

Relationship of predation potential to mortality of *Calanus finmarchicus* on Georges Bank, northwest Atlantic

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Abstract

Based on 29 cruises on Georges Bank between January and June, conducted as part of the U.S. Global Ocean Ecosystem Dynamics program, we describe seasonal and spatial variability of early life history mortality for the planktonic copepod *Calanus finmarchicus* and relate mortality to an index of predation potential from a suite of suspension-feeding predators. Emphasis is placed on the earliest life history phase wherein peak mortality occurs. Instantaneous mortality rates for a combined egg-through-nauplius-3 stage show a recurrent seasonal pattern of a modest elevation in January followed by a seasonal peak in May of all 5 study yr. Spatial differences exist in mortality rates, with a higher probability of mortality on the southern flank in winter and a pronounced seasonal maximum on the bank crest in May. Three hypotheses associated, respectively, with egg hatching success, advection, and invertebrate predation were evaluated to account for the seasonal and spatial mortality patterns. Variations in egg-hatching success are inconsistent with the observed seasonal patterns of loss. Off-bank advection, particularly on the southern flank, appears to be the dominant loss term in January. Apart from this winter period, egg mortality is associated with predation potential. Comparison of an index of daily rates of egg loss with an index of consumption rates of eggs by suspended hydroids, hydromedusae, and five species of planktonic copepods show general agreement between mortality and predation in both seasonal variation and spatial patterns. Of the predator taxa, late copepodid and adult *C. finmarchicus*, supplemented by planktonic hydroids, appear to have the largest quantitative predation effect.

Zooplankton populations in temperate latitudes characteristically experience strong seasonal forcing of water column stability, temperature, phytoplankton production, horizontal transport, and the influence of predators.

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Efforts to understand the mechanisms controlling zooplankton population dynamics have traditionally focused on effects of the first three of these processes. These seasonal drivers are usually emphasized in numerical simulations that seek to reproduce zooplankton population dynamics. Although alternative perspectives have been presented, focusing on the seasonality of predation (e.g., Ohman 1983; Davis 1984a,b; Purcell and Decker 2005) and advective losses (e.g., Lewis et al. 2001), the role of the loss term in governing the temporal and spatial variability of suspension-feeding marine zooplankton remains an understudied aspect of zooplankton ecology.

An impediment to addressing mortality and other losses in the marine pelagic environment, apart from specialized environments such as lagoons (Landry 1978), embayments (Uye and Liang 1998), and fjords (Eiane et al. 2002), has been the difficulty of sampling the same planktonic population over time. A basic concern is that the residence time (τ) of the water and organisms in the study region

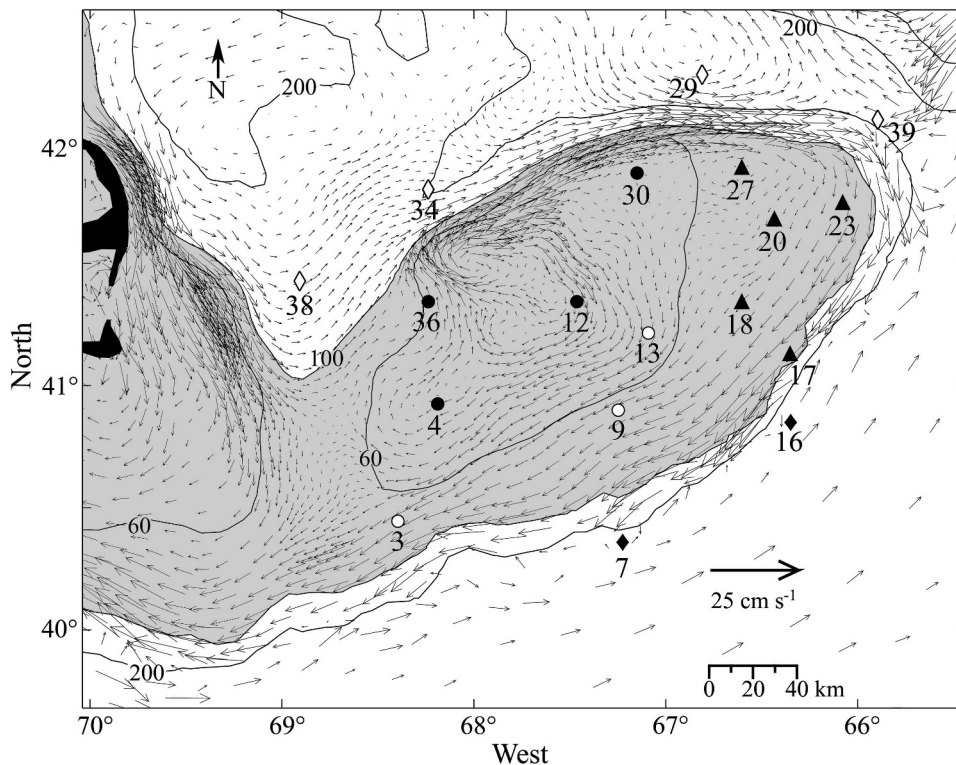


Fig. 1. Bathymetry and depth-averaged residual flow field on Georges Bank, from Werner et al. (1996), with modifications. Gray indicates region within the 100-m isobath. Stations where *C. finmarchicus* was sampled for this study are coded by region: filled circle = bank crest; filled triangle = northeast peak; filled diamond = slope; open circle = southern flank; open diamond = Gulf of Maine.

should be greater than the generation time of the organisms (T_{gen} ; Aksnes et al. 1997). The constraint $\tau > T_{\text{gen}}$ is unlikely to be met in coastal ecosystems with high flow rates and complex circulation. For example, for zooplankton with T_{gen} of 40 d in a coastal region with directional mean currents of 20 cm s^{-1} , the sampling pattern would need to extend at least 700 km to encompass members of the same population. This is rarely practical.

However, the Georges Bank region, on the open continental shelf, is well-suited to the problem. Because of topographically rectified tidal currents, there is retentive clockwise recirculation on the bank (Fig. 1) that intensifies with the onset of density stratification in spring–summer (e.g., Werner et al. 1996). As a consequence, the mean on-bank residence time is approximately 46–56 d (Flagg et al. 1982; Page et al. 1999), which compares favorably with the generation time of the dominant copepods. Drifters deployed in late winter and spring made as many as three complete circuits in the on-bank circulation, remaining on-bank for approximately 6 months (Limeburner and Beardsley 1996). Also, because Georges Bank is only ca. 175 km wide, the spatial scale of sampling necessary to encompass the entire life history is therefore tractable. Moreover, this study site has a zooplankton assemblage typical of mid- to high latitudes in the North Atlantic, with congeners found in parallel environments elsewhere in the ocean.

In the context of the U.S. Global Ocean Ecosystem Dynamics (GLOBEC) Georges Bank/Northwest Atlantic

program, we sought to determine whether seasonal and spatial variability of population growth of planktonic copepods (here focusing on *Calanus finmarchicus*) is influenced by variable rates of population loss. We define the subpopulation of interest as the potentially interbreeding *Calanus* occurring on the specific bathymetric feature of Georges Bank. In this region Davis (1984b) argued that the simulated predation potential of carnivorous zooplankton (especially chaetognaths, ctenophores, and the copepod *Centropages*) was sufficient to control population growth of *C. finmarchicus* and other co-occurring smaller-bodied copepods.

In order to address the possible role of variable losses to this geographically defined subpopulation, we apply inverse methods to estimate the time- and space-dependent mortality rates experienced by *C. finmarchicus* early life history stages on Georges Bank. “Mortality” as solved for here encompasses all loss terms, whether of biological or physical origin. If such rates of mortality prove to be relatively constant in time and invariant in space (e.g., as assumed by Lynch et al. 1998), this result would justify the traditional emphasis on other factors in studies of copepod population dynamics.

