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A comparative study of *Calanus finmarchicus* mortality patterns at five localities in the North Atlantic

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We compare the patterns of stage-specific mortality of *Calanus finmarchicus* at five localities across the North Atlantic Ocean during the spring—summer period of active population growth: Georges Bank, a continental shelf locality in the NW Atlantic, based on 30 broadscale survey cruises in the US GLOBEC program; the northern North Sea, studied during the historic FLEX program with sampling four times daily for 73 days; Ocean Station M in the central Norwegian Sea, based on an 80-day daily time-series; and Lurefjorden (sampled weekly in late winter—early summer) and Sørfjorden (sampled monthly), two fjords in southwestern Norway characterized by markedly different guilds of predators. The mortality estimation methods included Wood's Population Surface Method, the Vertical Life Table (VLT) method, and a modified VLT, according to the study site and copepod recruitment schedules. Contrary to assumptions implicit in many simulation models and indirect methods for estimating zooplankton mortality, both rates and stage-specific patterns of mortality of *C. finmarchicus* vary appreciably across the North Atlantic. Characteristics of local environments, including the predator field in particular, appear to strongly influence mortality schedules in different regions. In at least two sites (Georges Bank and Ocean Station M), mortality rates of early stages of *C. finmarchicus* are density-dependent. We attribute this density-dependent mortality to egg cannibalism, which introduces non-linear population responses to changing environmental conditions. Region-specific biological interactions can substantially modify the effects of physical climate variability and render simple linear relationships between climate and zooplankton abundance unlikely.

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Introduction

There is considerable interest in being able to forecast the consequences of climate change on pelagic communities. Such forecasts are complicated by the growing recognition of natural ocean—atmosphere variations on multi-decadal time scales (e.g. Mantua *et al.*, 1997; Brinton and Townsend, 2003; Lavaniegos and Ohman, 2003). Recent awareness has also grown regarding the non-stationary characteristics of some time-series: the dominant processes leading to population change during some time periods may be quite different from those in others (e.g. Solow, 2002). In the case of the marine zooplankton, among the more striking examples of non-stationarity is that of the interannual variation in *Calanus finmarchicus* in the North Sea, which showed a close, inverse relationship with the North Atlantic Oscillation (NAO) from 1958 through 1995 (Fromentin and Planque, 1996; Reid and Beaugrand, 2002). Subsequently, the relationship that had held for 38 years broke down and variations of *C. finmarchicus* became completely uncorrelated with the NAO (Reid and Beaugrand, 2002). Among processes that have been hypothesized to account for this changing pattern, one consideration is temporal changes in biogeographic distributions (Beaugrand *et al.*, 2002) and several other hypotheses have been advanced (Heath *et al.*, 1999; Reid

and Beaugrand, 2002). However, a central point emerging from such observations is that forecasting changes in populations will not be successful in the absence of a direct mechanistic understanding of the processes that contribute to such correlations.

The traditional approach to forecasting population trends of the zooplankton is to assume that the production and ultimately standing stock of zooplankton are limited principally by variability of food, chiefly phytoplankton, and hence to assume that the problem distills to one of better understanding of phytoplankton production. To oversimplify this perspective, climatic factors are thought to act through the classical schemes of turbulent mixing, nutrient enrichment, primary production, and transport processes to govern zooplankton abundance. While it is generally acknowledged that zooplankton mortality can be an important modulator of the preceding processes, so little is known about the rates and contributing factors to zooplankton mortality, in a quantitative sense, that the issue is usually avoided altogether. In the absence of specific information on the processes governing death rates of natural populations, the shortest path is often taken, i.e. simply to assume zooplankton mortality is constant in order to better focus on the processes thought to be of primary interest.

Furthermore, detailed demographic studies that permit mortality to be estimated directly in the field are demanding and have rarely been attempted. In many ocean environments, ocean circulation and mixing make them unsuitable for such studies. This has led some investigators to seek alternative means to estimate mortality in indirect ways. Among these are relationships that assume mortality rates can be approximated from easily measured independent variables such as body mass (Peterson and Wroblewski, 1984), adult fecundity and habitat temperature (Hirst and Kiørboe, 2002), or depth in the water column (Aksnes and Giske, 1990). Such approaches assume that stage-specific patterns and daily rates of mortality are predictable by the independent variable (body size, temperature, depth, etc.) alone. An implicit assumption is that mortality is little influenced by regional differences in the environment, i.e. that ocean environments with the same physical characteristics will lead to spatially uniform rates and stage-specific patterns of mortality.

In the present study we test the hypothesis of spatial uniformity of rates and patterns of mortality of *Calanus finmarchicus*. This species is a key member of pelagic foodwebs in the temperate−boreal North Atlantic. It formed the focus of the recent Trans-Atlantic Study of *Calanus* (TASC) program (Tande and Miller, 2000). In the spirit of comparative regional study initiated by TASC, we assess whether mortality patterns are essentially uniform in different sectors of the North Atlantic, such that they can be inferred from independent variables without regard to the specific local circumstances. Our study contrasts five regions in which *C. finmarchicus* is a dominant member of the zooplankton assemblage (Figure 1). We draw on our own
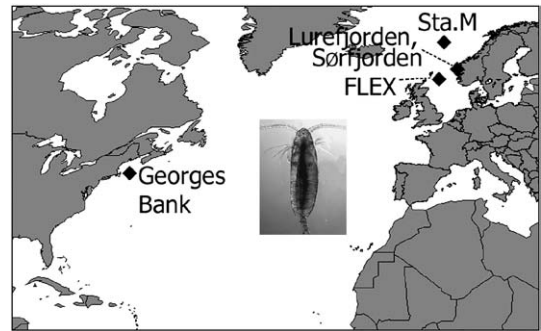

Figure 1. Locations of the five study sites in the North Atlantic. Further details are provided in Table 1.

recent investigations that have utilized comparable numerical methods for mortality estimation. Two of the study regions are continental shelf localities (Georges Bank, studied as part of the US GLOBEC Northwest Atlantic program (Ohman *et al.*, 2002), and the northern North Sea, the focus of historic Fladen Ground '76 experiment (FLEX; Krause and Trahms, 1983). Two are Nordic fjords (Lurefjorden and Sørfjorden) that are geographically close to one another but have markedly different guilds of predators (Eiane, 1999; Eiane *et al.*, 2002). The last is a deep ocean site at Ocean Station M, near the center of the Norwegian Sea (Irigoien *et al.*, 1998; Hirche *et al.*, 2001).

