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On birth and death in the sea

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Key words: copepods, population dynamics, mortality estimation, density dependence, life history trade-offs, *Calanus*, *Pseudocalanus*

Abstract

We present the first comparative study of the stage-specific patterns of mortality of *Calanus* and *Pseudocalanus*, two widely distributed genera that are representative of a relatively large-bodied, broadcast spawning calanoid copepod and a relatively small-bodied, egg-brooding calanoid. The study site is Georges Bank, a continental shelf locality in the Northwestern Atlantic with retentive circulation that renders it suitable for studies of population dynamics. Based on extensive mortality estimates from 30 cruises, we find that co-occurring *Calanus finmarchicus* and *Pseudocalanus* spp. have markedly different patterns of stage-specific mortality, the former bimodal and the latter relatively uniform with respect to developmental stage. Neither taxon exhibits a monotonic decline in mortality with developmental stage, nor are rates of mortality predictable in a useful manner by copepod body size or by ambient temperature. Young stages of the broadcast-spawning *C. finmarchicus* show conditional density-dependence of mortality rates, i.e. mortality rates are independent of population density when adult females are low in abundance but positively related to population density at high female abundances. This density-dependence, which is probably attributable to egg cannibalism, introduces a quadratic mortality term into population dynamic models. The egg-brooding *Pseudocalanus* spp., in contrast, show no evidence of density-dependent mortality. The two taxa illustrate a life history trade-off: the broadcast-spawning *Calanus* exhibits birth rates that are greatly elevated with respect to those of *Pseudocalanus*, but there is a compensatory cost in very low survivorship of the freely spawned eggs. Both the high fecundity, high mortality life history of *Calanus* and the low fecundity, low mortality life history of *Pseudocalanus* appear to have approximately equal fitness in this study site.

Introduction

The genera *Calanus* and *Pseudocalanus* are among the most prevalent zooplankton taxa found in north temperate and boreal latitudes. Often one or both of these genera include the most common zooplankters found in the oceanic water column. As a consequence, they have invited considerable attention by experimentalists and field ecologists, as well as by ecosystem modelers. In a series of insightful studies, Frost and collaborators began contrasting different aspects of the biology and ecology of representative species of these genera. Such studies have included comparisons of *Calanus* and *Pseudocalanus* with respect to feeding behavior (Frost, 1974), mating behavior (Griffiths &

Frost, 1976), grazing impact (Steele & Frost, 1977), rates of somatic growth (Vidal, 1980; Frost, 1980), reproductive responses and susceptibility to food limitation (Runge, 1985; Frost 1985), and diel vertical migration behavior (Ohman et al., 1983; Frost, 1988; Frost & Bollens, 1992).

Such studies are of interest beyond the particular taxa concerned. The two genera are representative of relatively large- and small-bodied calanoid copepods, differing ca. 10-fold in body mass (Frost, 1980), which co-occur in many regions of the world ocean. In addition to differences in body size, they represent a contrast in reproductive mode. Adult females of all members of the genus *Calanus* freely spawn their eggs into the water column while all *Pseudocalanus* species

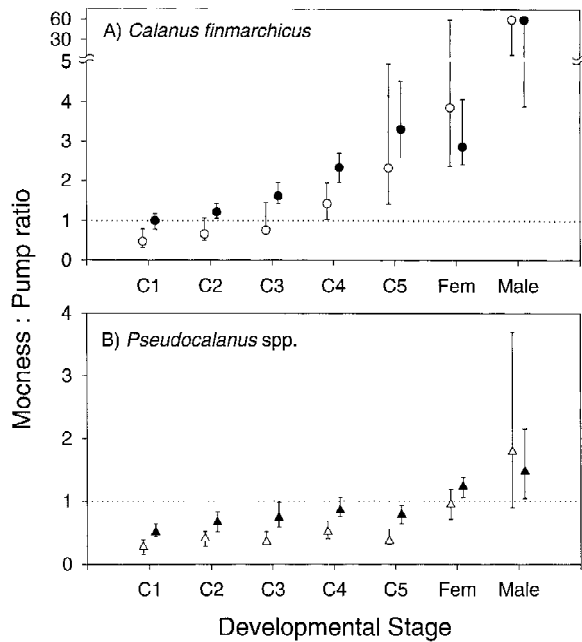


Figure 1. Ratio of Mocness:Pump collections for copepodid and adult stages of (A) *Calanus finmarchicus* and (B) *Pseudocalanus* spp. on Georges Bank. Values are the median \pm 95% nonparametric confidence limits for the ratio of Mocness collections to: centrifugal pump (filled symbols) or diaphragm pump (open symbols) collections. Where no individuals were collected by the pump, the ratio was arbitrarily set to 60. The 1:1 line indicates equal collection efficiency of Mocness and pump. Water column integrated abundances were compared at stations where the maximum difference in sampling depths between pumps and Mocness was less than 15 m. $N=162$ –206 paired comparisons for the centrifugal pump and 59–68 comparisons for the diaphragm pump.

carry their eggs in an attached egg mass. Such differences in mode of egg laying clearly influence the maximum egg production potential of the two taxa, with the physiological maximum egg production rate of *Calanus* being about an order of magnitude higher than that of *Pseudocalanus* (Frost, 1985). The implications of such differences in fecundity have been explored in life history models by Kiørboe & Sabatini (1994, 1995).

Despite the extensive attention given to *Calanus* and *Pseudocalanus* (see also Corkett & McLaren, 1978; Davis, 1987; Mauchline, 1998; Heath & Coombs 1999; Tande & Miller, 2000, amongst others), a conspicuous element of the population biology of both genera remains remarkably poorly understood. This concerns the rates of mortality in natural populations, the time/space variability of mortality rates in different geographic locales, and the causative agents of mortality. Even for some of the best studied cope-

pods in the ocean, for which many of the processes leading to variability in birth rates are reasonably well understood, there is scant information available on death rates. Work with *Pseudocalanus newmani* (Ohman & Wood, 1995) and *Calanus finmarchicus* (Ohman & Hirche, 2001), in different ocean basins, has suggested that variability in death rates may be at least as important as variability in birth rates in explaining fluctuations in abundance in the sea.

The present study seeks to contrast the stage-specific patterns of mortality for representatives of *Calanus* and *Pseudocalanus* co-occurring temporally and spatially in the same geographic study site. We focused this study on subpopulations occurring on Georges Bank, a continental shelf locality in the northwestern Atlantic ocean. Pelagic secondary production in this region in spring–summer is dominated by *Calanus* and *Pseudocalanus* (Davis, 1987). The study site takes advantage of retentive circulation (e.g. Naimie et al., 2001) that makes possible studies of population dynamics. Georges Bank has been the focus of the intensive U.S. GLOBEC Northwest Atlantic research program (e.g. volumes edited by Wiebe & Beardsley, 1996; Wiebe et al., 2001). Although we focus principally on summarizing results from 5 years of BROADSCALE Survey cruises, we also draw on a short term drifting tracking study for comparisons of egg production rates between the two taxa of interest.