We have previously presented overall average mortality rates for *C. finmarchicus* and *Pseudocalanus* spp. on Georges Bank across the entire life history (Ohman et al. 2002). The *C. finmarchicus* data from the same cruises were analyzed by Li et al. (2006) using a different approach that

explicitly incorporated a model of the climatological circulation in the region. They used an adjoint method to infer the temporal–spatial variations in rates of molting, mortality, and upstream supply that could account for the observed population stage structure. Li et al. (2006) inferred these rates for post-nauplius 3 (N3) stages and found encouraging agreement with the results from Ohman et al. (2002). They also concluded that biological reaction terms are more important than advective and diffusive fluxes in governing the annual population dynamics of *C. finmarchicus* on Georges Bank.

Here we analyze temporal and spatial variations in loss rates of the eggs and youngest naupliar stages. These stages experience the highest probability of mortality both on Georges Bank and in other regions of the North Atlantic (Ohman et al. 2004; Hirst et al. 2007 for *Calanus helgolandicus*) and therefore constitute an important bottleneck to population growth. We also seek to determine the causative agents of mortality. The U.S. GLOBEC program included a formidable field study of 5 successive yr of monthly broadscale survey cruises through the primary growing season of winter–spring copepod assemblages, together with assessments of physical characteristics of the water column, composition of carnivorous zooplankton, and other specific process-oriented studies (see Wiebe et al. 2006). We use this information to address three hypotheses to explain *C. finmarchicus* mortality patterns: seasonal variations in egg hatching success, off-bank losses caused by advection, and predation. To our knowledge, a comparable analysis has not been carried out for marine copepods in an open marine system.

Carnivorous zooplankton are a likely source of mortality for young stages of *C. finmarchicus* (e.g., Eiane et al. 2002). Numerous species of suspension-feeding copepods, including the genus *Calanus*, also readily ingest copepod eggs or/and nauplii. Bonnet et al. (2004) summarize evidence for predation on copepod nauplii by a total of 22 copepod species, including at least nine species that ingest larval stages of conspecifics and are truly cannibalistic. Cannibalism introduces important nonlinearities into population dynamics (Ohman and Hirche 2001) and ecosystem models (Steele and Henderson 1992). Because copepods typically dominate the mesozooplankton on Georges Bank in terms of both numbers of individuals (Durbin and Casas 2006) and biomass, they represent a potentially important source of predation mortality for both embryonic and larval stages of copepods, as well as for other microplankton.

Materials and methods

Sampling was conducted on 29 U.S. GLOBEC broad-scale survey cruises on Georges Bank monthly from February to June 1995 and from January to June 1996–1999 (details in Durbin and Casas 2006). Early developmental stages of copepods were sampled with a plankton pump, and later developmental stages through adults, and carnivorous zooplankton, were sampled with a 150- μm -mesh, 1- m^2 Mocness. On rare occasions under inclement weather conditions a 200- μm -mesh, 0.60-m-diameter bongo net was substituted for the Mocness and towed from near

bottom to the surface. A centrifugal plankton pump was used from 1995 through May 1998, but analyses of stage-specific abundances of animals corrected for stage duration revealed that this pump did not adequately sample nauplius stages 1 and 2 (N1 and N2; Ohman et al. 2002), perhaps because of physical damage. A diaphragm pump was then used from June 1998 to June 1999. The diaphragm pump produced a sampling bias against N1 only. To obtain consistent abundance estimates across all cruises, we consider only N3 and later stages. Pumped samples were retained on a 50- μm -mesh screen in 1995 and on a 35- μm -screen from 1996 to 1999. All available samples from stations designated as priority 1 (3, 7, 9, 12, 16, 18, 20, 29, 36, and 38), together with those from most priority 2 stations (4, 13, 17, 27, 30, 34, and 39; see Fig. 1) from April to June in 1995 and on March–May cruises in 1998 and 1999 (see Durbin and Casas 2006), were used for mortality estimation.

The daily per capita egg production rate of *C. finmarchicus* adult females was obtained from application of a morphological reproductive index (Runge 1987; Runge and Roff 2000) to a random sample of a minimum of 30 adult females analyzed from each of the stations for which mortality was estimated. As described in Ohman et al. (2002), the calibration of the reproductive index against experimental incubations of egg production rate of *C. finmarchicus* females conducted during U.S. GLOBEC Georges Bank process cruises yielded the regression equation $CPR = 12.37 \cdot RI - 2.46$ ($n = 60$, $r^2 = 0.74$; Runge et al., 1997), where CPR is egg production rate as carbon (% body carbon d^{-1}) and RI is the reproductive index expressed as the fraction of females predicted to spawn. Female carbon mass (FC , $\mu\text{g C female}^{-1}$) was estimated from a relationship with female prosome length (PL , mm), measured at each station: $\ln FC = 3.04 \ln PL + 1.97$ ($r^2 = 0.60$). Daily egg production rate (B , eggs $\text{female}^{-1} \text{d}^{-1}$) was then obtained from

$$B = \frac{CPR \cdot FC}{100 \cdot EC} \quad (1)$$

where EC is the average egg carbon content, assumed to be constant at $0.23 \mu\text{g C egg}^{-1}$. This calculation method, which is an alternative to the modified relationship described in Niehoff and Runge (2003), was used because the appropriate RI was measured at all stations in the same way across all years. B was then multiplied by the abundance of adult females m^{-2} (A_f), measured from counts of the Mocness samples integrated over the water column, to obtain the daily recruitment of eggs produced $\text{m}^{-2} \text{d}^{-1}$ for each station. Variations in abundance of all developmental stages of *C. finmarchicus* are reported in Durbin and Casas (2006).

The vertical distribution of *C. finmarchicus* N3 was assessed from vertically stratified pump sampling in three strata and the weighted mean depth was calculated for each station. The temperature at the weighted mean depth was determined from each station's CTD casts. Temperature-dependent development times for each developmental stage from egg through N3 were obtained from Bělehrádek functions (Campbell et al. 2001).

Knowledge of the daily recruitment rate of eggs m^{-2} , ambient water column temperature, and abundance and vertical distribution of N3 was used to estimate the average instantaneous mortality rate from egg release through the development of N3. This rate is applicable across egg, N1, N2, and N3; we refer to it as the egg–N3 mortality rate. Although there are stage-specific variations of mortality rates (Ohman et al. 2004), the sampling bias precluded direct estimation of egg mortality separately from mortality of the earliest naupliar stages. A modified vertical life table method was used to estimate instantaneous mortality rates, as detailed in Ohman et al. (2002). Briefly, the egg–N3 mortality rate (m , d^{-1}) was solved from:

$$\frac{A_{N3}}{BA_f} = \frac{\exp^{-mD_{E-N2}} [1 - \exp^{-mD_{N3}}]}{m} \quad (2)$$

where A_{N3} = abundance of N3 m^{-2} , D_{E-N2} = development time (d) from egg through N2, D_{N3} = development time (d) of N3, and m = mortality rate (d^{-1}) for egg–N3; other symbols are defined above. A total of 256 mortality estimates was made from iterative solutions to Eq. 2, for an average of nine stations for each of the 29 cruises.