Methods

Georges Bank

Georges Bank is a region with a relatively long on-bank residence time of fluid (Naimie *et al.*, 2001) and zooplankton, especially after the onset of seasonal stratification, making it particularly appropriate for demographic studies. This is one of the major reasons it was selected as a study site for US GLOBEC. Sampling was conducted on 30 broadscale survey cruises from 1995 to 1999. Each year, six monthly cruises were carried out from January to June (February to July in 1995). Vertically stratified samples were taken with both a plankton pump and a 153-μm mesh MOCNESS and the appropriate sampling device chosen for each developmental stage of *C. finmarchicus* (Durbin *et al.*, 2000; Ohman *et al.*, 2002). Abundances were integrated vertically per square meter. A sampling bias against nauplius 1 and 2 (N1 and N2) of *Calanus* was detected when a centrifugal pump was used and a bias against N1 was found when a diaphragm pump was substituted. We presume that the bias arose due to mechanical disturbance of fragile nauplii. Hence, the earliest stage for which mortality could be estimated was a combined egg-through-N3 (egg−N3) stage with the centrifugal pump (February 1995 to June 1998) and a combined egg-through-N2 (egg−N2) stage with the diaphragm pump (June 1998 to June 1999). Such combined stages reflect mortality between the

production of eggs and the end of N2 or N3. Temperatures used to predict development rates from Campbell *et al.* (2001a) were obtained from the mean depth of each developmental stage at each station sampled. Egg input to the water column by *C. finmarchicus* was obtained from assessments of a gonadal index, calibrated against experimental determinations of egg production rates (Runge *et al.*, submitted for publication). Other explicit details related to sampling and the mortality solution methods, using the Vertical Life Table method (VLT; Aksnes and Ohman, 1996) for stages after nauplius 2 (N2) and the modified VLT for earlier developmental stages, can be found in Ohman *et al.* (2002). The VLT assumes constancy of stage ratios, but not of absolute abundances, as addressed further below.

In April 1997 and April 1999, developing cohorts of copepods were tracked on Georges Bank by following two to three mesh sock drifters drogued at 20-m depth for 6−11 days. Each day a series of five pump profiles was made for younger developmental stages, and three bongo tows made for adults using a 200-μm mesh net. Aliquots from each group of daily replicated samples were pooled for enumeration of abundance of each developmental stage.

FLEX − northern North Sea

These data originate from the intensive study of Krause and Trahms (1983) and were kindly provided by M. Krause. Samples were taken from the RV "Meteor" at the central station in the FLEX '76 study in the northern North Sea using 10-l Niskin bottles on a rosette, from 26 March to 6 June 1976. Samples were taken as often as four times per day, at standard depths of 3, 10, 20, 30, 40, 50, 60, 75 or 80, 100 m, and, from 9 May onward, near the bottom at 150 m. Each sample was enumerated entirely, without subsampling (Krause and Trahms, 1983).

We initially expected that Niskin bottle collection would be suitable for nauplii and early copepodids, but not for adults of *Calanus*. However, Williams and Lindley (1980a) found reasonable agreement between zooplankton dry biomass estimated by a high speed towed sampler (on continuous transect lines) and this water bottle sampling (at a fixed geographic location). Krause and Radach (1989) reported that comparisons of depth-integrated abundances from their water bottle series with net collections showed higher abundances in the water bottles. In mesocosm experiments in Espegrend, Norway, direct comparisons of *Calanus* collected by water bottles with those recovered from drained mesocosms showed no bias against C5, adult male, or adult female *Calanus* by the bottles (data from Rey, 2000). Hence, we include mortality estimates for all stages of *C. finmarchicus* here, although we apply a cautionary note to the rates obtained for the late copepodids and adults.

Mortality estimates were restricted to the period between 19 April and 17 May because this period corresponded to the spring bloom (Krause and Trahms, 1983) when development rates might be expected to be food-satiated. We also focused on this time period because it appears to be an interval without the introduction of different water masses. After 17 May a storm moved through the study site and sampling was interrupted briefly. Comparison of development times predicted from Belehrádek functions (Campbell *et al.*, 2001a) with measurements made for *C. finmarchicus* during the FLEX experiments (Williams and Lindley, 1980b) reveals that *Calanus* was developing through each copepodid stage at rates corresponding to temperature-dependent maximum rates. Appropriate temperatures were obtained from the temperature (Soetje and Huber, 1980) at the weighted mean depth of each developmental stage (N1-through-adults) in each daily vertical profile. Mortality estimation employed the Population Surface Method (PSM; Wood, 1994) after subsampling the data at 2-day intervals to reduce the number of parameters to estimate, thereby permitting the software to converge on a solution. The PSM is a non-parametric method that makes no assumptions about an underlying demographic model, other than the constraints that the population changes relatively smoothly from one age class to the next, as described by the McKendrick−van Foerster equation, and that mortality rates are non-negative. The wiggliness parameter is selected by generalized cross-validation, as described by Wood (1994). All stage abundances were given a weight of 1. Further details are provided in Eiane and Ohman (2004).

Ocean Station M

Sampling and experiments were carried out at Ocean Station M, in the central Norwegian sea gyre, for 80 days from 22 March to 9 June 1997 (Irigoien *et al.*, 1998; Hirche *et al.*, 2001). Zooplankton were sampled between 100 m and 0 m with a WP2 net bearing a 53-μm mesh and experimental egg production incubations were done daily (Niehoff *et al.*, 1999). Although there is considerable mesoscale variability in copepod abundances at this location, the development of a well-defined generation of *C. finmarchicus* is clear and hydrographic results suggest that a single water mass was sampled (Hirche *et al.*, 2001), as discussed further below. To reduce the influence of small-scale patchiness, time-series of stage abundance and egg production were first smoothed with one pass of a four-point running mean. Methods for estimation of egg mortality are in Ohman *et al.* (2002). Here we add the mortality rates of the remainder of the life-history stages living in epipelagic waters by fitting the PSM (Wood, 1994) to the smoothed time-series of the spring generation (G_1) individuals for nauplius 1−2 (N1−N2) through copepodid stage 4. The time-series was subsampled at 2-day intervals, as above, and all stage abundances given a weight of 1. Copepodid stage 5 and adults, which occurred deeper in the water column (cf. Niehoff *et al.*, 1999), were excluded from

our analysis. In this site N1—N2 of *C. finmarchicus* were not differentiated from each other, nor were N4—N6.

Developmental stage durations for this site appeared to be food-limited prior to the spring bloom (Hirche *et al.*, 2001). Therefore, based on comparison with Hirche *et al.* (2001), the stage durations employed in the PSM were twice the Belehrádek values (Campbell *et al.*, 2001a), for feeding stages (N3—C5) until the bloom, and thereafter equal to the temperature-dependent rates. The temperature used was the average temperature in the upper 100 m of the water column.

Lurefjorden and Sørfjorden

Sampling details and solution methods are provided in Eiane (1999) and Eiane *et al.* (2002) and are summarized in Table 1. Both fjords are relatively deep and have shallow entrance sills and long residence times of water and zooplankton, making them appropriate for sampling the same population over time.