Materials and methods

Sampling

Sampling was carried out on 30 BROADSCALE Survey cruises on Georges Bank and the immediately surrounding region from 1995 through 1999. Samples were taken on 6 monthly cruises each year from January through June, except in 1995 (February–July). The stations from which mortality estimation was conducted were the cardinal stations at which both pump and net samples were taken (Stations 3, 9, 18, 20, 29, 36, 38; also Station 7 in 1995 and 1996; also Stations 30 and 34 in 1998 and 1999; also Stations 4, 34, 39 in January 1996 and Stations 4, 13, 16 in January 1999). See Figure 1 in Durbin et al. (2000a) for station locations. At each station, the population was sampled with a plankton pump and a 1 m², 153- μ m mesh Mocness (Wiebe et al., 1985; Durbin et al., 2000a). A centrifugal pump was used from February, 1995 through May 1998 and a diaphragm pump from

June 1998 through June 1999. Inspection of the catch curves by developmental stage, corrected for stage-specific differences in development times, revealed that nauplius stages 1 and 2 of *Calanus finmarchicus* and nauplius 1 of *Pseudocalanus* were undersampled by the centrifugal pump. This observation motivated the switch to the diaphragm pump, for which the catch of N2 of *Calanus* was improved but N1 of both species continued to be undersampled. As a consequence of the bias against N1 of both species, our general recommendation for future sampling of copepod nauplii is to use large volume water bottles rather than pumps. For both pumping systems, pumps were connected to 6.4 cm diameter ribbed suction hose that emptied into a receiver tank aboard ship. The contents of the tank were drained through a 0.035 mm mesh (0.050 mm in 1995). Flow rates were approximately 500 l min⁻¹ with the centrifugal pump and 240 l min⁻¹ with the diaphragm pump. Sample volumes were measured with a Signet flow meter. Pump sampling depths were 0–15 m, 15–40 m and 40–70 m (bottom depth permitting).

Three depth strata were sampled with the Mocness, usually 0–15 m, 15–40 m and 40–100 m (bottom depth permitting). Where bathymetry allowed, a fourth sample was taken from 100 m to the bottom. Abundances were vertically integrated across all sampled depth strata at each station and expressed as numbers per m² of sea surface. Mean depths (Z_m) for each developmental stage were calculated from:

$$Z_m = \frac{\sum_{i=1}^k N_i \left(\frac{\Delta Z_i}{2} + Z_{i,s} \right)}{\sum_{i=1}^k N_i}, \quad (1)$$

where for each depth stratum from $i = 1 \dots k$, where k is the total number of strata sampled, N_i = animal density (number per m³), ΔZ_i = thickness of stratum (in m), and $Z_{i,s}$ = upper depth boundary of stratum (in m).

Samples were fixed in 4% buffered formaldehyde, then all naupliar stages, copepodids, and adults of *Calanus finmarchicus* (Gunnerus) and *Pseudocalanus* spp. were distinguished and enumerated at the University of Rhode Island (Durbin et al., 2000a). The designation *Pseudocalanus* spp. in this locality probably includes three species, viz. *P. moultoni* Frost, *P. newmani* Frost, and *P. minutus* (Krøyer, 1845). The first two species were explicitly recognized from Georges Bank in Frost's (1989) revision of the genus. We infer that *P. minutus* is occasionally expatriated to the region from the nearby Scotian Shelf, where its

occurrence has been confirmed (Frost, 1989). From the data presented in Bucklin et al. (2001), averaged over five BROADSCALE Survey cruises in 1997, *Pseudocalanus* females were an equal mix of *P. newmani* (51.1%) and *P. moultoni* (48.9%, $N=2720$ total animals sequenced), with a monthly progression from February to June of 44.7%, 45.5%, 46.6%, 47.3%, 59.3% *P. moultoni*. Calculation of differential mortality rates of these two species must await routine, rapid molecular discrimination of thousands of individual nauplii.

The daily recruitment rate of *Calanus finmarchicus* eggs into the water column was estimated as the product of the daily egg production rate per female times the vertically integrated abundance of adult females. Daily egg production rate was obtained from a reproductive index based on morphological analysis of the state of gonad development of adult females (cf. Runge, 1987). The reproductive index was calibrated against experimental incubations of egg production rate of *C. finmarchicus* females in the environs of Georges Bank ($r^2=0.74$, Runge et al., 1997). Female abundances were obtained from vertically integrated Mocness abundances.

Temperature at the mean depth occupied by each developmental stage at each station was determined from CTD casts. The temperature-dependent duration of each developmental stage of *C. finmarchicus* at each station was determined from the Belehrádek functions in Campbell et al. (2001a). Stage durations for *Pseudocalanus* spp. were determined from hybrid values for *P. newmani* (eggs from McLaren et al., 1989, post-embryonic stages from Landry, 1983) and *P. moultoni* (McLaren et al., 1989).

Mortality estimation

Mortality estimation for nauplius through adult stages was done using the vertical life table approach, which estimates the joint mortality rates for each successive pair of developmental stages (Aksnes & Ohman, 1996). For two subadult stages mortality (m) is estimated from an iterative solution to:

$$\frac{\exp^{mD_i} - 1}{1 - \exp^{-mD_{i+1}}} = \frac{N_i}{N_{i+1}} \quad (2)$$

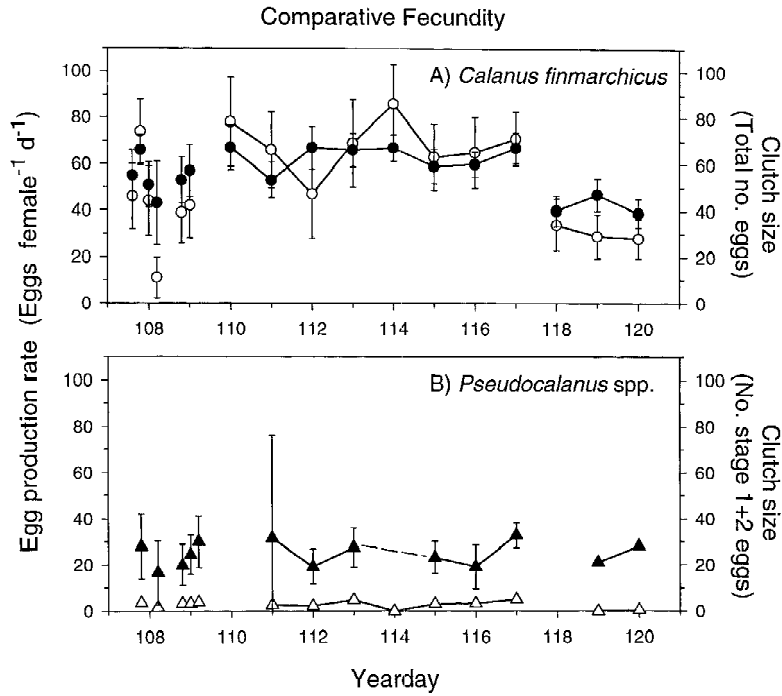


Figure 2. Comparative fecundity of (A) *Calanus finmarchicus* and (B) *Pseudocalanus* spp. on Georges Bank, 18–30 April, 1999 (yearday 108–120). Daily egg production rate (open symbols) and clutch size (filled symbols), mean \pm 95% C.L. On day 108, experimental animals were collected at 2 stations (Stations 1 and 2) on the bank Crest and at 2 stations (Stations 3 and 4) on the Southern Flank, and on day 109 at 3 stations (Stations 5, 6 and 8) on the NE Peak. Multiple daily stations are offset on the abscissa for clarity. The lines connect stations occupied while tracking a mesh sock drifter drogued at 20 m. A front was crossed between days 117 and 118 (see R/V Endeavor Cruise 322 Report for details).