To compare mortality rates with predation potential, we focused on the egg stage because predation potential by planktonic consumers on eggs is much better constrained by available data than predation on naupliar stages. We converted instantaneous mortality rates (m , d^{-1}) to an index of numbers of eggs lost daily (EL , eggs $m^{-2} d^{-1}$) by integrating the instantaneous mortality rate over a day and multiplying by the daily rate of egg production, BA_f :

$$EL = BA_f(1 - e^{-m}) \quad (3)$$

Abundances of omnivorous or predatory copepods and other carnivorous zooplankton m^{-2} were obtained from vertical integration of three Moccness samples per station, or occasionally from bongo nets sampling the entire water column. Five-year monthly mean abundances were calculated for each available station (see Durbin and Casas 2006), multiplied by estimated predation rates, then mapped using EasyKrig as described in Durbin and Casas (2006). Predation rates on eggs of *C. finmarchicus* were determined from experiments done on Georges Bank or nearby waters at 6°C. Predation rates are compared at a standardized prey density of 10 eggs L^{-1} (Table 1). Where the minimum prey concentration used in experiments was higher (Sell et al. 2001), the clearance rate was assumed to be constant and used to estimate the ingestion rate at the lower prey density. The ability of *C. finmarchicus* copepodid stage 4 (C4) to ingest eggs was established by analogy with *C. helgolandicus* (Bonnet et al. 2004) and its ingestion rates were scaled relative to those of *C. finmarchicus* copepodid stage 5 (C5) from Daro's (1980) grazing experiments. Predation rates by small hydromedusae were approximated as 0.5 eggs medusa $^{-1} d^{-1}$ (B. Sullivan, with reference to *Obelia* in Sullivan and Banzon 1990). We assume that nonmotile eggs are eaten by hydromedusae at somewhat lower rates than are nauplii. Predator consump-

Table 1. Daily predation rates on *Calanus finmarchicus* eggs by omnivorous or carnivorous zooplankton occurring abundantly on Georges Bank, at a standardized prey concentration of 10 prey L^{-1} and temperature of 6°C.

Predator or omnivore	Predation rate (prey predator $^{-1} d^{-1}$)	Source
<i>C. finmarchicus</i> female	8.3	J. Runge et al. unpubl.
<i>C. finmarchicus</i> C5	1.6	J. Runge et al. unpubl.
<i>C. finmarchicus</i> C4	1.2	cf. Bonnet et al. 2004; Daro 1980
<i>Temora longicornis</i> female	2.0	Sell et al. 2001
<i>Centropages typicus</i> female	1.8	Sell et al. 2001
<i>Centropages hamatus</i> female	1.8	analogy with <i>C. typicus</i>
<i>Metridia lucens</i> female	0.6	Sell et al. 2001
Hydromedusae	0.5	B. Sullivan pers. comm.
Hydroids (<i>Clytia</i> spp.)	0.34	Madin et al. 1996

tion potential was obtained by multiplying predator abundance m^{-2} by per capita egg predation rates.

Hatching success of *C. finmarchicus* eggs was measured in 65 experiments on Georges Bank by Runge et al. (2006). Experiments were carried out on nine Georges Bank process cruises in 1995, 1997, and 1999, in all study months but January. Four batches of 50 eggs each were transferred from eggs produced in shipboard incubations into scintillation vials filled with filtered seawater. Eggs were incubated at the temperature of the egg production experiments for 3–4 d, then fixed in formaldehyde, and the numbers of nauplii and unhatched eggs were enumerated upon return to the laboratory ashore.

Results

Temporal patterns—The instantaneous mortality rate of *C. finmarchicus* egg–N3 varied seasonally on Georges Bank (Fig. 2). In each of the 5 study yr there was significant variability with time (Kruskal-Wallis, hereafter K-W, $p \leq 0.05$ in each year, $df = 5$), with a minimum in mortality rate in February–March and a maximum in May (Fig. 2a). In the 4 yr for which estimates were available, mortality rates were somewhat elevated in January relative to February and March. The 5-yr composite mean over all stations and all years illustrates the overall seasonal variation ($p < 10^{-9}$, K-W), with a 2.4-fold variation in instantaneous mortality from the minimum in March to the maximum in May (Fig. 2b).

In contrast to mortality rates, mean hatching success of *C. finmarchicus* eggs varied only between 70% and 82% and showed no seasonal trend (Fig. 3, $p > 0.05$, $df = 4$, K-W). Here we summarize the data of Runge et al. (2006) as overall means by month across all years studied, in a manner comparable to the mortality rates. There was no evidence for a maximum in average hatching success in March and a minimum in May, as would be required to account for observed mortality rates.

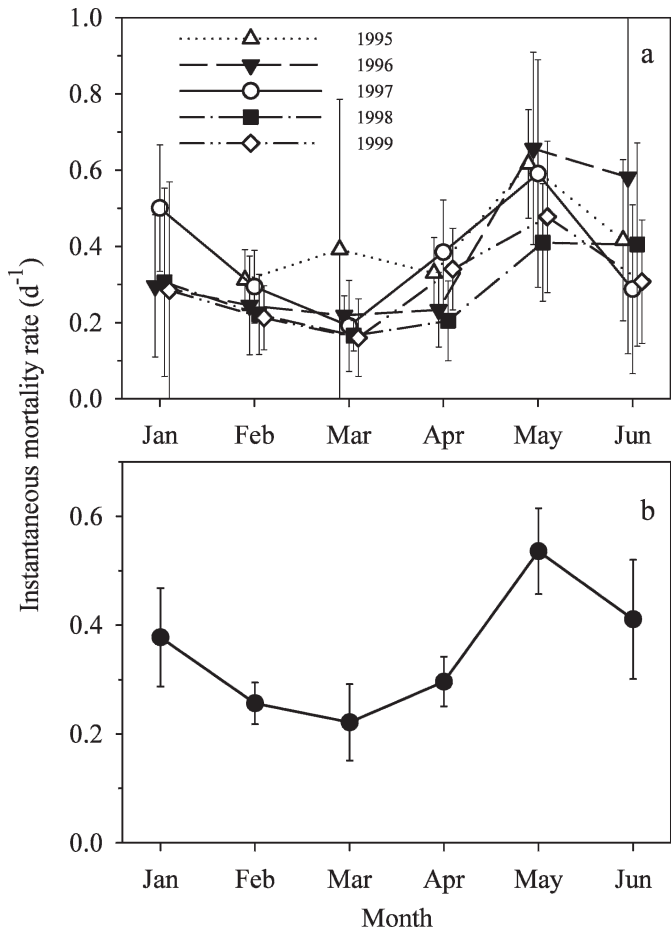


Fig. 2. *C. finmarchicus*. Seasonal variations in Georges Bank-wide averages of egg-N3 instantaneous mortality rate for (a) each of the 5 study yr and (b) all 5 yr combined. Mean \pm 95% C.I.

To estimate the effects of predation, we focused specifically on eggs. The seasonal pattern of our index of integrated daily egg loss, averaged across the bank, exhibits significant seasonal variability (Fig. 4a; $p < 0.0001$, K-W, $df = 5$) with a maximum of approximately 53,000 eggs lost $m^{-2} d^{-1}$ in May. There is a minimum in January because of the much smaller number of adult females, and therefore eggs produced, at that time of year. Variations in predation potential by a suite of omnivorous copepods (*C. finmarchicus*, *Centropages hamatus*, *Centropages typicus*, *Temora longicornis*, and *Metridia lucens*), suspended hydranths of the hydroid phase of *Clytia* spp., and hydromedusae also exhibited a distinct seasonal trend (Fig. 4b; $p < 10^{-9}$, K-W, $df = 5$), with a minimum in February and pronounced maximum in May. The index of estimated predation potential in May was approximately 65,000 eggs eaten $m^{-2} d^{-1}$.