Results

Georges Bank

When applying the Vertical Life Table (VLT) method it is important to have ample replication of stage ratios (Aksnes and Ohman, 1996) and to substantiate the assumption that the observed ratios of developmental stages remain relatively stable for intervals of time corresponding to the durations of each successive pair of developmental stages. We addressed this issue on two cohort tracking cruises on Georges Bank, where sampling was done while following drifters. We report results for both *C. finmarchicus* and *Pseudocalanus newmani* + *moultoni*, in order to more fully test the assumption. The conditions were quite different on

Table 1. Locations and sampling details for the five principal study sites.

	Georges Bank	FLEX	Ocean Station "M"	Lurefjorden	Sørfjorden
Geographic location	41°N 67°30′W	58°55′N 0°32′E	66°N 2°E	60°40′N 5°10′E	60°25′N 5°30′E
Maximum depth (m)	∼200	∼150	∼2000	430	360
Sampling dates	Feb 1995—June 1999	26 March—6 June 1976	22 March—9 June 1997	27 Feb—12 June 1996	5 March—12 June 1996
Sampling interval	Monthly; first six months of each year (up to 20 priority 1 and priority 2 stations per cruise)	Up to four times daily	Daily; weekly for multi-net profiles	Weekly	Monthly
Sampling methods (a)	Pump	Rosette with 10-l Niskin bottles	WP2 net	Pump (30—0 m)	Pump (30—0 m)
(mesh size (μm))	(35 or 50)	(30)	(53)	(60)	(60)
Sampling methods (b)	MOCNESS	—	Multi-net	Multi-net	Multi-net
(mesh size (μm))	(153)		(150)	(180)	(180)
Egg production rates	Assessed from reproductive index (Runge *et al.*, 1997)	No	Yes	No	No
Mortality estimation methods	VLT* and modified VLT†	PSM‡	PSM‡ and delay differential§	PSM‡	PSM‡
Key references	Durbin *et al.*, 2000; Ohman *et al.*, 2002; Runge *et al.*, 1997	Krause and Trahms, 1983	Irigoien *et al.*, 1998; Niehoff *et al.*, 1999; Hirche *et al.*, 2001; Ohman and Hirche, 2001	Eiane *et al.*, 2002	Eiane *et al.*, 2002

*Vertical Life Table method (Aksnes and Ohman, 1996).
†Modified Vertical Life Table method (Ohman *et al.*, 2002).
‡Population Surface Method (Wood, 1994).
§Delay-differential method (Ohman and Hirche, 2001).

the two cruises: in April 1997 there was strong evidence of food limitation of development (Crain and Miller, 2001) and egg production (Campbell *et al.*, 2001b) of *C. finmarchicus*, while in April 1999 rates of development and egg production were relatively high (Wagner and Runge, unpubl.). Nevertheless, in both instances, the proportional stage composition remained relatively constant during the first week of the tracking exercise. In 1997, both *Calanus* and *Pseudocalanus* showed considerable consistency of stage composition throughout the 6 days (Figure 2). In 1999, the drifters crossed a front between 27 and 28 April, after which a separate subpopulation appeared to have been sampled. The average coefficient of variation of ratios of successive developmental stages of *C. finmarchicus* was 46.5% and 50.3% in 1997 and 1999, respectively, and for *Pseudocalanus* spp. it was 44.0% and 57.5% in the 2 years, including all dates sampled in April 1999. According to the simulations of Aksnes and Ohman (1996), this level of variation would introduce minimal bias into the mortality estimates by the VLT. We advise users of the VLT to directly validate associated assumptions before applying the method.

The average mortality rates for *C. finmarchicus* from all 30 broadscale survey cruises on Georges Bank between January and June showed considerable variation across the life history (Figure 3a). Note that the earliest life-history phase for which we could resolve mortality rates in this study site was the combined egg−N2 (June 1998 to June 1999 only) and also that the VLT solution method provides mortality estimates for successive stage pairs, but not for individual stages. Peak mortality of $0.50 \, \mathrm{d}^{-1}$ was observed in the earliest phase of the life history, egg−N2, followed by a rapid decline in mortality to near-zero values at N3/N4. Subsequently, a secondary increase in mortality rates to $0.15 \, \mathrm{d}^{-1}$ occurred in the late naupliar and early copepodid stages, followed by a decline to relatively stable values of $0.05-0.07 \, \mathrm{d}^{-1}$ through the C5/adult female. Georges Bank was the only one of the five localities studied where a secondary mode of increased mortality occurred in the late naupliar stages.

Mortality rates early in the life history of *C. finmarchicus* were found to be conditionally density-dependent (Figure 4a). That is, egg−N2 mortality rates were independent of adult population size at low adult abundances, but became
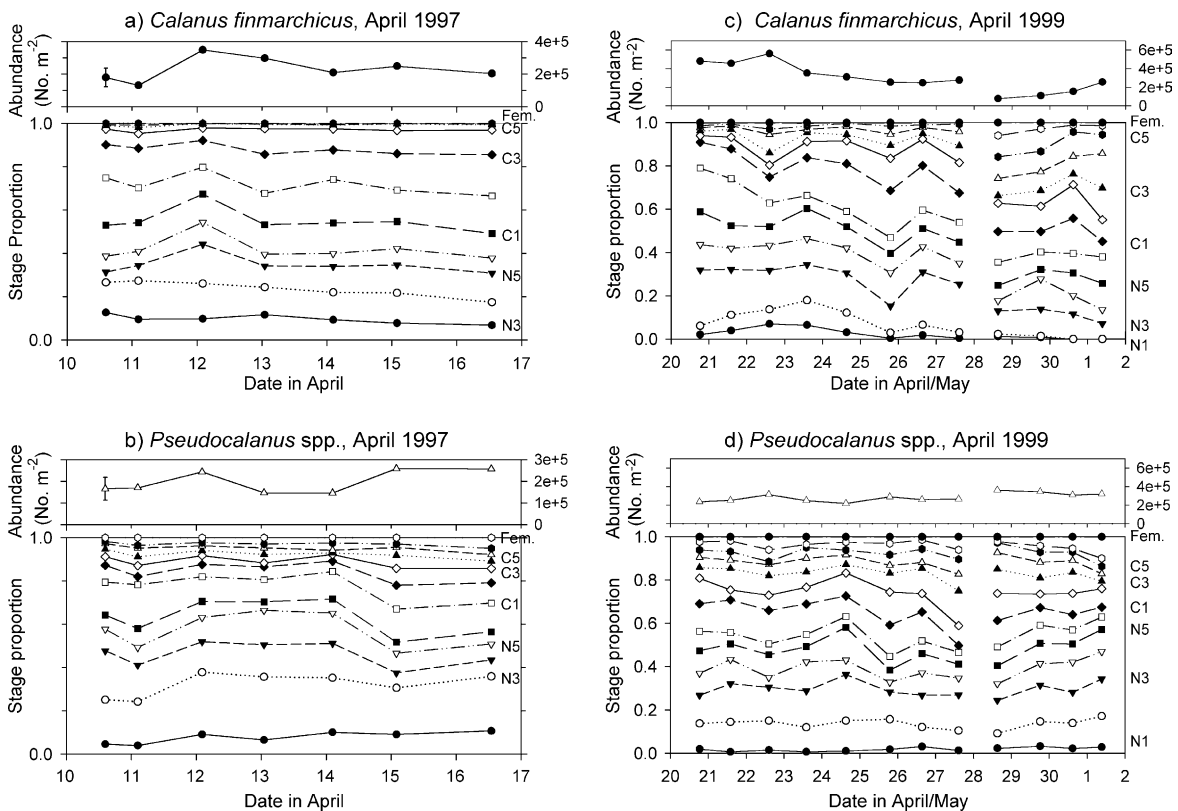