and for joint copepodid 5/adult (C5/adult female or C5/adult male) mortality, from:

$$m = \frac{\ln\left(\frac{N_{C5}}{N_{Ad}} + 1\right)}{D_{C5}}, \quad (3)$$

where D_i is the duration (in d) and N_i is the abundance per m^2 of the i th developmental stage, and N_{Ad} is the abundance of either adult males or adult females. We assumed a 1:1 sex ratio of C5's and a common development time for C5's of both sexes. For *C. finmarchicus*, we also estimated the combined mortality for the egg-through-the first quantitatively sampled stage, which was N_3 (i.e. egg- N_3) for the time period sampled with the centrifugal pump and N_2 (i.e. egg- N_2) for the interval sampled with the diaphragm pump. The relation used was derived from Equation (11a) in Aksnes et al. (1997):

$$\frac{N_3}{BN_f} = \frac{\exp^{-mD_{E-N_2}} [1 - \exp^{-mD_{N_3}}]}{m}, \quad (4)$$

where N_3 =number of nauplius stage 3 per m^2 , B =egg production rate (eggs female $^{-1}$ d $^{-1}$), N_f =number

of adult females per m^2 , D_{E-N_2} =development time (d) from onset of egg through end of N_2 , D_{N_3} =development time (d) of N_3 , and m =the joint mortality rate for egg- N_3 . Where egg- N_2 estimates were made instead of egg- N_3 , all variables subscripted N_3 in Equation (4) should be changed to a subscript of N_2 and the development time in the first exponential should be D_{E-N_1} (=development time from onset of egg through end of N_1). Estimation of egg mortality was not done for *Pseudocalanus* spp. because we did not have estimates of their egg production rates from Broadscale Survey cruises. In total, we obtained 5341 mortality estimates.

Drifter tracking

The fecundity of *C. finmarchicus* and *Pseudocalanus* spp. was compared in experimental incubations during a drifter tracking experiment on Georges Bank, from 18 April to 1 May 1999. The centroid of initially three, and subsequently two, mesh sock drifters drogued at 20 m depth was followed to guide all sampling and collection of experimental animals. Adult female

copepods were sorted immediately after capture with a bongo net. Forty *C. finmarchicus* females were placed individually in petri dishes (30 ml). At 8 h intervals, eggs were counted and removed from the incubation vials. The total eggs produced over 24 h gives the daily egg production rate. *Pseudocalanus* spp. females, verified to be mixture of *P. moultoni* and *P. newmani*, were examined and their eggs assigned to 6 stages of development based on morphology. The number of eggs in the first two stages, which together lasted approximately 1 day, was enumerated. The daily egg production rate was obtained from the product of the proportion of females carrying stage 1+2 eggs (average number of females examined per station=49) times the average clutch size of stage 1+2 eggs (average number of clutches enumerated=7).

The hatching success of *C. finmarchicus* eggs produced during incubations was assessed by incubating batches of 50 randomly selected eggs for 72 h at 5–7 °C. Hatching success of *Pseudocalanus* eggs was measured by teasing egg masses off females and adding an individual egg mass with known number of eggs to a scintillation vial for 6 d or more at 5–7 °C ($N=103$ –158 eggs per experiment). The embryonic duration of *Pseudocalanus* eggs is approximately 4.6 d at 6 °C (McLaren et al., 1989). Eggs and nauplii were preserved and enumerated. In initial trials with *Pseudocalanus*, eggs attached to females were added to vials. However, late stage eggs fell off females and settled to the bottom of the container where they were colonized by bacteria associated with settled phytoplankton and hence usually failed to hatch. In subsequent trials, eggs were removed from females and no phytoplankton was added. Hydrographic data and drifter tracks may be found in R/V Endeavor Cruise 322 Report (Durbin et al., 1999).

The linear dimensions of formaldehyde-preserved individuals of *C. finmarchicus* and *Pseudocalanus* spp. ($N=14$ –15 per stage, except $N=8$ in the case of adult female *Pseudocalanus*) from each developmental stage from N1 through adult females were measured. Specimens of both taxa originated from the same field samples collected on Georges Bank in April 1999.

Results

Sampling

Comparisons of the relative capture efficiency of different developmental stages of *Pseudocalanus* spp.

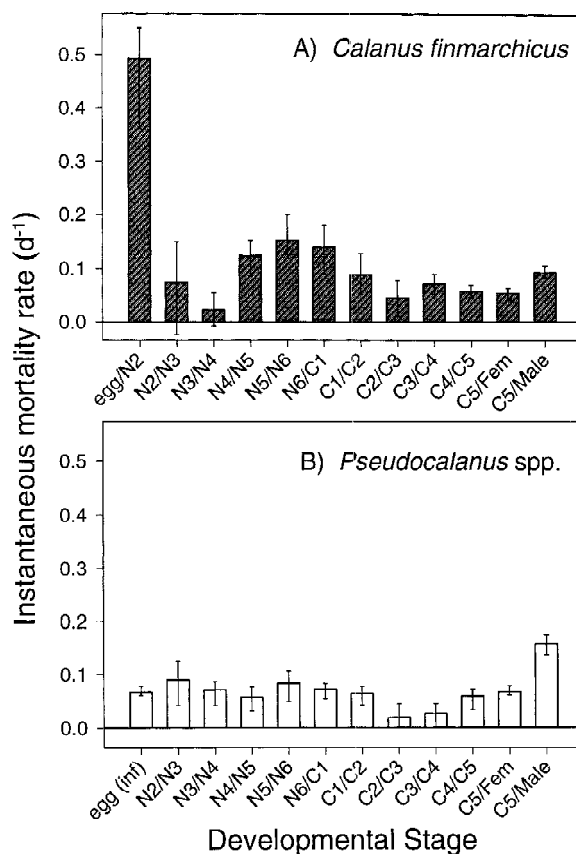


Figure 3. Summary stage-specific instantaneous mortality rates on Georges Bank for (A) *Calanus finmarchicus* ($N=2555$) and (B) *Pseudocalanus* spp. ($N=2786$). Median \pm 95% nonparametric confidence limits. Mortality estimates are derived from 30 Broadscale Survey cruises, 1995–1999, except for egg/N2 and N2/N3 for *Calanus finmarchicus*, which are based only on diaphragm pump samples taken in June 1998 and January–June 1999. In the case of *Pseudocalanus* spp., egg mortality rates are inferred to be equivalent to the C5/female rates; direct estimates were not made.

and *Calanus finmarchicus* by the Mocness and plankton pumps are illustrated in Figure 1. In relation to the centrifugal pump, the Mocness is the preferred collector for C2 and later stages of *C. finmarchicus* and for adults of *Pseudocalanus*. In relation to the diaphragm pump, the Mocness is the preferred collector for C4 and later stages of *Calanus* and adult males of *Pseudocalanus*. Consequently, for *Calanus finmarchicus* when the centrifugal pump was used, abundances of all naupliar stages and copepodids through C1 were taken from the pump samples and all later stages from the Mocness. When the diaphragm pump was used, abundances through C3 were taken from the pump. For *Pseudocalanus*, all naupliar stages as well as copepodid stages through C5 were taken from the pump

and measures of adult abundances from the Mocness samples.