Especially notable as a predator of *Calanus* eggs was *C. finmarchicus* itself, the dominant source of egg predation in May, as well as in all other months except January (Fig. 4b). *C. finmarchicus* C4 and C5 comprised the most quantitatively significant source of egg consumption, supplemented by adult females (Fig. 5). Although the daily predation rate by individual *C. finmarchicus* C4 and C5 was appreciably lower than that of adult females, the abun-

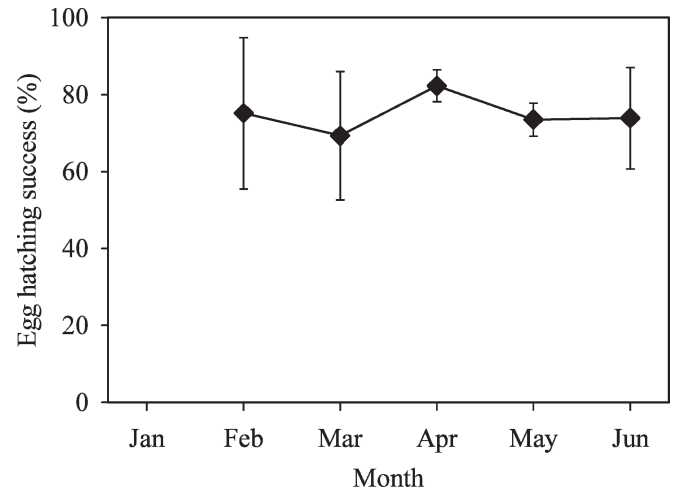


Fig. 3. *C. finmarchicus*. Seasonal variations in Georges Bank-wide averages of egg hatching success for all study years combined. Composite of results from Runge et al. (2006). Mean \pm 95% C.I. No experiments were conducted in January.

dance of C4 and C5 was substantially higher, especially in April–May, because of the passage of a developing generation (Durbin and Casas 2006). Planktonic hydroids were another very significant source of potential egg predation, with peak seasonal predation effects in May–June (Fig. 4b). *C. typicus* dominated egg predation potential in January, thereafter diminishing seasonally in importance, whereas its congener *C. hamatus* made its largest contribution in May–June. Hydromedusae and the planktonic copepods *T. longicornis* and *M. lucens* made a small contribution to *Calanus* egg predation.

Spatial patterns—The amplitude of the seasonal cycle in *C. finmarchicus* egg-N3 mortality rates varied spatially across Georges Bank, with the most pronounced seasonal increase to a May peak occurring on the bank crest and fringes of the Gulf of Maine (Fig. 6, $p < 10^{-9}$, K-W, $df = 5$; see Fig. 1 for definition of regions). Conversely, although there was significant seasonal variability in mortality rates on the southern flank, slope, and northeast peak ($p < 0.001$, K-W, $df = 5$), mortality rates in January were comparable to rates in May. Mortality rates differed significantly between the two regions in April–June ($p < 0.02$), but not in January–March ($p > 0.10$, two-sample t -tests).

These spatial patterns are illustrated in further detail in spatial contours of mortality rates (Fig. 7). The region from the northeast peak to the slope was a contiguous area of elevated mortality in January, at which time losses on the rest of Georges Bank were small. The seasonal progression of egg mortality reached a maximum in the shallow waters of the bank crest and bordering stations of the Gulf of Maine in May, thereafter diminishing in June. At that time there were local minima in mortality rates across most of the northeast peak and southern flank (Fig. 7).

Spatial patterns in estimated predation rates were generally consistent with these spatial patterns in mortality rates, apart from winter. In January, none of the predators showed a spatial pattern of predation potential that was

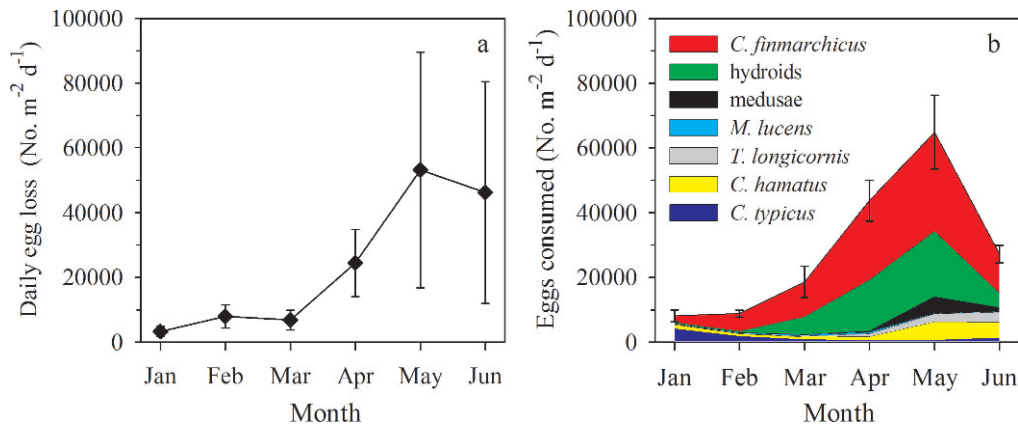


Fig. 4. *C. finmarchicus*. Seasonal variations in estimated (a) daily egg loss and (b) daily predation potential on eggs for all 5 study yr combined, by *C. finmarchicus* (C4, C5, and adult females), hydroids, hydromedusae, *M. lucens*, *T. longicornis*, *C. hamatus*, and *C. typicus*. Mean \pm 95% C.I.

consistent with the local maximum in egg mortality in the southern flank–slope region (Fig. 7). *C. typicus* was the most important potential source of egg mortality at this time of year, but it was concentrated on the bank crest (Fig. 8a). In January, the region of high *C. typicus* predation potential overlapped the spatial minimum in mortality rate. However, through most of the rest of the year, predation potential to a large extent overlapped mortality rates. The primary predators on *C. finmarchicus* eggs all showed overall seasonal maxima in predation potential in either May or June (Fig. 8). Early in the year, consumption potential by *C. finmarchicus* C4 + C5 + adult females was highest principally around the northern periphery of the bank, then became more widespread across the entire bank in April–May, retracting to leave a doughnut hole of reduced consumption in June (Fig. 8e). The other potential egg predators in late spring–early summer (*C. hamatus*, *T. longicornis*, suspended hydroids of *Clytia* spp., and hydromedusae) all developed seasonal

maxima in predation potential on the bank crest in May or June. Notable among these taxa were planktonic hydroids because of their widespread occurrence and high abundance in the shallow bank crest, where hydranths are resuspended off the bottom and into the water column by tidal shear.

The total estimated predation potential by all egg predators combined also showed a maximum in May, particularly on the bank crest (Fig. 8g). Apart from January, which was excluded because of the relationship with advective loss as described below, the spatial pattern of our index of egg predation was correlated ($p < 0.001$, Spearman's rank) with the spatial pattern of estimated mortality rates.

Discussion

Causative agents of mortality on Georges Bank—Our results demonstrate a seasonally recurrent pattern of early

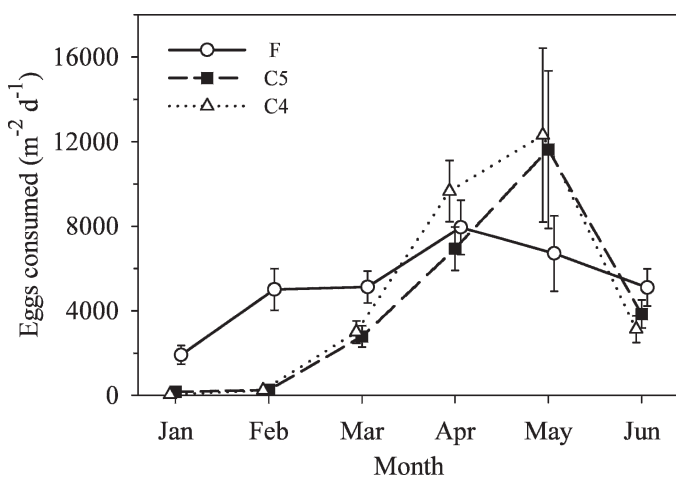


Fig. 5. Seasonal variations in daily predation potential on *C. finmarchicus* eggs by three developmental stages of *C. finmarchicus* (C4, C5, and adult females [F]) for all 5 study yr combined. Mean \pm 95% C.I.