Figure 2. Temporal variations in total abundance and developmental stage composition of two copepod taxa on cohort tracking cruises on Georges Bank in April 1997 and April 1999. Daily sampling was conducted while following a mesh sock drifter. (a) *Calanus finmarchicus* in April 1997, (b) *Pseudocalanus* spp. (*newmani + moultoni*) in April 1997, (c) *C. finmarchicus* in April 1999, and (d) *Pseudocalanus* spp. in April 1999. Error bars on the first day in panels (a) and (b) are the 95% CL.

directly proportional to adult abundance at high population abundances. Such a relationship was also found for egg−N3 mortality rates, for which the data set is larger, as discussed more fully in Ohman et al. (2002).

FLEX − northern North Sea

The FLEX region is another continental shelf region. Estimates of egg mortality rates are not available for this
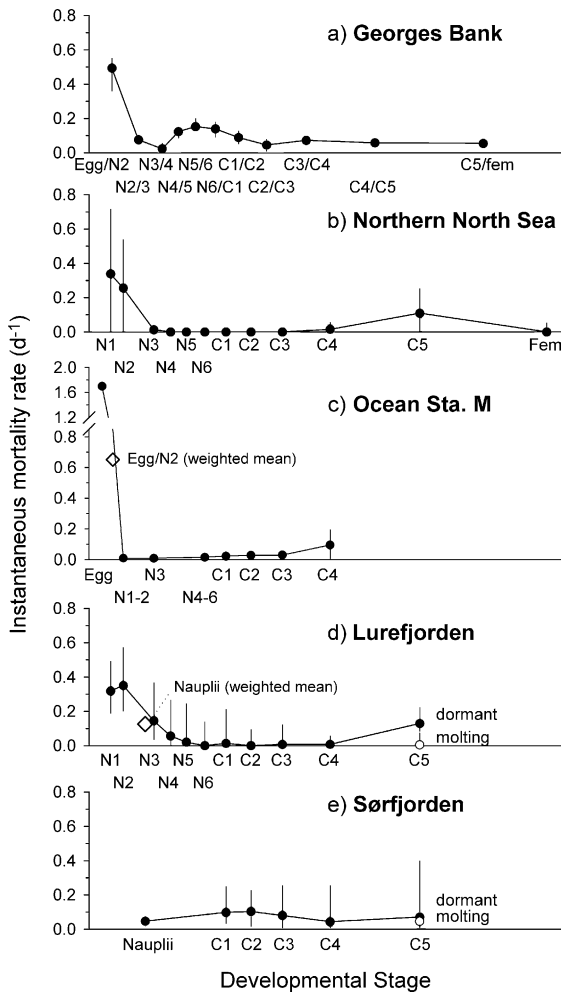

Figure 3. Variations in *Calanus* mortality rate with developmental stage in the five study sites. (a) Georges Bank, (b) the central FLEX region of the northern North Sea, (c) Ocean Station M, (d) Lurefjorden, and (e) Sørfjorden. Abscissa labels in panel (a) indicate the stage pairs for which mortality estimates were made. Open diamond in panel (c) indicates the weighted mean mortality rate for egg-through-N2 for comparison with the value in panel (a). Open diamond in panel (d) indicates the weighted mean mortality rate for all naupliar stages for comparison with the value in panel (e). "Dormant" indicates the mortality rate if C5s have begun to enter dormancy and "molting" indicates the mortality rate if all C5s are molting directly to the adult. Values are mean ± 95% CL except panel (a), which illustrates median ± non-parametric 95% CL.

region because systematic egg production measurements were not conducted during the FLEX study. Mortality rates for *C. finmarchicus* in the period of mid-April to mid-May, an interval over which evidence indicates that the same population was sampled, declined markedly from maxima for stages N1 and N2, to near-zero values through the early copepodid stages (Figure 3b). If the water bottles remained relatively unbiased samplers for late copepodid stages, the resulting pattern is that of a gradual increase in instantaneous mortality rates from C4 to C5 (to $0.11\ \mathrm{d}^{-1}$), and thereafter a decline for adult females.

Ocean Station M

This open ocean locality is the only site where *Calanus* egg mortality could be estimated independently of other developmental stages. The average egg mortality rates between late March and early June were high, $1.7\ \mathrm{d}^{-1}$, and declined quickly to near-zero values for the naupliar stages (Figure 3c). As in the FLEX region, a secondary increase in mortality of late naupliar−early copepodid stages was not observed. Mortality rates increased slightly to copepodid stage 4.

Also plotted in Figure 3c is the weighted mean value of egg−N2 mortality at Ocean Station M, for direct comparison with the values obtained on Georges Bank. When expressed over a comparable part of the life history the average value of egg−N2 mortality in the open ocean ($0.65\ \mathrm{d}^{-1}$) is slightly higher than the corresponding value on the continental shelf ($0.50\ \mathrm{d}^{-1}$). As observed on Georges Bank at high abundances, mortality rates of the youngest developmental stages (here, the eggs) were found to be directly proportional to the abundance of adult female *C. finmarchicus* (Figure 4b). Both regressions in Figure 4 remain significant ($\mathrm{p}<0.01$) if the two highest points are eliminated from either analysis.

