

The lost generation of *Calanus pacificus*: Is the diatom effect responsible?

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Abstract

An apparent mismatch between periods of high reproduction (spring) and high copepodite abundance (autumn) has been observed for the copepod *Calanus pacificus* in Dabob Bay, Washington, U.S.A. This persistent pattern leads to a lost generation of progeny that are produced in spring but do not recruit to the juvenile and adult populations, and this is likely due to a combination of factors including advective losses, predation mortality, and nonviability of progeny. Here we test the hypothesis that observed detrimental effects of diatoms on the viability of copepod embryonic and naupliar stages (the diatom effect) are the primary reason for the observed patterns of reproduction and abundance. Furthermore, we test how assumptions about egg production rate and naupliar viability can affect calculations of copepod recruitment. To test these hypotheses, we developed a numerical model to quantitatively explore how certain parameters may have affected the population of *C. pacificus* population in Dabob Bay. Predation mortality was the most significant contributor to population losses, while advective losses and naupliar viability were of lesser importance, and the model results were more sensitive to parameterization of naupliar viability than egg production rate. Although brief instances of low naupliar viability caused a 25–30% reduction in cumulative stage I copepodite abundance over time when compared with the assumption of persistent high naupliar viability, the lost generation of *C. pacificus* in Dabob Bay is likely due to predation mortality, not the diatom effect.

In marine planktonic copepods, egg production rate, viability of the offspring, predation rate, and advective flux rate are factors affecting recruitment of copepodite stages from spawned eggs. Since 1994, there have been a number of laboratory studies examining the viability of copepod progeny when females are fed different food types, and many of these studies suggest that diets high in diatoms can reduce reproductive success compared to diets with alternative or mixed prey types (see reviews in Paffenhof 2002; Ianora et al. 2003). This phenomenon has been termed the “diatom effect” (cf. Halsband-Lenk 2005), but its relevance to field populations has been ambiguous. Egg production rate has been widely shown to be positively correlated with concentration of chlorophyll (e.g., Bunker and Hirst 2004); however, there does not appear to be any relationship between egg hatching success (the proportion of spawned eggs that hatch, which is often >80%) and

diatom concentration (Irigoien et al. 2002). None of the studies to date quantitatively assessed how observed decreases in naupliar viability affected the population dynamics of the species being observed. In this paper, we present the results of a modeling investigation to explore whether an observed diatom effect could have decreased the recruitment success of the copepod *Calanus pacificus* (Copepoda: calanoida) in Dabob Bay, Washington, U.S.A.

In Dabob Bay, there is a resident population of *C. pacificus*, which annually progresses through three generations from February to September (Osgood and Frost 1994a). The population reaches its maximum abundance in autumn and its minimum abundance in late spring (Fig. 1; Osgood and Frost 1994a; Pierson et al. 2005b). In contrast, the maximum egg production rate (EPR) occurs in late spring, while the minimum EPR occurs in summer, before the abundance maximum (Fig. 1; Runge 1985; Frost 1988). This paradoxical pattern leads to a lost generation in which the large number of eggs produced early in the year does not result in increases in juvenile (copepodite) abundances. Similar patterns have been observed for the congeners *Calanus finmarchicus* in the St. Lawrence Bay estuary and *Calanus helgolandicus* in the English Channel (Plourde et al. 2001; Irigoien and Harris 2003), low recruitment success was observed early in the year, whereas abundance of copepodites increased later in the year even though egg production was lower. In contrast, the *C. finmarchicus* populations on Georges Bank and in the Norwegian Sea