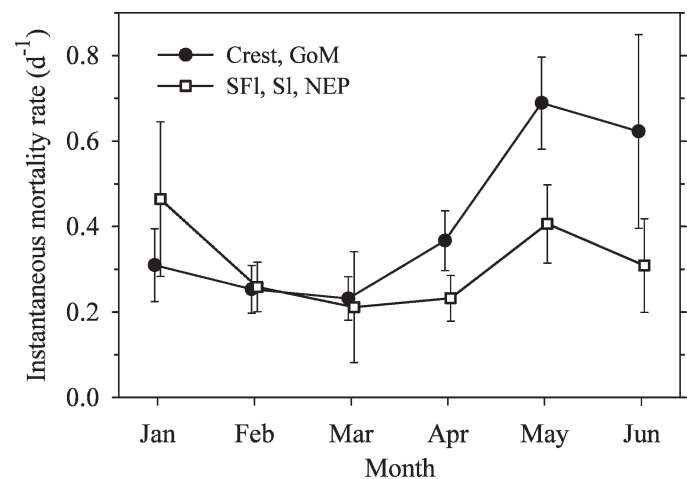


Fig. 6. *C. finmarchicus*. Seasonal variations in egg–N3 instantaneous mortality rate for two station clusters: the bank crest + Gulf of Maine (Crest, GoM) and the southern flank + slope + northeast peak (SFI, SI, NEP), for all 5 study yr combined. Mean \pm 95% C.I.

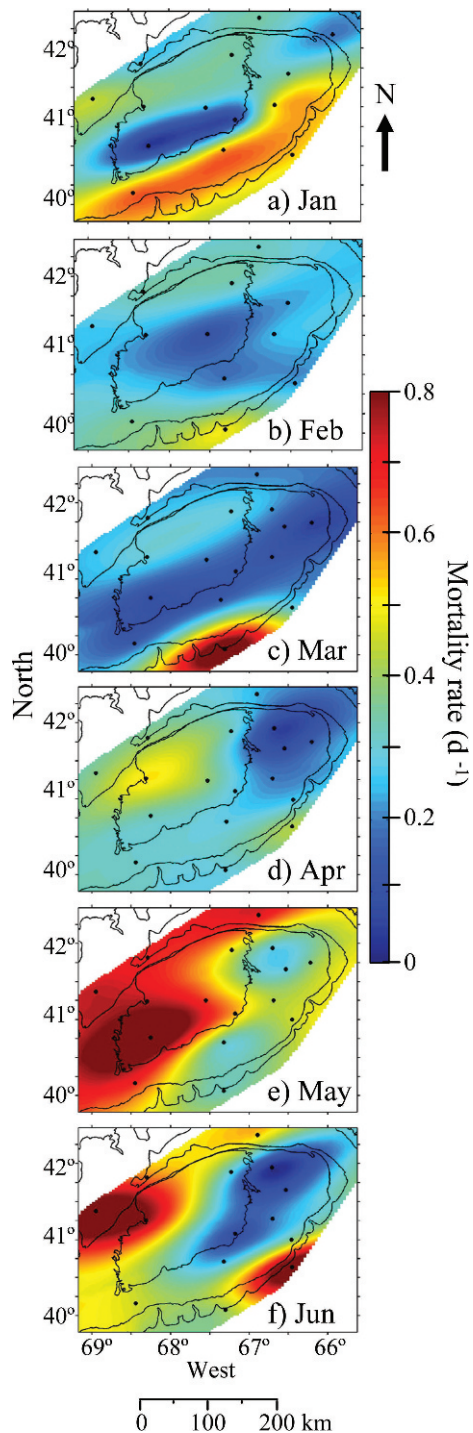


Fig. 7. *C. finmarchicus*. Spatial and seasonal variations in egg-N3 instantaneous mortality rate (d^{-1}) for all 5 study yr combined.

life history mortality of *C. finmarchicus* on Georges Bank. Mortality rates of *C. finmarchicus* egg-N3 were slightly elevated in January, declined to a seasonal minimum in March, then reached a maximum value in May. This pattern occurred in all 5 yr of the field study. There were also regional differences on Georges Bank in the amplitude of this seasonal cycle, with a reduced winter minimum and

more pronounced May maximum at stations on the bank crest and the fringe of the Gulf of Maine, and the opposite pattern at stations on the eastern limb of the bank. We considered three principal hypotheses to account for these seasonal and spatial patterns of mortality: variations in egg hatching success, off-bank losses caused by advection, and predation.

Seasonal variations in egg hatching success are not consistent with the seasonal trend in mortality, and in some instances oppose it. Analysis of individual experiments revealed that there were occasions when egg hatching success was nearly 100% and rare occasions when it dropped below 40% (Runge et al. 2006), but we do not have measures of toxins, diets, or mating success necessary to explain these individual cases. As one indirect and imperfect index of food availability, we found no relationship between egg hatching success and total chlorophyll *a* at the same stations ($p > 0.10$, $r^2 = 0.06$, $n = 48$). Although the presence of diatom-derived toxic compounds (Ianora et al. 2003), dietary deficiency (Poulet et al. 2006), or fertilization limitation (Kjørboe 2007) could occasionally depress egg hatching success to low levels on Georges Bank, neither the restricted amplitude of variation of hatching success nor the absolute rates of hatching failure are sufficient to account for the 2.4-fold seasonal variation in mortality rates that we observed.

Circulation on Georges Bank is a complex interaction of tidal currents, wind-driven flow, inflow from the Scotian Shelf and Gulf of Maine, shelf-slope frontal exchanges, impingement of Gulf Stream rings, and other processes. Most relevant to the present analysis is the climatological average seasonal and spatial patterns of winds and circulation, commensurate with the climatological average patterns of copepod mortality. Direct measurements of seasonal variations in off-bank losses caused by advection are not available. However, the drifter study of Limeburner and Beardsley (1996) suggested that near-surface drifters along the southern flank tended to move off-bank in response to strong wind events. A summary of wind climatology (Manning and Strout 2001) for the 6 months relevant to the present study shows that wind stress over Georges Bank attains a maximum in January, with winds predominantly from the north-northwest, and reaches a minimum in May (Fig. 9). This seasonal trend is the opposite of that expected if wind-driven transports were to account for the seasonal pattern of mortality rates. In particular, elevated mortality rates in May and June are not consistent with advective loss as an explanation, because winds have declined substantially and the retentive on-bank residual tidal circulation becomes stronger with the seasonal intensification of stratification (Naimie et al. 2001). Flagg et al. (1982) reported average on-bank residence times of drifters at 10-m depth of 45 ± 8 d in winter-spring, increasing to 66 ± 28 d in summer, also opposing the trend toward a seasonal maximum in mortality in May-June reported here.