Comparative fecundity

In April, 1999, the fecundity of *C. finmarchicus* and *Pseudocalanus* spp. was compared. The daily egg production (EPR) of *C. finmarchicus* ranged between 11.1 and 85.8 eggs female⁻¹ d⁻¹ (52.5±10.8, mean±95%), with clutch sizes between 39 and 67 eggs per clutch (Fig. 2). Both clutch size and EPR decreased when the drifters crossed a front into lower chlorophyll water (R/V Endeavor Cruise 322 Report, Durbin et al., 1999). The EPR of *Pseudocalanus* spp. ranged between 0 and 5.1 eggs female⁻¹ d⁻¹, (2.72±0.95, mean±95%) with the clutch size of young eggs (stages 1 and 2 only) between 17 and 33 eggs. *Pseudocalanus* clutch size did not decline across frontal waters, but EPR may have (Fig. 2). The mean rate of egg production by *Calanus* was 19 times than of co-occurring *Pseudocalanus*.

The egg hatching success of both species was high, averaging 88.9±4.0% (N=11 experiments) for *C. finmarchicus* and 84.8±6.4% for *Pseudocalanus* spp. (N=3).

Comparative mortality

The average mortality rates of *C. finmarchicus* and *Pseudocalanus* spp. differ appreciably. For *C. finmarchicus*, the highest mortality is found in the combined egg-N2 stage, then declines to progressively lower values in the N2/N3 and N3/N4 (Fig. 3A). There is significant heterogeneity of mortality rates by developmental stage, whether egg/N2 rates are included ($P < 10^{-10}$, Kruskal–Wallis 1-way ANOVA=186.856, df=11) or excluded ($P < 10^{-10}$, K-W=122.884, df=10). Mortality rates increase in the late naupliar stages and C1 ($P < 0.05$), then decline again to constant levels from C2/C3 through the adult female. The C5/adult male rates are consistently higher than the C5/adult female rates ($P < 0.05$). Note that mortality estimates are averages from 1995 to 1999 for N3/N4 and later stages, but averages from June 1998 to June 1999 for the egg/N2 and N2/N3 stages. Egg/N2 mortality could only be assessed when the diaphragm pump was used.

The bimodal pattern of stage-specific mortality rates observed in *C. finmarchicus* was not observed in *Pseudocalanus* spp. Significant heterogeneity in mortality by developmental stage was detected for *Pseudocalanus* spp. ($P < 10^{-10}$, K-W=197.758,

df=10), but there is an approximately equal probability of mortality for most developmental stages, with a small decrease in the C2/C3 and C3/C4 stages ($P < 0.05$) and about a 2-fold increase in mortality rate for the adult males (Fig. 3B). Notably, the increase in mortality of late naupliar stages seen in *C. finmarchicus* is not observed in late naupliar stages of *Pseudocalanus*. The hypothesis of no difference between frequency distributions of mortality rates for the two taxa was rejected, whether *C. finmarchicus* egg/N2 mortality rates were included ($P < 0.001$, Kolmogorov–Smirnov 2-sample test) or excluded ($P < 0.01$). Pairwise comparisons revealed that *C. finmarchicus* and *Pseudocalanus* spp. mortality rates differed in the egg stage, N4/N5, N5/N6, N6/C1, C3/C4 and C5/Male stages ($P \leq 0.05$).

The *Pseudocalanus* egg mortality rates in Figure 3B are based on the inference that the mortality rate of the eggs is the same as that of the adult females, as females carry their eggs. This assumption has been verified for a population of *Pseudocalanus newmani* in a different environment (Ohman & Wood, 1996), and is further substantiated by the relatively high hatching success of *Pseudocalanus* eggs on those occasions when it has been measured on Georges Bank. If the differences between *Calanus* and *Pseudocalanus* in stage-specific mortality rate commencing at N4 were explainable by size-specific differences in encounter rates with predators, one would expect to see appreciable differences in size between these taxa, beginning at the N4 stage. Figure 4 shows that while total length, body width, and aspect ratio (total length/width) do differ for later developmental stages of the two taxa, such metrics begin diverging at the N6 (or N5) stage, or later, and not expressly at the N4. Furthermore, such size and shape differences become more pronounced with later stages despite the relative similarity of late-stage mortality rates. Hence, size, at least as measured by linear dimensions, by itself is not sufficient to explain the mortality rate differences between taxa.

If the vertical distributions of late naupliar stages of the two taxa differed substantially, their encounter rates with predators located in vertically restricted regions of the water column could account for the mortality differences observed. Figure 5 shows that there is about a 5 m average vertical offset in vertical distribution between the two taxa through the naupliar stages, which decreases somewhat in the early copepodid stages and increases for the C5s and adult males. (See Durbin et al., 2000b for a more complete ana-

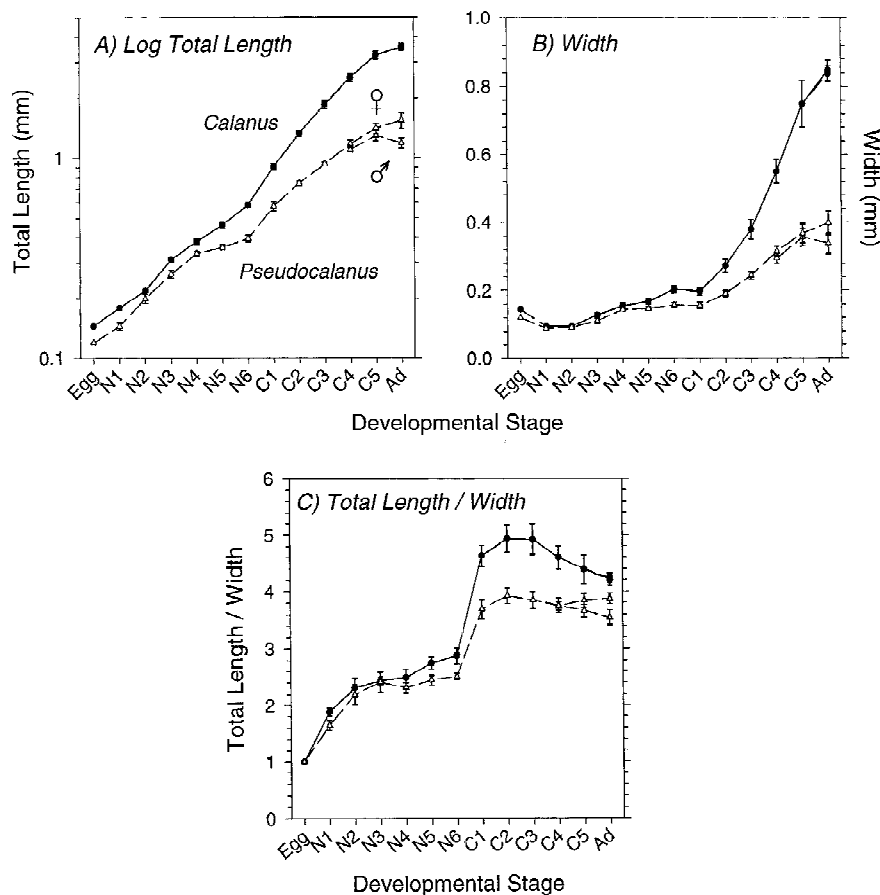


Figure 4. Comparative dimensions of *Calanus finmarchicus* and *Pseudocalanus* spp., from field samples on Georges Bank in April 1999. (A) LogTotal length, (B) Body width, and (C) ratio of Total length/body width. Males and females were measured separately for the adults of *C. finmarchicus* (total lengths not distinguishable on this plot) and for C4 through adults of *Pseudocalanus* spp. (mean \pm 95% C.L.).