Lurefjorden and Sørfjorden

The contrasting patterns of *Calanus* mortality in Lurefjorden and Sørfjorden between March and mid-June have been presented and discussed in Eiane (1999) and Eiane et al. (2002). Although eggs were sampled in the water column in that study, we did not have available corresponding egg production rate determinations from which egg mortality rates could be properly assessed. The *Calanus* population is thought to be dominated by *C. finmarchicus* in these fjords, but *C. helgolandicus* and *C. glacialis* can also be present, so we refer to them as *Calanus* spp. In Lurefjorden, which is characterized by elevated abundances of carnivorous zooplankton and few fish, mortality rates of early *Calanus* nauplii were high, then declined to near-zero values for the late nauplii through early copepodids (Figure 3d). Assignment of correct mortality rates for the C5s depends on whether in mid-June they begin to enter dormancy (filled symbol, Figure 3d) or continue to molt to adults (open symbol). The molting status was not directly assessed, but
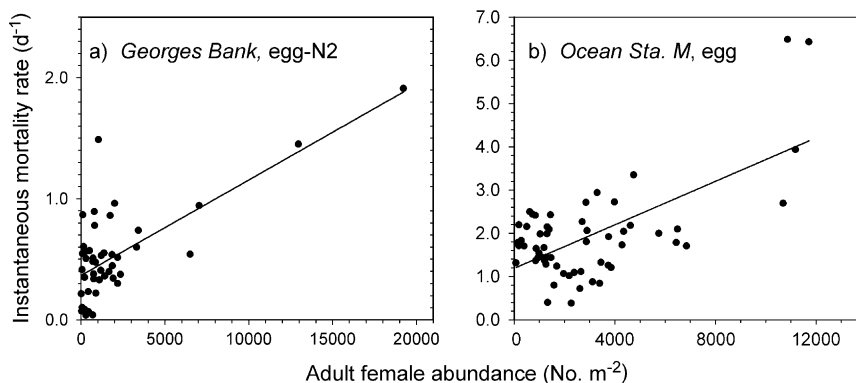
Figure 4. Relationship of early stage mortality of *Calanus finmarchicus* to the abundance of adult females on (a) Georges Bank (egg−N2 mortality rates) and (b) Ocean Station M (egg mortality rates). Regressions: Georges Bank: $Y = 0.000079X + 0.3673$, $r^2 = 0.490$, $p < 0.0001$; Station M: $Y = 0.000252X + 1.1915$, $r^2 = 0.415$, $p < 0.0001$.

we consider it more likely that this population was beginning to enter dormancy at this time.

In Sørfjorden the stage-specific pattern of mortality exhibited low and relatively constant rates across the entire life history (Figure 3e). To compare the naupliar mortality rates in Lurefjorden, where sampling was sufficiently frequent to resolve stage-specific rates, with the more infrequent sampling in Sørfjorden, the weighted mean mortality rate of all nauplii was calculated in Lurefjorden (open symbol, Figure 3d). Accordingly, the average rates of naupliar mortality in Lurefjorden ($0.13 \, d^{-1}$) were appreciably higher than in Sørfjorden ($0.05 \, d^{-1}$). In neither fjord was there a secondary hump in late naupliar/early copepodid mortality, as seen on Georges Bank.

Differences between adult male and adult female mortality were estimated on Georges Bank where the adult rates were estimated as the C5/adult stage pair. The C5/males rates (0.093 ± 0.084, mean $\pm$ 95% CL) were nearly twice those of the females (0.054 ± 0.041). Elevated mortality rates of adult males are consistent with the reduced mouthparts and non-feeding males characteristic of this lineage of calanoid copepods.

Discussion

Our results are inconsistent with the assumption of geographic uniformity of rates and patterns of mortality for *Calanus finmarchicus* in different sectors of the North Atlantic (Figure 3). The five geographic regions studied show distinctive patterns of mortality that reflect responses to local conditions. Furthermore, we did not find a characteristic mortality schedule for those ocean environments that share similar geomorphology (either continental shelves or fjords). The two continental shelf sites compared, Georges Bank and the northern North Sea, differed appreciably in mortality patterns of late naupliar and early copepodid stages. The two fjords studied by Eiane *et al.*

(2002) showed mortality schedules as different from one another as those seen between any two of the five sites in the North Atlantic. These two fjords are located approximately 20 km apart, indicating that the geographic separation of two localities, by itself, is not sufficient grounds for extrapolating mortality schedules. Instead, the differences are attributable to markedly different guilds of predators in the two fjords (Eiane *et al.*, 2002). McCaffrey (2000) found that the differences between these fjords in copepod mortality patterns can substantially alter rates of secondary production by *C. finmarchicus*, even if the abundance of copepods surviving to the adult stage were the same in the two environments.

The implication of our overall result is that the regional setting in which the *Calanus* is found, and in particular the predator field, must be considered in assessing the regional dynamics and responses to climate change of *C. finmarchicus*. This conclusion will surprise few readers. Nevertheless, it is at variance with numerous 1-D models that seek to represent zooplankton in a spatially uniform North Atlantic. This result is also inconsistent with several indirect approaches that have been proposed to estimate zooplankton mortality (see below).

Regional contrasts

The secondary increase in mortality of late naupliar/early copepodid stages of *C. finmarchicus* found on Georges Bank and not elsewhere is noteworthy. In contrast to *Calanus*, *Pseudocalanus newmani + moultoni* co-occurring with *Calanus* on Georges Bank did not show elevated mortality risk at that phase of the life history. Ohman *et al.* (2002) concluded that *Metridia lucens* and other omnivorous or carnivorous zooplankton that have a strong preference for *Calanus* nauplii over *Pseudocalanus* nauplii (Sell *et al.*, 2001) are responsible for the interspecific differences on Georges Bank. We hypothesize that predators with the prey selection characteristics of *M. lucens* are

considerably less abundant in the other study regions considered here. However, we do not currently have sufficient information to positively identify all predators with such feeding behavior, and so we cannot yet evaluate this hypothesis directly.

We have only one truly deepwater open ocean site in this study, which limits our ability to rigorously compare mortality rates in oceanic vs. nearshore environments. From this one site, we observe that egg mortality rates of *C. finmarchicus* were relatively high and all naupliar and early copepodid stages showed quite low rates. Additional study sites in oceanic environments are clearly needed. An increase of C5 mortality rates relative to C4s was suggested in three sites in which stage-specific rates could be resolved, and a similar pattern was observed by Irigoien *et al.* (2000) south of Iceland. In the FLEX region the rates declined in the adult female stage. From the FLEX study there is evidence that adult females live deeper in the water column than C5s both day and night (Williams and Lindley, 1980b; Krause and Radach, 1989; Eiane and Ohman, 2004), which was also true on Georges Bank (Durbin *et al.*, 2000; Ohman *et al.*, 2002). In these relatively shallow-water locales where there is limited opportunity for diel vertical migration, the persistent deeper habitat occupied by the adult females seems to make them less vulnerable than C5s to visually hunting predators.

The mortality rates reported by Matthews *et al.* (1978) for *C. finmarchicus* in Korsfjorden, western Norway were variable and generally quite high, but are now thought to have been strongly influenced by transport processes (Aksnes and Magnesen, 1983). Working in Lindåspollene, a fjord in southwestern Norway, Aksnes and Magnesen estimated higher rates of mortality for early copepodid stages of *C. finmarchicus* than we found, although the stage durations they used appear to be too brief.