Comparison of the average rate of loss across all cruises ($29.0\% \text{ d}^{-1}$ when expressed as a finite rate, Table 2) with the average off-bank advective loss in equivalent units ($1.8\text{--}2.2\% \text{ d}^{-1}$) estimated from the reciprocal of on-bank

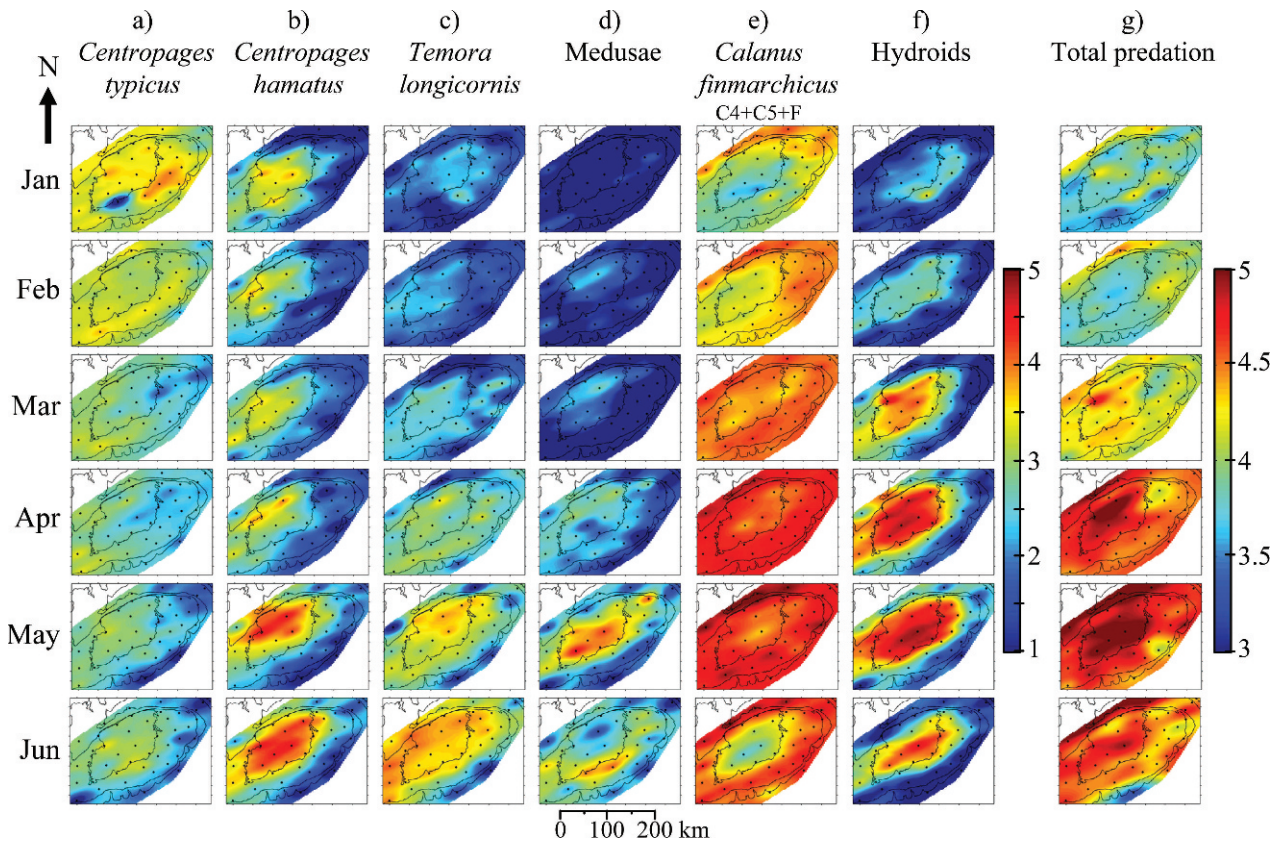


Fig. 8. Spatial and seasonal variations in predation potential on *C. finmarchicus* eggs by six individual taxa of carnivorous or omnivorous zooplankton and by all predators summed, for 5 study yr combined. (a) *C. typicus*, (b) *C. hamatus*, (c) *T. longicornis*, (d) medusae, (e) *C. finmarchicus* C4 + C5 + Females (F), (f) hydroids, and (g) total predation by all sources combined. Contours show estimates of log numbers prey consumed $m^{-2} d^{-1}$. Note different color scale for panels in (g).

residence times (Flagg et al. 1982; Page et al. 1999), reveals that typical mortality rates are 13–16 times higher than can be accounted for by the typical advective losses. Hence, advective losses both have the wrong seasonal trend and are, on average, far too low to account for the seasonal peak of mortality rates.

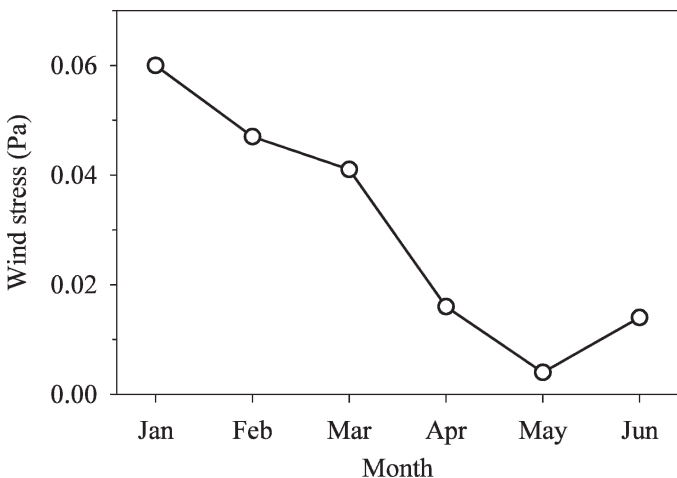


Fig. 9. Monthly mean wind stress on Georges Bank between 1975 and 1997, from Manning and Strout (2001). Resultant of eastward and northward winds.

However, concerning the winter period of high winds, Lewis et al. (2001) simulated the consequences of variations in winter wind stress for plankton retention on Georges Bank. They found that tracer organisms originating in the vicinity of the southern flank were the most vulnerable to off-bank transport, and observed that losses were high in conditions of northwest winds. Page et al. (1999) calculated residence times of water at 10–50-m depth from a circulation model and consistently found lower residence times in the southern flank (often ca. 20 d) than on the bank crest (often 50–60 d), especially in winter, in accord with our spatial patterns. These results agree in both seasonal timing and spatial pattern of elevated winter

Table 2. Comparison of average mortality rate of *Calanus finmarchicus* egg-N3 with average advective losses on Georges Bank. Advective losses are approximated as the reciprocal of the mean residence times from Flagg et al. (1982; 56 d for drifters drogued at 10 m) and Page et al. (1999; 46 d for modeled tracers between 10 and 50 m).

Source of loss	Instantaneous rate	Finite rate	Reference
Mortality rate	0.34 d^{-1}	$\approx 29.0\% d^{-1}$	present study
Advection	—	$\approx 1.8\% d^{-1}$	Flagg et al. 1982
Advection	—	$\approx 2.2\% d^{-1}$	Page et al. 1999

mortality with the results we observed on the edge of the southern flank, leading to the conclusion that off-bank advection is the dominant source of population losses of early stage *C. finmarchicus* from Georges Bank on the southern flank in winter.

Li et al. (2006) reported spatial and seasonal patterns of post-N3 mortality of *C. finmarchicus*, in contrast to our analysis of mortality in the youngest developmental stages wherein the highest losses occur. Their temporal-spatial average pattern of stage-specific mortality rates for post-N3 stages show a very similar pattern to that seen in Ohman et al. (2002), with a relatively small difference in absolute rates. We cannot directly compare time-space variations in rates from the present study with theirs, because of the lack of overlapping parts of the life history considered. The closest comparison we can make is between their rates for N4 and our rates for egg-N3. Li et al. show a maximum in N4 mortality rates in January-February, declining monotonically toward a minimum in May-June. This seasonal trend differs from the May maximum that we consistently observed for younger developmental stages in each of our 5 study yr. Unlike Li et al.'s results, our pattern is consistent with trends in predation. In addition, the spatial location of their winter maximum was on the bank crest, with low rates on the northeast peak and most of the southern flank. Those spatial patterns are essentially the opposite patterns to what we found. Our spatial patterns in mortality are consistent with low predation on the bank crest in January and high winter advective loss on the northeast peak/southern flank. Our patterns also agree with expectations from high hydroid predation on the bank crest in May; few hydroids are present in January.