lysis of vertical distributions of *Calanus* nauplii.) Such relatively small vertical offsets by themselves seem unlikely to account for observed differences in mortality rates, especially since there is no marked tendency for differences to increase at the N4 stage. At individual stations, where conditions are more stratified or better mixed, the vertical offsets may be considerably larger or smaller than these averages, and there also may be regional differences between taxa in diel vertical migration behavior. However, a consistent and significant vertical offset in average vertical position of both of these taxa and their predators would be necessary to account for the differences in average mortalities seen in Figure 3. The relative similarity in vertical distributions between *Calanus* and *Pseudocalanus* in this environment further suggests that depth-dependent differences in horizontal advection (Eiane et al., 1998) are unlikely to account for the observed differences in mortality rates.

The possibility that intergeneric differences in swimming behavior, and consequently in vulnerability to predators, accounts for the differences observed is discussed below.

The mortality rate of the aggregated egg-N2 stage was estimated from seven cruises when the diaphragm pump was used. Egg-N2 mortality rates show a relationship with the abundance of adult females sampled concurrently in the water column (Fig. 6A). This relationship is relatively weak at low abundances of adult females, but becomes pronounced at female abundances exceeding approximately 2000 females m^{-2} . The earliest developmental stage for which mortality of *Calanus finmarchicus* was estimated consistently on all cruises was the aggregated egg-N3 stage. The egg-N3 mortality rate shows a nonlinear relationship with the abundance of adult females (Fig. 6B). Early stage mortality is again independent of female abundance at low female abundance, but the relationship becomes

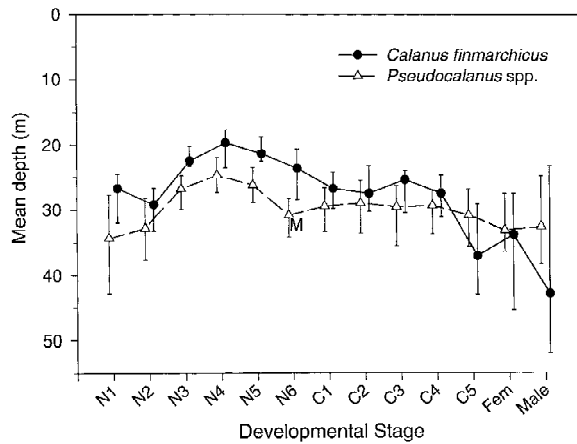


Figure 5. Mean depth, by developmental stage, for *Calanus finmarchicus* and *Pseudocalanus* spp. in the environs of Georges Bank. All stations sampled, irrespective of time of day, are included. Error bars show 95% C.L.

density-dependent at higher female abundances. In the case of *Pseudocalanus* spp., if we infer that the instantaneous mortality rate of eggs is approximated by that of females, there is no evidence of density-dependent egg mortality across any range of female densities (Fig. 6C).

We explored the relationship between mortality rate and body mass (as C content) and mortality rate and ambient temperature. Although Loess fits (Cleveland & Devlin, 1988) suggested that these relationships may not be linear in log-log space, nonlinear curves fitted to these data showed virtually no improvement in r^2 and thus we present the linear relations here to facilitate comparisons. Linear fits to the log-transformed data suggest a weak negative trend with body size (Fig. 7) and a weak positive trend with temperature (Fig. 8). ANCOVA revealed that the slopes of the relationships were significantly different between the two copepod taxa for both mass ($P < 0.0001$) and temperature ($P < 0.001$), hence the data are shown for each separately. However, for both *Calanus* and *Pseudocalanus*, these independent variables fail to account for most of the variability in the observations. At any given C content or temperature, observed mortality rates vary by approximately 2 orders of magnitude. Between 81 and 96% of the variability in copepod mortality rates remains unexplained by either body mass or by temperature. A multiple regression incorporating both temperature and C content accounted for 5.3% of the variability in *Pseudocalanus* spp. mortality and 27.2% of the variability in *C. finmarchicus* mortality.

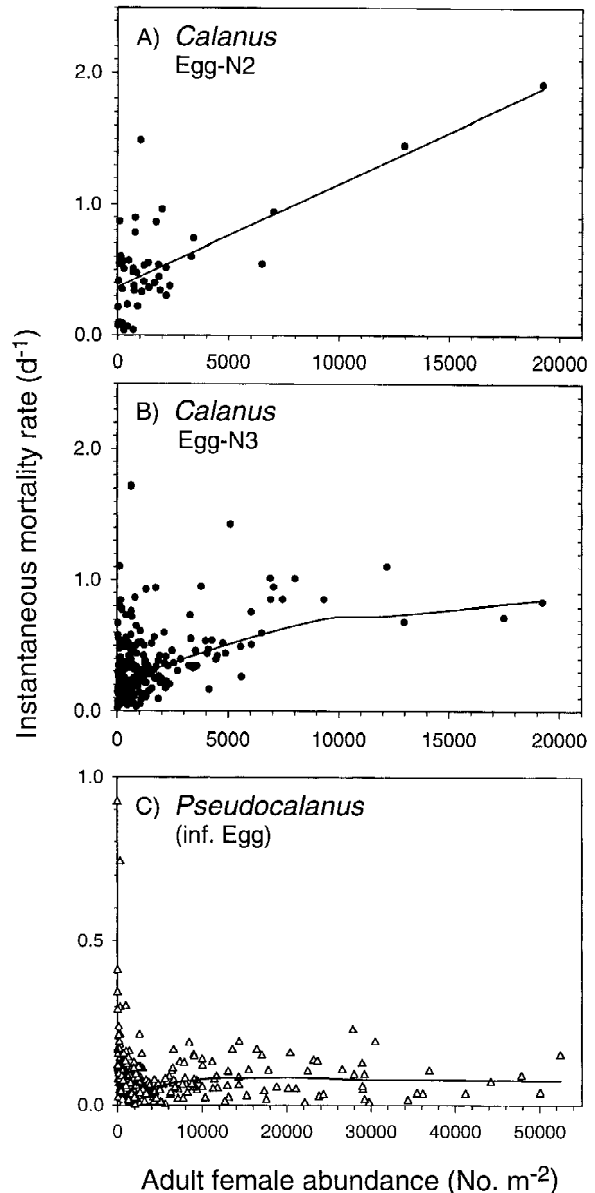


Figure 6. Instantaneous mortality rates of young developmental stages versus the abundance of adult females, for (A) *C. finmarchicus* egg/N2 (June 1998 and January–June 1999), (B) *C. finmarchicus* egg/N3 (January 1995–June 1999), and (C) *Pseudocalanus* spp. inferred egg mortality (January 1995–June 1999). The line in (A) is a linear regression ($r^2=0.49$) and in (B) and (C) is a Loess fit (Cleveland & Devlin, 1988).