Differences between Georges Bank and the Norwegian Sea in the slope of the density-dependent relationships are to be expected, as egg mortality was resolved separately at Station M but only the combined egg-through-N2 mortality was resolvable on Georges Bank. The weighted mean mortality of egg-through-N2 mortality at Station M was only slightly higher than that on Georges Bank, suggesting that the absolute rates, as well as some of the causal factors, may be similar between the two regions. We have suggested elsewhere (Ohman and Hirche, 2001; Ohman *et al.*, 2002) that the most parsimonious explanation for the density-dependent mortality in both regions is cannibalism by late copepodids and adult females of *Calanus* on their own young (cf. Runge and Roff, 2000; Runge *et al.*, pers. obs.). Resuspended hydroids are an important additional source of egg mortality on Georges Bank inside the tidal mixing front, but they would be lacking in the deepwater open ocean environment. Density-dependent mortality related to cannibalism has also been reported for populations of *Acartia* in shallow-water coastal environments (e.g. Landry, 1978). Such density-dependence makes linear relationships between changing climate variables and population responses unlikely. Density-dependent mortality can interact with both the mean and variability of climate state to give non-linear population responses (Coulson *et al.*, 2001).

Egg hatching success has not been found to be a major source of *Calanus* egg mortality at either Ocean Station M (Ohman and Hirche, 2001) or Georges Bank (electronic supplement in Irigoien *et al.*, 2002, in comparison with the present results).

Suitability of methodology

In comparing mortality schedules in five regions of the North Atlantic the reader should bear in mind that these studies are from not only different locations, but also different years, for differing durations, with different sampling methods. However, as these are among the more comprehensive seasonal studies of *Calanus finmarchicus* in the North Atlantic they bear inspection for patterns of similarity and differences. At Georges Bank, the one location where we have mortality estimates in multiple years, the mortality patterns across the life history were similar from year-to-year (ms in prep.). We also note that the seasonal trends in abundance of *C. finmarchicus* at Ocean Station M (Hirche *et al.*, 2001) are similar to the trends observed there four decades earlier (Østvedt, 1955), although we do not have mortality estimates from the earlier study. It remains possible that interannual differences have confounded our comparison of sites, but, if so, this emphasizes the need to address both interannual and spatial variations in mortality patterns.

Knowledge of stage durations is important for all methods utilized. Aksnes and Ohman (1996) have modeled and others have directly examined (Aksnes and Ohman, 1996; Ohman *et al.*, 2002; Eiane and Ohman, 2004) the robustness of mortality estimates to errors in stage durations. Both mortality patterns and rates are relatively insensitive to errors of a factor of 2. The optimum approach would be to have concurrent measures of molting rates at each sampling interval. Concerning the use of a different solution method on Georges Bank, there is no evidence that this has influenced the regional contrasts in a significant way. Direct comparison of results from the VLT method and the PSM method, when the assumptions of both were met, found comparable results (Aksnes and Ohman, 1996; Eiane and Ohman, 2004).

Advection and other sources of patchiness complicate efforts to estimate mortality in field populations and render the problem intractable in many situations. However, the mixing of different populations was minimized in three of our study sites because two of them are semi-enclosed fjords (Lurefjorden and Sørfjorden) with limited exchange with the coastal ocean. The third site is a highly retentive bank (Georges Bank), with tidally rectified circulation that leads to a protracted on-bank residence times. Moreover,

on Georges Bank the solution method for most of the life history employs stage ratios rather than stage abundances; ratios of developmental stages generally show much less spatial variability than absolute abundances, which is a primary motivation for applying the VLT method (cf. Aksnes and Ohman, 1996). In the North Sea site, we selected a relatively short time interval during which physical data suggested a lack of intrusions of different water masses. Furthermore, the stage structure of the population sampled in the FLEX region indicated the temporal progression of a developing generation of *C. finmarchicus* (Eiane and Ohman, 2004). At Ocean Station M, Hirche *et al.* (2001) discuss evidence from hydrographic data, hind-casting particle tracking models, and drifter trajectories that the *C. finmarchicus* population of only the southwestern Norwegian Basin was sampled in their time-series. It is inevitable that different patches within this water mass were sampled, although such patches are estimated to have originated from a radius of no more than 100 km (Hirche *et al.*, 2001). The smoothing step carried out here reduces the influence of the occasional outlier in daily time-series at Station M. Moreover, the Population Surface Method has been shown through simulation study (Wood, 1994) and empirical comparisons (Ohman and Wood, 1996) to recover underlying population dynamics and give robust mortality estimates even in the presence of moderate levels of sampling variability. Patchiness surely exists at Station M, but with appropriate numerical methods it need not obscure the underlying basic patterns of development of a copepod generation and stage-specific differences in mortality.

Calanus growth experiments in mesocosms in Espegrend, Norway (Hygum *et al.*, 2000; Rey, 2000) provide mortality rates measured in a nearly optimal environment, against which our rates for natural populations can be compared. Although the mesocosms were certainly not free of predators, they were initiated with sorted eggs of *Calanus* and would have experienced no cannibalism at the outset and very low abundances of most other potential predators. Accordingly, mortality rates averaged 0.012 d^{-1} in the low food concentration treatment and 0.011 d^{-1} at high food, apparently with little difference across the life history (Hygum *et al.*, 2000). In comparison, the rates observed in all five study sites in the North Atlantic were appreciably higher than these nearly optimal rates, confirming that natural populations experience significantly higher losses than might be expected due to physiological shortcomings alone.

Indirect approaches to mortality estimation

With the paucity of morality estimates from direct demographic study, a number of indirect approaches have been attempted. Allometric relationships have been found between mortality rate and body size (Peterson and Wroblewski, 1984), or body size and patchiness as a covariate (McGurk, 1987), when variations in adult body size are considered over several orders of magnitude for diverse marine organisms. However, such summaries across diverse taxa are poor descriptors of the body size-dependence of copepod mortality rates (Hirst and Kiørboe, 2002). Moreover, the allometric approach cannot account for regional differences that we observe in the present study for animals of the same developmental stage and very similar sizes.

Another approach related to allometry assumes that, at steady-state, the lifetime fecundity of an organism should be exactly compensated by mortality. This general method has been applied to organisms such as marine fishes (Gunderson and Dygert, 1988) and, more recently, to planktonic copepods of two different types of life history (Hirst and Kiørboe, 2002). Although the latter authors conclude that the mortality predicted from body mass and temperature "generally match the field measurements well with respect to rates and patterns," this assessment appears rather optimistic. Field estimates of egg mortality rates for broadcast spawning taxa are consistently higher than expected from the independent variable, often by 1−2 orders of magnitude (Figure 6a in Hirst and Kiørboe, 2002), while post-hatch mortality rates of larger broadcast spawners are underestimated by temperature at high temperature and overestimated by body mass at high body mass. Notably, the variability in mortality rates observed at any given adult body mass or temperature is usually 1−2 orders of magnitude, even where the mean is approximated by the independent variable.