It is possible that N4 shows a completely different pattern of mortality than egg-N3, as well as different causal agents of loss. Alternatively, differences in the solution method used in the two studies could be responsible. The method employed by Li et al. explicitly includes modeled advection and diffusion, in addition to estimating molting rates and inverting for mortality rates. Their method assumes that the physical circulation is perfectly described by the model at all grid points and that the climatological circulation is applicable at all times. Differences between expected and observed copepod stage abundances are ascribed only to biological terms; therefore, any errors in the physical circulation are forced to be absorbed by mortality. The circulation model employed by Li et al. had coarser temporal resolution (bimonthly) than the copepod sampling (monthly); this could have contributed to systematic errors in circulation and therefore in mortality when applied to individual monthly cruises. Also, Li et al. utilized vertically averaged climatological mean temperature and chlorophyll to estimate molting rates for all developmental stages, whereas we used vertically resolved, weighted mean temperatures for each sampling location, sampling time, and developmental stage, thus taking into account cruise- and site-specific variations for each individual estimate.

It is noteworthy that the dominant sources of predation mortality for *C. finmarchicus* eggs are *Calanus* itself and suspended hydroids. Neither is considered among classical

zooplankton predators. Although the importance of hydroids may be peculiar to the shallow shelf environment of Georges Bank, because of the combination of both suitable benthic habitat and vigorous tidal currents that resuspend hydranths into the water column (Madin et al. 1996; Concelman et al. 2001), it is likely that cannibalism by *Calanus*—and egg predation by other suspension-feeding copepods—is a widespread phenomenon. Because *C. finmarchicus* can reach high densities and relative dominance in many parts of its range (Tande and Miller 2000), it may have such density-dependent, self-limiting capabilities elsewhere (Ohman and Hirche 2001). In the present study site the numerous C4 and C5 stages of *C. finmarchicus* have a larger estimated effect than do adult females at most times of year. Cannibalism by copepods has been invoked in numerous other studies (e.g., Landry 1978; Uye and Liang 1998; Bonnet et al. 2004).

Davis (1984b) proposed that predators have sufficient consumption potential to regulate the growth and abundance of copepods on Georges Bank, including *C. finmarchicus*. His simulation addressed predators on post-embryonic stages, with particular attention to chaetognaths and ctenophores, treating *Centropages* spp. as predators on copepod nauplii. Although the two former taxa probably do contribute to the mortality of later developmental stages of *C. finmarchicus*, especially in summer beyond the seasonal period treated here, and *Centropages* spp. are contributors to the mortality of *C. finmarchicus* eggs, cannibalism by *Calanus* and predation by hydroids appear to be the dominant source of predation governing survivorship of the egg stages of *C. finmarchicus*.

Eiane et al. (2002) compared average mortality of *Calanus* populations in two fjords, one dominated by carnivorous zooplankton and the other by planktivorous fish, and observed markedly different survivorship patterns, with considerably higher losses in younger developmental stages in the fjord populated with abundant zooplankton. The contrast in survivorship patterns between these two fjords was as great as observed in three other studies in the North Atlantic, including Georges Bank, pointing to the importance of inter-site differences in predator fields in accounting for regional differences in mortality (Ohman et al. 2004). An analysis of time-dependent egg mortality rates of *C. finmarchicus* in the Norwegian Sea suggested that onset of population growth there is influenced as much by a seasonal decline in egg mortality as by the increased food supply associated with the spring phytoplankton bloom (Ohman and Hirche 2001).

Predation estimates—Predation rates are affected by variations in prey concentration, turbulence, temperature, and the presence of alternate prey. None of these factors is well known for the complete ensemble of *Calanus* egg predators considered here. We chose to compare predation rates at a consistent prey density, to assess the relative effect of different co-occurring taxa based on empirically measured rates, although it is highly unlikely that the same prey density is encountered by all predators at all times. Table 3 indicates that measured densities of nauplii (which

Table 3. Estimates of densities of copepod eggs and nauplii from relatively fine-resolution vertical sampling. GB = Georges Bank.

Region	Species	Vertical resolution (m)	Developmental stage	Peak density (No. L ⁻¹)	Reference
GB, southern flank	mixed	5–20	nauplii	7–160	Incze et al. 1996
GB	<i>Calanus finmarchicus</i>	10–35	nauplii	5	Durbin and Casas 2006
GB, southern flank	mixed	10	nauplii	50	Lough 1984
GB, southern flank	mixed	1	nauplii	14*	Gallager et al. 2004
Gulf of Maine	<i>C. finmarchicus</i>	1–3	nauplii	5	Durbin et al., unpubl.
English Channel	<i>Calanus helgolandicus</i>	unspecified	eggs	2.5	Bonnet et al. 2004
North Sea	<i>C. helgolandicus</i>	unspecified	eggs	70	Bonnet et al. 2004 (inferred)

* Detection probability of nauplii unknown; optical method.

are more frequently reported than those of eggs) have often been found at or near our assumed level; egg concentrations would be expected to be higher still, because of high early stage mortality (Ohman and Hirche 2001; Hirst et al. 2007). The abundance of *Calanus* eggs can far exceed our assumed concentration (Table 3). Moreover, conventional sampling methods, including pump sampling, typically integrate over relatively large vertical distances and are certain to miss vertical thin layers (Owen 1989; Gallager et al. 2004) and other microscale patches that may be important to predators. Mullin and Brooks (1976) pointed out that most planktonic consumers could not survive at food concentrations typically measured in the ocean and inferred that consumers must find prey patches that we typically do not resolve. Despite ensuing advances in sampling techniques, it is likely that predators find prey aggregations that we have not sampled. Thus our predator consumption rates are often likely to be conservative estimates, but perhaps are overestimates at other times. For this reason, we consider these only an index of predation potential rather than an accurate quantitative measure of eggs ingested.

To assess the effects of prey density on the predation rates by the suite of predators considered here, we calculated our index of predation potential at prey densities of 1, 10, and 30 eggs L⁻¹ (Fig. 10). At the two higher prey densities, predation potential consistently exceeded the index of egg mortality. Although this was not the case at the lowest prey density, there was a consistent relationship

between mortality and predation potential ($p < 0.001$, Spearman's rank), suggesting that irrespective of the uncertainty in prey densities encountered in the field, variations in predation were associated with variations in egg loss.

Furthermore, we have not taken into account the effects of small-scale turbulence that serves to increase the relative motions of predators and prey and thereby augment encounter rates (Rothschild and Osborn 1988). Werner et al. (1996) concluded that turbulence on Georges Bank increased contact rates between larval fish and their zooplankton prey by two to five times and permitted larvae to attain realistic growth rates. We are not able to quantify the effects of turbulence on the specific predators treated here, but note that turbulence-enhanced contact rates would consistently enhance the probability of *Calanus* egg encounters with predators in the bank crest and make that a particularly perilous region. Indeed, the bank crest is where the doughnut hole of diminished abundance of *C. finmarchicus* emerges in June (Fig. 8).