Discussion

This is the first study to contrast the stage-specific patterns and rates of mortality of *Calanus* and *Pseudocalanus*, despite a sizable existing literature on many other aspects of their biology and ecology

(Mauchline, 1998). The extensive Broadscale Survey cruises conducted during the U.S. GLOBEC Northwest Atlantic program afforded an unusual opportunity to satisfy the intensive demands for biological and physical data needed to solve for species- and stage-specific mortality rates for both taxa. Our results illustrate that there are appreciable differences in the rates and patterns of mortality for *C. finmarchicus* and *Pseudocalanus* spp. co-occurring within the same geographically restricted study site.

The pronounced difference in earliest stage mortality between the two taxa is not unexpected, as *Calanus* is a broadcast spawner whose freely spawned eggs might be expected to suffer high losses in the ocean due to a variety of causes, while *Pseudocalanus* females carry their eggs in an attached egg mass, which consequently would be expected to experience considerably reduced mortality rates. This dichotomy between rates of egg mortality in broadcast and brooding copepods was explored by Kiørboe & Sabatini (1994, 1995), whose results suggest that the faster rates of development and different scaling of egg size with adult female size in broadcast spawning copepods affords them the capacity to produce a sufficient number of small eggs to compensate their greatly elevated mortality. However, the hypothesized differences in egg mortality between life histories that were modeled by Kiørboe and Sabatini were based on empirical measurements of mortality rates of only a single species of egg-brooding marine copepod, *Pseudocalanus newmani* (Ohman, 1986; Ohman & Wood, 1996). There is a pressing need for appropriate field studies to expand the number of mortality estimates for natural populations in diverse field environments, particularly for taxa that carry their eggs (see also Liang & Uye, 1997) and for populations of all life histories residing in the open ocean.

The conditional density-dependence of *C. finmarchicus* egg-N2 mortality, which appears to operate only at high densities of *Calanus* females, is not in complete agreement with Strong's (1986) suggestion of 'density-vague' relationships. In this concept, which has been criticized (e.g. Berryman, 1991), the effects of population density are thought to occur at both low and high, but not at intermediate densities. We observed no effect of population density at either low or intermediate densities. This conditional density-dependence in *Calanus* also contrasts with the complete lack of population density-related egg mortality inferred for *Pseudocalanus*. The most likely explanation for the relationship between *Calanus* egg

mortality and female abundance at high egg densities is cannibalism on freely suspended *Calanus* eggs, which would not occur for the brooded eggs of *Pseudocalanus*. Experimental work has shown that adult females (Runge & Roff, 2000) and C5's (Runge et al., unpubl.) of *C. finmarchicus* ingest eggs and nauplii of conspecifics, and do so with clearance rates that are comparable to optimal clearance rates measured on other microzooplankton prey (cf. Ohman & Runge, 1994; Irigoien et al., 1998). Another principal source of mortality on *Calanus* eggs is predation by suspended hydranths of the hydroid *Clytia* spp., which have been shown experimentally to ingest eggs and nauplii of *C. finmarchicus* on Georges Bank (Madin et al., 1996). Such hydroids are particularly abundant on the shallow, tidally mixed bank crest (Concelman et al., 2001). If we apply experimentally measured clearance rates by *Calanus* and hydroids, together with their measured abundances at each station, these two sources of predation alone are in most cases sufficient to account for the early stage mortality observed. Omnivorous copepods such as *Metridia* and *Centropages* are likely to further contribute to *Calanus* egg mortality (Sell et al., 2001), and chaetognaths and other predators to post-embryonic mortality (cf. Sullivan & Meise, 1996). Careful consideration of the predation potential by these taxa, and their spatial variations, will be presented elsewhere. However, in summary, it appears that the principal source of early stage *Calanus* mortality at low population densities is predation on eggs and young nauplii by suspended hydroids, while at high densities of adults, egg cannibalism is the principal source of predation mortality. The brooded eggs of *Pseudocalanus* do not incur either source of mortality.

A similar, but still stronger effect of density-dependence of egg mortality on adult female abundance has been found for *C. finmarchicus* in the open ocean at Ocean Station M in the central Norwegian Sea (Ohman & Hirche, 2001). The mortality patterns differ between the Norwegian Sea and Georges Bank in that density-dependent egg mortality found at Station M at low *Calanus* abundances was not observed on Georges Bank. A primary difference in the predator communities of the two environments is the lack of planktonic hydroids in the deep-water, oceanic environment of the Norwegian Sea. Where hydroids are lacking, egg mortality appears to be more closely related to the presence of cannibalistic females. The significance of this density-dependent relationship of early stage mortality is that it results in a nonlinear

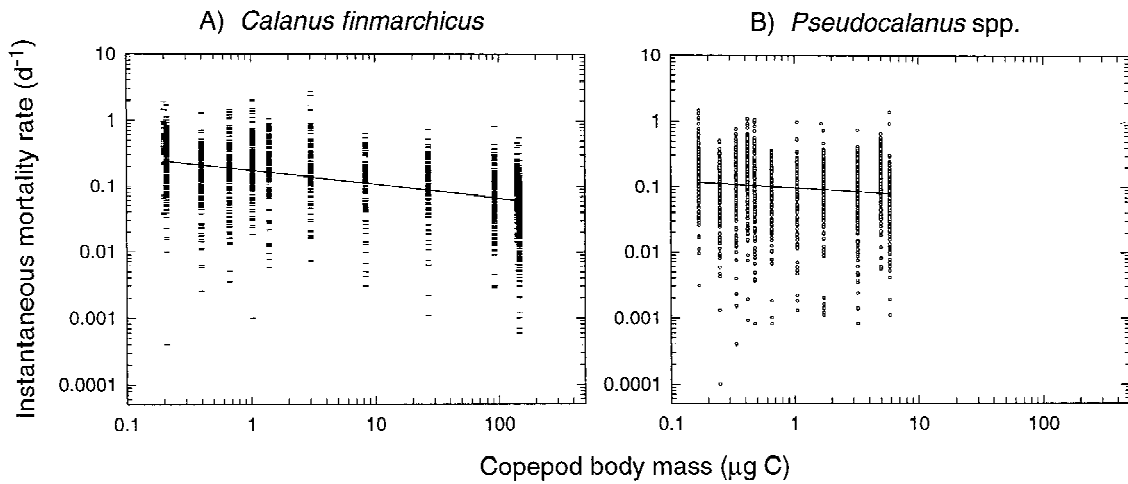


Figure 7. Relationship between instantaneous mortality rate and copepod body mass (as carbon), for (A) *C. finmarchicus* ($\text{Log } Y = -0.210 \text{ Log } X - 0.763$, $r^2 = 0.194$, $P < 0.0001$) and (B) *Pseudocalanus* spp. ($\text{Log } Y = -0.110 \text{ Log } X - 1.018$, $r^2 = 0.015$, $P < 0.0001$). Only non-negative values were included in the regressions. Estimates of the carbon content of each copepod developmental stage were obtained from Campbell et al. (2001a) for *C. finmarchicus* and Davis (1984b) for *Pseudocalanus*.