Dam and Tang (2001) also apply a steady-state assumption, but their objective is not to predict mortality rates, but rather to provide upper plausible bounds for mortality rates that are sustainable for sequential generations. This is intended as a reference limit or guide, rather than an expected rate.

Myers and Runge (1983) used life-history theory to explain seasonal changes in copepod body size and mortality rates as an evolutionarily stable strategy in environments with seasonal changes in predation pressure. This approach takes account of the seasonal changes of the predator field in the study site of interest, but it appears not to have been applied outside the original test data of *Acartia hudsonica* (=*clausi*) in Jakles Lagoon.

Aksnes and Giske (1990) have suggested that the mortality risk to copepods can be characterized *a priori* as a function of their depth in the water column. This generalized characterization of risks does not predict specific regional differences we observed between such environments as Georges Bank and the northern North Sea.

Apart from the life-history analysis of Myers and Runge (1983), such indirect approaches are not suited to the seasonal population dynamics of individual species. Although time-dependent variations in mortality are not the focus of the present analysis, they have been found to be key factors explaining temporal abundance variations of *C. finmarchicus* (Ohman and Hirche, 2001), *Pseudocalanus newmani* (Ohman and Wood, 1996), and a variety of other

taxa. Furthermore, none of the indirect approaches consider the possibility of mortality rates that vary as a function of population density, as observed in both a continental shelf and an open ocean study site.

In conclusion, we found regional variations in stage-specific mortality in five localities in the North Atlantic. Such differences are inconsistent with a suite of indirect methods that have been proposed to estimate zooplankton mortality. In those situations where the predator field has been well characterized, regional variations are clearly relatable to different types of predators with different prey selection characteristics. We expect that such differences in predator fields underlie the remaining geographic variations, although this issue requires direct quantitative test. Just as local variations in the primary production cycle can generate different rates of population increase, spatial differences in the rates, patterns, and causal agents of mortality will influence the dynamics of *Calanus finmarchicus* in different sectors of the Atlantic. Explicit consideration of the interaction of the regional biotic environment with climatic factors will increase our ability to forecast future changes in marine zooplankton populations.

Acknowledgements

References

Aksnes, D. L., and Giske, J. 1990. Habitat profitability in pelagic environments. Marine Ecology Progress Series, 64: 209−215.

Aksnes, D. L., and Magnesen, T. 1983. Distribution, development, and production of *Calanus finmarchicus* (Gunnerus) in Lindåspollene, western Norway, 1979. Sarsia, 68: 195−208.

Aksnes, D. L., and Ohman, M. D. 1996. A vertical life table approach to zooplankton mortality estimation. Limnology and Oceanography, 41: 1461−1469.

Beaugrand, G., Reid, P. C., Ibañez, F., Lindley, J. A., and Edwards, M. 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. Science, 296: 1692−1694.

Brinton, E., and Townsend, A. 2003. Decadal variability in abundances of the dominant euphausiid species in southern sectors of the California Current. Deep-Sea Research II, 50: 2469−2492.

Campbell, R. G., Wagner, M. M., Teegarden, G. J., Boudreau, C. A., and Durbin, E. G. 2001a. Growth and development rates of the copepod *Calanus finmarchicus* reared in the laboratory. Marine Ecology Progress Series, 221: 161−183.

Campbell, R. G., Runge, J. A., and Durbin, E. G. 2001b. Evidence for food limitation of *Calanus finmarchicus* production rates on the southern flank of Georges Bank during April 1997. Deep-Sea Research II, 48: 531−549.

Coulson, T., Catchpole, E. A., Albon, S. D., Morgan, B. J. T., Pemberton, J. M., Clutton-Brock, T. H., Crawley, M. J., and Grenfell, B. T. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. Science, 292: 1528−1531.

Crain, J. A., and Miller, C. B. 2001. Effects of starvation on intermolt development in *Calanus finmarchicus* copepodites: a comparison between theoretical models and field studies. Deep-Sea Research II, 48: 551−566.

Dam, H. G., and Tang, K. W. 2001. Affordable egg mortality: constraining copepod egg mortality with life history traits. Journal of Plankton Research, 23: 633−640.

Durbin, E. G., Garrahan, P. R., and Casas, M. C. 2000. Depth distribution of *Calanus finmarchicus* nauplii on the Georges Bank during 1995 and 1996. ICES Journal of Marine Science, 57: 1686−1693.

Eiane, K. 1999. Pelagic food webs: structuring effects of different environmental forcing. Dr Scientific Thesis, University of Bergen, Norway, 1−121.

Eiane, K., Aksnes, D. L., Ohman, M. D., Wood, S., and Martinussen, M. B. 2002. Stage-specific mortality of *Calanus* spp. under different predation regimes. Limnology and Oceanography, 47: 636−645.

Eiane, K., and Ohman, M. D. 2004. Stage specific mortality of *Calanus finmarchicus*, *Pseudocalanus elongatus* and *Oithona similis* on Fladen Ground, North Sea, during a spring bloom. Marine Ecology Progress Series, 268: 183−193.

Fromentin, J.-M., and Planque, B. 1996. *Calanus* and environment in the eastern North Atlantic. II. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. Marine Ecology Progress Series, 134: 111−118.

Gunderson, D. R., and Dygert, P. H. 1988. Reproductive effort as a predictor of natural mortality rate. Journal du Conseil International pour l'Exploration de la Mer, 44: 200−209.

Heath, M. R., Backhaus, J. O., Richardson, K., McKenzie, E., Slagstad, D., Beare, D., Dunn, J., Fraser, J. G., Gallego, A., Hainbucher, D., Hay, S., Jonasdottir, S., Madden, H., Mardaljevic, J., and Schacht, A. 1999. Climate fluctuations and the spring invasion of the North Sea by *Calanus finmarchicus*. Fisheries Oceanography, 8(Suppl.): 163−176.

Hirche, H.-J., Brey, T., and Niehoff, B. 2001. A high-frequency time series at ocean weathership station M (Norwegian Sea): population dynamics of *Calanus finmarchicus*. Marine Ecology Progress Series, 219: 205−219.

Hirst, A. G., and Kiørboe, T. 2002. Mortality of marine planktonic copepods: global rates and patterns. Marine Ecology Progress Series, 230: 195−209.

Hygum, B. H., Rey, C., Hansen, B. W., and Tande, K. 2000. Importance of food quantity to structural growth rate and neutral lipid reserves accumulated in *Calanus finmarchicus*. Marine Biology, 136: 1057−1073.

Irigoien, X., Harris, R. P., Head, R. N., Lindley, J. A., and Harbour, D. 2000. Physiology and population structure of *Calanus finmarchicus* (Copepoda: Calanoida) during a Lagrangian tracer release experiment in the North Atlantic. Journal of Plankton Research, 22: 205−221.