We have also not attempted to correct for variations in predation rates with temperatures that depart from 6°C, as this would require assumptions about the temperature dependence of predator behavior for diverse types of organisms ranging from cnidarians to crustaceans. Assuming a Q₁₀ of 2, any resulting bias in our approach would serve to somewhat overestimate predation rates in March (by ~10%), when they are low anyway, and to underestimate predation rates (by ~30%) later in the season as the

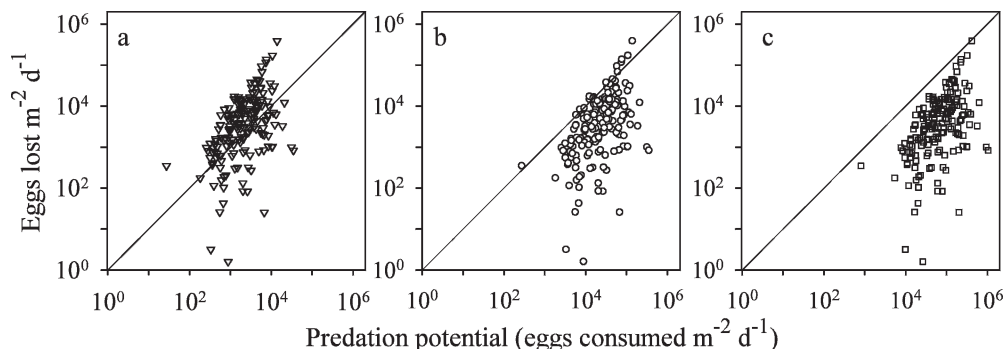


Fig. 10. Relationship between egg mortality of *C. finmarchicus* and predation potential by an ensemble of egg predators at three densities of *C. finmarchicus* eggs: (a) 1 egg L⁻¹, (b) 10 eggs L⁻¹, and (c) 30 eggs L⁻¹. Clearance rates are assumed to be constant. Data correspond to locations where mortality rates and predators were measured at the same station and time. Line indicates 1 : 1 relationship.

water column warms. This is a relatively minor source of uncertainty in relation to other unknowns.

The influence of alternative prey on these predators is difficult to assess. Landry (1981) suggested that *Calanus pacificus*, when offered its own nauplii and a diatom, switches so as to feed disproportionately on the more prevalent prey type. J. Runge and S. Plourde (unpubl.) found that *C. finmarchicus* adult females and C5s readily ingest eggs at high clearance rates. Females showed nearly three times higher clearance rates on eggs in filtered seawater as compared with eggs in the presence of diatoms (*Thalassiosira weissflogii*). Experiments with natural prey suspensions found that clearance rates by *C. finmarchicus* are appreciably higher on microzooplankton than on phytoplankton (Ohman and Runge 1994). Basedow and Tande (2006) found consistently higher clearance rates of *C. finmarchicus* on conspecific nauplii (N1 and N2) than on diatoms (*T. weissflogii*), and no effect of the presence of diatoms on clearance rates of nauplii offered concurrently. Bonnet et al. (2004) found that rates of cannibalism on eggs of *C. helgolandicus* were appreciably higher than on nauplii and that clearance rates on nauplii were independent of clearance rates on eggs. Overall we conclude that the behavior of *C. finmarchicus* in prey mixtures, and that of co-occurring predators on *Calanus* eggs, requires further attention, but the rates applied here are reasonable estimates.

A number of taxa were not considered among the dominant predators on *Calanus* eggs in situ. These include the cyclopoid copepod *Oithona*, which can be abundant in the region. *Oithona* prefer motile prey (Paffenhöfer 1993; Castellani et al. 2005), and they are unlikely to detect or ingest copepod eggs. *Sagitta* are also very abundant on Georges Bank (Davis 1984b). However, chaetognaths use vibration receptors for prey detection (Saito and Kiørboe 2001) and generally do not respond to nonswimming prey such as eggs. Ctenophores show relatively low abundance on Georges Bank in the first half of the year (Sullivan and Meise 1996), although ctenophores may be abundant in summer (Davis 1984b) and abundance estimates may be biased by artifacts of dissolution in preservatives (Sullivan and Meise 1996). Prey preferences and feeding rates of cydippid larvae are not well known. Overall annually averaged predation estimates by Steele et al. (2007) suggest that ctenophores account for no more than 10% of consumption of mesozooplankton carbon. Fish larvae may ingest *Calanus* eggs and nauplii, but they are likely too dilute to affect the dynamics of the copepod populations in this general region (Pepin and Penney 2000).

Alternative sources of loss—Additional factors potentially contributing to loss as measured here could include developmental failure of early naupliar stages, parasitism, or egg sinking. Pierson et al. (2005) recorded occasions of reduced naupliar survival when female *C. pacificus* were grazing almost exclusively on diatoms harmful to hatching success. Observations of possibly defective nauplii hatching from eggs during shipboard experiments on Georges Bank were recorded but not quantified (Runge et al. 2006). In general, we would expect reduction in naupliar survival to

track hatching success, which does not show seasonal variation. We have no information on the types or quantitative significance of parasites of *C. finmarchicus* eggs on Georges Bank. We infer that eggs' sinking to the benthos is unlikely to be a significant source of mortality, and here depart from Durbin and Casas (2006). The highest egg mortality rates are observed in May over the bank crest, a region with vigorous tidal currents that resuspend organisms from the seafloor. Indeed, this vertical motion is why benthically derived hydroids are so abundant in the water column in that region (Concelman et al. 2001). Vigorous resuspension is likely to accelerate contact between hydroids and eggs. We consider it unlikely that many eggs would penetrate the benthic boundary layer and contact the bottom. This vertical recirculation differs from the shallow waters of Long Island Sound, where egg sinking could be an important loss term (see Dam and Tang's [2001] reinterpretation of Peterson and Kimmerer 1994).

Mortality estimation methods—The assumptions of the vertical life table method have been previously reviewed (Aksnes and Ohman 1996; Aksnes et al. 1997) and most apply to the modified method we applied here. The constraint of relative constancy of egg production rates, stage abundances, and stage durations implies that none are changing markedly over a time period equivalent to the duration of the stages considered here (several days). We previously tested this assumption on Georges Bank with two cohort-tracking cruises and found that, within the limits of sampling error, both egg production rates and stage ratios were generally stable within a parcel of water followed for several days (Ohman et al. 2002). On a time scale of days, the temperature of the physical environment does not change markedly, apart from a situation wherein organisms cross abrupt fronts. We obtained >98% positive mortality estimates, which further corroborates the assumption of short-term constancy. The method also assumes that stage durations are known. In our case, the durations of embryo, N1, and N2 stages are well-described by temperature (e.g., Campbell et al. 2001). The duration of N3 will be influenced by food concentration and food quality as well as temperature, but neither the in situ diet of N3, the relationship of naupliar stage duration with diet, nor the role of maternally invested lipids in N3 nutrition are well known. Slightly more than half of the total developmental sequence from egg through N3 is not affected by available food, but the N3 stage could, at times, be food limited. At such times we would somewhat overestimate the egg–N3 mortality.

The method also assumes there is no stage-specific sampling bias. We became aware of a sampling bias against N1 and N2 in our initial sampling, which led us to make mortality estimates using the N3 stage abundances, for which there is no evidence of bias by our pump sampling. Although the resulting combined egg–N3 estimates are on average unbiased, they likely underestimate the mortality rates of eggs and overestimate the mortality rates of early naupliar stages. Where it has been possible to resolve mortality rates of eggs alone, the eggs of *Calanus* spp. have

much higher mortality rates than do the early naupliar stages (e.g., Ohman et al. 2004; Hirst et al. 2007). Hence, our estimates of daily losses of eggs should be considered only an approximate index of variability in egg mortality, rather than a correct absolute measure. Accordingly, it is probably only fortuitous that the magnitude of seasonal egg loss corresponded approximately with the magnitude of consumption by predators.

Early life history mortality of a geographically localized subpopulation of *C. finmarchicus* on an open continental shelf in the Northwest Atlantic showed a recurrent pattern of seasonal variation of population losses in all 5 study yr. The local maximum in winter on the southern flank is attributable mainly to off-bank transport, whereas the predominant seasonal peak loss in May–June is consistent with predation by an assemblage of suspension-feeding copepods, dominated by cannibalistic *C. finmarchicus* and supplemented by resuspended benthically derived hydroids in the bank crest. Analyses of seasonal and spatial dynamics of zooplankton populations need to consider the variable patterns of loss terms and the potential for self-limitation of natural populations.

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