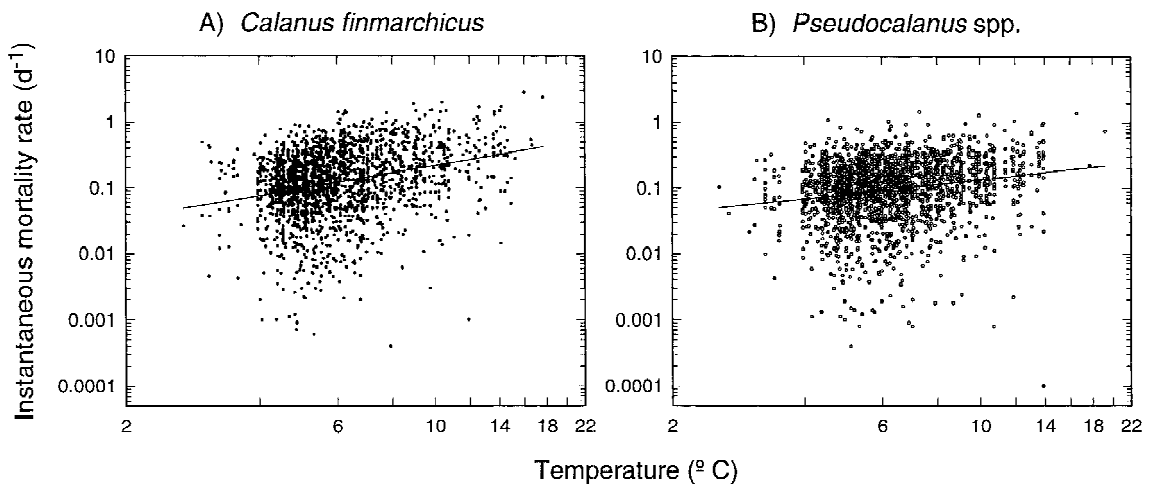


Figure 8. Relationship between instantaneous mortality rate and ambient temperature, for (A) *C. finmarchicus* ($\text{Log } Y = 1.153 \text{ Log } X - 1.814$, $r^2 = 0.081$, $P < 0.0001$) and (B) *Pseudocalanus* spp. ($\text{Log } Y = 0.738 \text{ Log } X - 1.606$, $r^2 = 0.039$, $P < 0.0001$). Only non-negative values were included in the regressions.

mortality term. Such nonlinearities, in the form of a quadratic mortality function, introduce markedly different dynamics into models of marine ecosystems, when compared to zooplankton mortality modeled as a linear function of zooplankton abundance (Steele & Henderson, 1992; Fasham, 1995; Edwards & Yool, 2000).

We do not have egg viability measurements corresponding to each estimate of egg mortality to assess the component of mortality attributable to unsuccessful egg hatching. However, on those occasions when egg hatching success has been measured, it tends to

be high, as on the cohort tracking cruise reported above. Runge et al. (unpubl.) measured *C. finmarchicus* egg hatching success on 9 cruises between January and July, 1995–1999 and found that in most instances egg survivorship was relatively high (median of 79%; $n=69$). In only 3 of the 69 experiments did the average hatching success drop to below 50%. While we cannot rigorously test the diatom toxicity hypothesis (Miralto et al., 1999) here, we note that among these observations there was no seasonal trend in *C. finmarchicus* egg hatching success, in contrast to the expectation

from the toxicity hypothesis of a marked reduction during seasonal diatom blooms.

Perhaps as striking as the difference in egg mortality rates between *Calanus* and *Pseudocalanus* is the difference in late naupliar mortality. This intergeneric difference in N4-C1 mortality between *Calanus* and *Pseudocalanus* was not clearly attributable to differences in body size or vertical distribution. Rather, intergeneric differences in swimming behavior and thus in encounter rates with predators, and/or in escape responses from predators, is the likely explanation. Sell et al. (2001), working in the same study site as we did, found that the omnivorous copepod *Metridia lucens* ingested *Calanus finmarchicus* nauplii at rates 3–7 times higher than they ingested *Pseudocalanus* spp. nauplii of the same size. They suggested that *Pseudocalanus* nauplii are capable of stronger swimming, hence better escape responses, than *Calanus* nauplii. This result is entirely consistent with our mortality result and suggests that carnivorous zooplankton with prey selection characteristics similar to *Metridia lucens* are responsible for the intergeneric differences seen in mortality rates that we found *in situ*. A detailed analysis of this problem, together with comparative estimates of predation by planktivorous fish on Georges Bank and losses from other sources, is in progress. We note that the observed rates of instantaneous mortality of both copepod taxa are appreciably higher than can be accounted for by the average advective losses from Georges Bank (Limeburner & Beardsley, 1996; Naimie et al., 2001), although transient washout events can occur, especially in winter (Lewis et al., 2001).

Efforts to describe the mortality rates of pelagic invertebrates as simple allometric relations using body size as an independent variable (e.g. McGurk, 1987) have little utility in studies of copepod population dynamics. If we were to combine the data for both taxa, copepod body mass (as C) would account for only 6.7% of the variance in mortality rates. Similarly, we found ambient temperature to have very little explanatory value over the range 3–19 °C, in this environment. Again ignoring life history and taxonomic differences to combine results in a joint regression, only 5.5% of the variance in mortality rates for both species is accounted for by temperature. Although mortality rates show a tendency to increase with temperature, as predicted by Myers & Runge (1983), the effect is slight. The striking features of the relationships observed are the weak slopes and the extensive variance in mortality rates that remains unexplained by either variable. Intergeneric differences in life history characteristics,

behavior, and time-dependent predation risk are of first-order importance in understanding the variability unexplained by such simple regression relationships. Recent results by Eiane et al. (2002) illustrate that stage-specific mortality schedules for *Calanus* differ markedly when they encounter different guilds of selective predators.

Assumptions of mortality calculations

The vertical life method assumes that the ratio of successive developmental stages is at short-term equilibrium for an interval equal to the duration of the two stages combined (Aksnes & Ohman, 1996). This assumption implies that there are no well-defined recruitment trends over this time period. This appears to be a reasonable assumption until the late copepodid stages, as most stage pairs last a relatively short time (3–10 days until C4/C5, at which point it extends to about 18 days at 8 °C [Campbell et al., 2001a]). For these later and longer-lasting developmental stages, we would expect the positive and negative biases associated with recruitment trends of different directions to cancel one another in a data set as large as the one treated here. As was made clear by Aksnes and Ohman's numerical experiments, it is particularly important that replicated samples of stage ratios be used, a requirement that was clearly met in the present study.