Irigoien, X., Harris, R. P., Verheye, H. M., Joly, P., Runge, J., Starr, M., Pond, D., Campbell, R., Schreeve, R., Ward, P., Smith, A. M., Dam, H. G., Peterson, W., Threll, V., Koski, M., Smith, T., Harbour, D., and Davidson, R. 2002. Copepod hatching success in marine ecosystems with high diatom concentrations. Nature, 419: 387−389.

Irigoien, X., Head, R., Klenke, U., Meyer-Harms, B., Harbour, D., Niehoff, B., Hirche, H.-J., and Harris, R. 1998. A high frequency time series at weathership M, Norwegian Sea, during the 1997 spring bloom: feeding of adult female *Calanus finmarchicus*. Marine Ecology Progress Series, 172: 127−137.

Krause, M., and Radach, G. 1989. On the relations of vertical distribution, diurnal migration and nutritional state of herbivorous zooplankton in the northern North Sea during FLEX 1976. Internationale Revue gesamten Hydrobiologie, 4: 371−417.

Krause, M., and Trahms, J. 1983. Zooplankton dynamics during FLEX '76. *In* North Sea Dynamics, pp. 632−661. Ed. by J. Sündermann, and W. Lenz. Springer Verlag, Berlin.

Landry, M. R. 1978. Population dynamics and production of a planktonic marine copepod, *Acartia clausii*, in a small temperate lagoon on San Juan Island, Washington. Internationale Revue gesamten Hydrobiologie, 63: 77−119.

Lavaniegos, B. E., and Ohman, M. D. 2003. Long term changes in pelagic tunicates of the California Current. Deep-Sea Research II, 50: 2493−2518.

Mantua, N. J., Hare, S. R., Zhang, Y., Wallace, J. M., and Francis, R. C. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society, 78: 1069−1079.

Matthews, J. B. L., Hestad, L., and Bakke, J. L. W. 1978. Ecological studies in Korsfjorden, western Norway. The generations and stocks of *Calanus hyperboreus* and *C. finmarchicus* in 1971−1974. Oceanologica Acta, 1: 277−284.

McCaffrey, D. 2000. Dynamique de population de *Calanus finmarchicus* (Gunnerus, 1765) dans deux fjords norvégiens. Conséquences de la prédation sur la production secondaire et la stratégie de vie, pp. 1−32. DEA Océanologie Biologique et Environnement Marin, Université Pierre et Marie Curie, Paris VI.

McGurk, M. D. 1987. Natural mortality and spatial patchiness: reply to Gulland. Marine Ecology Progress Series, 39: 201−206.

Myers, R. A., and Runge, J. A. 1983. Predictions of seasonal natural mortality rates in a copepod population using life-history theory. Marine Ecology Progress Series, 11: 189−194.

Naimie, C. E., Limeburner, R., Hannah, C. G., and Beardsley, R. C. 2001. On the geographic and seasonal patterns of the near-surface circulation on Georges Bank − from real and simulated drifters. Deep-Sea Research II, 48: 501−518.

Niehoff, B., Klenke, U., Hirche, H.-J., Irigoien, X., Head, R., and Harris, R. 1999. A high frequency time series at weathership M, Norwegian Sea, during the 1997 spring bloom: the reproductive biology of *Calanus finmarchicus*. Marine Ecology Progress Series, 176: 81−91.

Ohman, M. D., and Hirche, H.-J. 2001. Density-dependent mortality in an oceanic copepod population. Nature, 412: 638−641.

Ohman, M. D., Runge, J. A., Durbin, E. G., Field, D. B., and Niehoff, B. 2002. On birth and death in the sea. Hydrobiologia, 480: 55−68.

Ohman, M. D., and Wood, S. N. 1996. Mortality estimation for planktonic copepods: *Pseudocalanus newmani* in a temperate fjord. Limnology and Oceanography, 41: 126−135.

Østvedt, O. J. 1955. Zooplankton investigations from weathership 'M' in the Norwegian Sea. 1948−49. Hvalrådets Skrifter. Scientific Results of Marine Biological Research, 40: 1−93.

Peterson, I., and Wroblewski, J. S. 1984. Mortality rate of fishes in the pelagic ecosystem. Canadian Journal of Fisheries and Aquatic Sciences, 41: 1117−1120.

Reid, P. C., and Beaugrand, G. 2002. Interregional biological responses in the North Atlantic to hydrometeorological forcing. *In* Large Marine Ecosystems of the North Atlantic. Changing States and Sustainability, pp. 27−48. Ed. by K. Sherman, and H. R. Skjoldal. Elsevier, Amsterdam.

Rey, C. 2000. Etude du développement, de la croissance, de la ponte et de leurs sources de variabilité chez des copépodes marins élevés en milieu contrôlé. Thèse Doctorat, Université Pierre et Marie Curie, Paris VI: 1−168.

Runge, J. A., and Roff, J. C. 2000. The measurement of growth and reproductive rates. *In* ICES Zooplankton Methodology Manual, pp. 401−454. Ed. by R. P. Harris, P. H. Wiebe, J. Lenz, H. R. Skoldal, and M. Huntley. Academic Press, San Diego.

Runge, J. A., Durbin, E., Plourde, S., and Gratton, Y. 1997. Spatial and temporal variation in egg production of *Calanus Finmarchicus* on Georges Bank: implications for the productivity of prey of cod and haddock larvae. ICES Annual Conference, Baltimore. ICES CM 1997/T:49, pp. 1−13.

Sell, A. F., Van Keuren, D., and Madin, L. P. 2001. Predation by omnivorous copepods on early developmental stages of *Calanus finmarchicus* and *Pseudocalanus* spp. Limnology and Oceanography, 46: 953−959.

Soetje, K. C., and Huber, K. 1980. A compilation of data on the thermal stratification at the central station in the northern North Sea during FLEX '76. "Meteor" Forschungs Ergebnisse, 22: 69−77.

Solow, A. R. 2002. Fisheries recruitment and the North Atlantic Oscillation. Fisheries Research, 54: 295−297.

Tande, K.S., and Miller, C.B. (Eds.), 2000. Population dynamics of *Calanus* in the North Atlantic. ICES Journal of Marine Science, 57: 1527−1874.

Williams, R., and Lindley, J. A. 1980a. Plankton of the Fladen Ground during FLEX 76. I. Spring development of the plankton community. Marine Biology, 57: 73−78.

Williams, R., and Lindley, J. A. 1980b. Plankton of the Fladen Ground during FLEX 76. III. Vertical distribution, population dynamics and production of *Calanus finmarchicus* (Crustacea: Copepoda). Marine Biology, 60: 47−57.

Wood, S. N. 1994. Obtaining birth and mortality patterns from structured population trajectories. Ecological Monographs, 64: 23−44.