (Heath *et al.* 2004; Head and Pepin, 2007). The assumption of constant rates of development and mortality among stage pairs would be clearly violated when both active and overwintering individuals are present (Aksnes and Ohman, 1996). This may have contributed to the recurrent negative mortality rates observed in autumn at HL2, corresponding to the period of entry into diapause (accumulation of C4 and C5; Figure 3c; Johnson *et al.*, 2008). Conversely, accumulation in C5 would likely cause a positive bias in estimated mortality rates in the C5–C6 stage pair in autumn. To explore the impact of high abundance of overwintering stages on estimates of mortality, we compared the relationship between mortality in stage pairs C4–C5 and C5–C6 and temperature during the period of population growth (May, June, July) and in autumn separately (Table 2, Figure 12). Daily mortality rate in stage pair C4–C5 in autumn was generally at the lower end of mortality values at any given temperature, supporting the expected effect of the presence of overwintering C5 on mortality estimates in this stage pair (Figure 12a). The same exercise with stage pair C5–C6 resulted in an even more substantial difference, with mortality estimates being consistently greater in autumn than during the population growth period, resulting in a markedly different relationship with temperature (Figure 12b, Table 2). To illustrate the impact of dormant stages on autumn mortality estimates, which we presumed would have significantly lower rates of loss relative to active animals, we re-estimated autumn mortality rates by applying a range of correction factors to reflect the proportion of deep-dwelling overwintering (C5) animals based on discrete sampling in autumn in the region: 40–90% of C5s dormant on the NLS (PP and EJHH, unpublished data); 85–95% dormant in the GSL (SP, unpublished data); 50–90% dormant on the SS (Sameoto and Herman, 1990). The result of these calculations indicates that the upper limit of these dormancy rates yields greater mortality at stage pair C4–C5, with a notable increase in the number of estimates > 0 (Figure 12a). Conversely, the same correction to the abundance of "active" C5 in autumn resulted in lower daily rates of mortality of C5–C6, which fell within the range of temperature-dependent mortality rates observed during the period of population growth (Figure 12b). It is clear from these simple calculations that the presence of active and dormant animals has a significant impact on the estimated mortality rates if there is insufficient knowledge of the proportion of animals in diapause. The issue can be even more complex in areas where a significant portion of dormant animals are present.
animals is stage 4 copepodites. Because of the inherent plasticity (interannual variability) in both the timing of the onset of diapause and the importance of early stages in autumn (Johnson et al., 2008), we feel it would be inappropriate to apply constant correction factors derived from data collected during only one or few years or at specific locations to our large-scale data. Therefore, we acknowledge a bias in autumn estimates of mortality rates of C4–C5 and C5–C6 stages and emphasize that mortality estimates of these later developmental stages in autumn should be considered with caution.

**Interplay between mortality, survival, and PopEpr in the control of recruitment**

The long-term stage-specific recruitment rate observed in different regions and periods illustrates the importance of considering both bottom-up and top-down processes in the understanding of *C. finmarchicus* dynamics (Twombly et al., 2007). *Calanus finmarchicus* showed a distinct pattern in stage-specific daily recruitment in the GSL during the growth period, with a greater loss during the egg–C1 stage than on the NLS and SS (Figure 9a). As temperature and phytoplankton biomass were quite similar in the GSL and on the NLS during the growth period (Figure 6), one could attribute this difference to region-specific differences in the cannibalism/predation field, an analysis beyond the scope of this study. In autumn, the higher daily rate of mortality on the SS, mainly associated with the warmer conditions, did result in a lower daily recruitment in egg to C3 relative to the GSL and NLS, indicating that surface-dwelling *C. finmarchicus* were doing poorly under conditions that could be considered as extreme for the species on the SS (Helaoueet and Beaugrand, 2009). In terms of population dynamics, our study showed that cohort survival represents the ultimate metric, allowing a clear extreme for the species on the SS (Helaoueet and Beaugrand, 2009). The need for a better description of mortality throughout the North Atlantic and, potentially, the impacts of environmental (e.g. climate) change.

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