Our method for estimating egg-N3 mortality assumes that rates of egg production and of egg and early naupliar development remain relatively constant for a period of a few days. Results from our cohort tracking cruise suggest that egg production estimates are relatively stable. Egg production estimates by Runge (unpubl.) suggest that at adjacent on-bank stations *C. finmarchicus* generally show similar reproductive indices and, therefore, similar inferred rates of egg production.

Our estimations also assume that stage durations can be well described as a function of temperature. This is certainly valid for the egg through nauplius 2 of both taxa, all of which are non-feeding stages. For feeding developmental stages of *Pseudocalanus*, several studies with varying amounts of evidence have concluded that development rates are not often food-limited *in situ* (e.g. Corkett & McLaren, 1978; Davis, 1984a; Ohman, 1985). Experimental work with *Calanus* spp. has established that the rate of stage development is less sensitive to low food concentrations than the rate of somatic growth (e.g. Vidal, 1980; Campbell et al., 2001a). In the experiments of

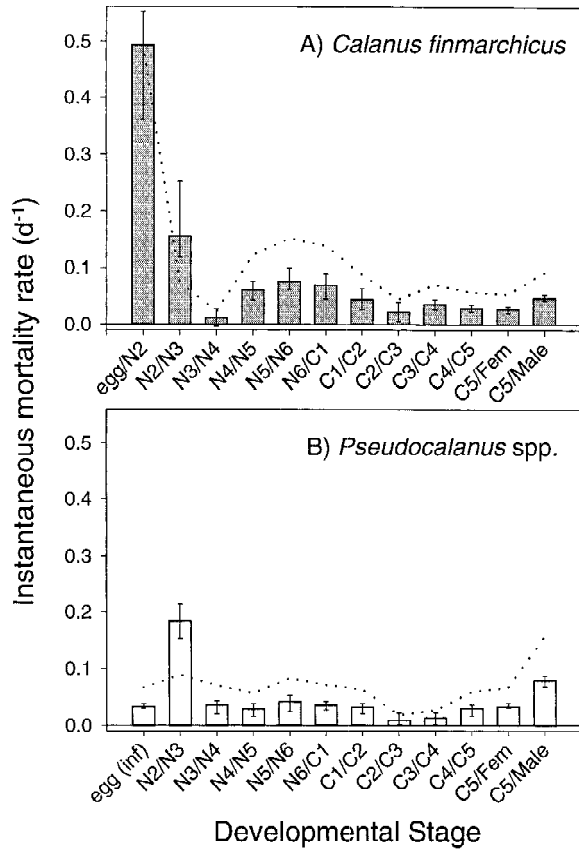


Figure 9. Effects on mortality estimates of increasing stage-specific development times by a factor of two from N3 through the adult to account for food limitation (median±95% confidence limits, bars and dashed lines). Dotted line in the background illustrates the average rates shown in Figure 3 above.

Campbell et al. (2001a) with *Calanus finmarchicus*, the observed difference in developmental rate from highest food concentrations (ca. 350 $\mu\text{gC l}^{-1}$) to lowest food concentrations (ca. 25 $\mu\text{gC l}^{-1}$) was about a factor of two for both nauplii and copepodites.

In Figure 9 we illustrate the maximal bias in mortality rates that would result if our temperature-dependent rates of development were incorrect by a factor of two. Slowed development via food limitation would generally decrease the average rate of mortality, but would not change the stage-specific patterns or the contrast between taxa. The exception is the mortality estimate for the N2/N3 stage, which changes appreciably because the duration of the N2 is unaffected by food variations, while the N3 stage is doubled. Although severe food limitation events can occur in the field, in which the rate of development is transiently slowed by considerably more than a factor of two (e.g. Campbell et al., 2001b; Crain & Miller,

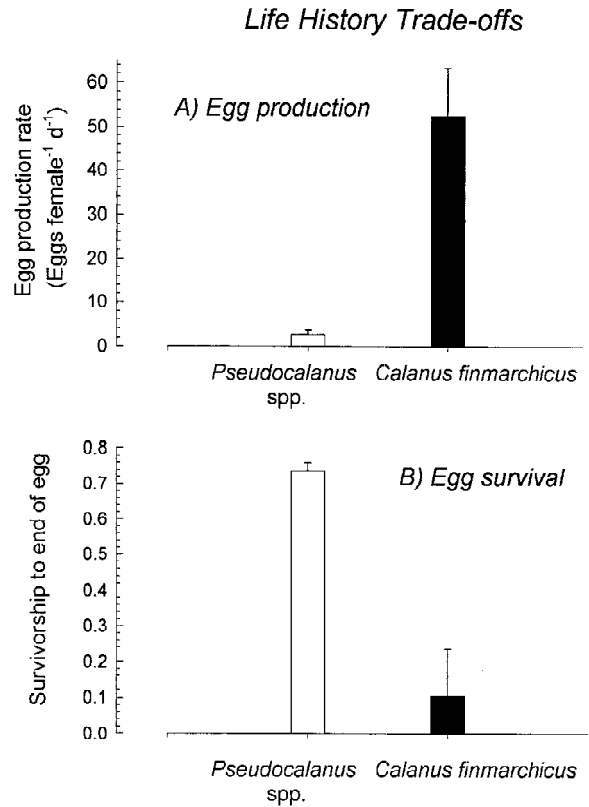


Figure 10. Life history trade-offs for *Calanus* and *Pseudocalanus*. (A) Comparative egg production rates for the two taxa and (B) comparative survivorship from the beginning to the end of the egg stage (mean±95% C.L.). *Calanus* egg survivorship was solved for from the egg/N2 and N2/N3 mortality rates by assuming that the N2/N3 mortality rate also applies to the N1 stage.

2001), such events appear not to be typical. Differential food limitation of different development stages (rather than a uniform doubling of development times) would significantly alter the rates from those presented in Figure 9 only if adjacent stages beyond N3 showed markedly different susceptibilities to limiting food, which appears unlikely. Furthermore, if we use reduced per capita egg production rate (EPR) of female *C. finmarchicus* on Georges Bank as an indicator of food-limited conditions, we found no evidence for consistently negative mortality rates (the expected direction of bias) for stations at which the EPR dropped below either 15, 10, or 5 eggs female⁻¹ d⁻¹. We conclude that we have not introduced undue bias in our mortality estimates by the procedure employed for estimating stage durations.

Conclusion

The two predominant copepod taxa on Georges Bank have different demographic characteristics. Figure 10 illustrates the trade-offs between fecundity and egg mortality that we observed on Georges Bank. The average egg production rate of *Calanus finmarchicus* was over 19 times that of *Pseudocalanus* spp., corresponding to a difference in instantaneous per capita birth rate of 4.1-fold. Compensating for this difference in fecundity is the marked difference in mortality. Expressed as survivorship to the end of the egg stage, it can be seen in Figure 10 that the survivorship of *Pseudocalanus* is 7 times that of *Calanus*. Moreover, *Pseudocalanus* does not incur the density-dependent losses experienced by *Calanus*, and appears to use behavioral means to reduce encounter rates with predators (or to escape more effectively from them). As the average annual abundance of *Calanus* and *Pseudocalanus* on Georges Bank is of similar magnitude, the fitness of these two contrasting life histories appears to be approximately equal in this study site and perhaps elsewhere in the north temperate ocean.

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