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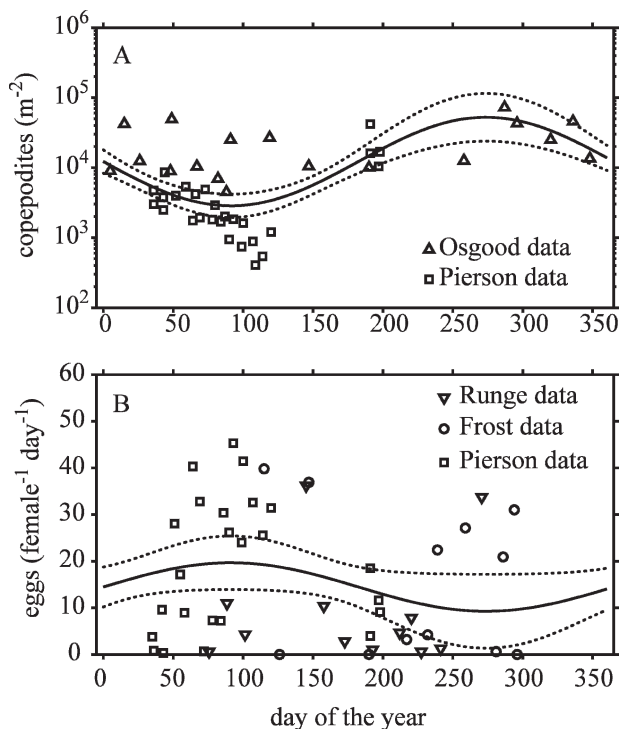


Fig. 1. Annual cycle of abundance of (A) all copepodite stages and (B) egg production rate for *C. pacificus* in Dabob Bay, Washington. Sine curves of the form $y = a \times \sin(x) + b$ were fit to all available data using a least squares approach to determine a and b (solid lines), and dotted lines show the 95% confidence interval of the curve fits. Abundance data came from Osgood and Frost (1994a) and Pierson et al. (2005a), and were $\log(x + 1)$ transformed before fitting curves. Egg production rate data came from Runge (1985), Frost (1988), and Pierson et al. (2005b).

show no decline in abundance throughout the early part of the year, suggesting that recruitment success is higher during this time in these regions (Hirche et al. 2001; Durbin and Casas 2006).

In order to address the hypothesis that the diatom effect may significantly influence copepod recruitment, we examined data collected as part of a larger project to determine if copepod reproduction is negatively effected by diatom blooms in situ (Frost 2005). It was shown that egg production rate in *C. pacificus* was generally positively correlated to chlorophyll *a* (Chl *a*) concentration; however, during blooms of diatoms of the genus *Thalassiosira* spp. (Horner et al. 2005), the naupliar viability of *C. pacificus* (defined as the number of spawned eggs surviving to the first feeding stage) decreased from a mean of $\sim 90\%$ survival to $<40\%$ in 2002 and $<70\%$ survival in 2003 (Pierson et al. 2005a). The observed negative effect of the diatoms on *C. pacificus* reproductive success was short-lived, and naupliar viability rebounded to the high levels ($>80\%$ survival) within one week. Although it was hypothesized that these ephemeral instances of decreased naupliar viability were not likely to have affected recruitment, a rigorous examination of that question was not undertaken (Pierson et al. 2005a).

We developed a numerical model of copepod recruitment to explore how the short-lived decreases in naupliar viability in 2002 and 2003 could have caused the observed lost generation of *C. pacificus* in those years. We compared model results to observations of copepodite abundances in Dabob Bay made between early February and late April, and we tested the model sensitivity to different parameterizations of EPR and naupliar viability. In addition, both an inverse model and a vertical life table were employed to estimate population loss rates based on observed egg production rates and copepodite abundances. These calculated loss rates were compared with estimates used in the model.

Methods

Data preparation—The methods and collection schedule for the data used in this study are given elsewhere (Horner et al. 2005; Pierson et al. 2005a,b). Briefly, 12 cruises were done approximately weekly between early February and late April in each of 2002 and 2003, to a station ($47^{\circ}46.14'N$, $122^{\circ}50.10'W$) in Dabob Bay, Washington, U.S.A. Upon arrival on station for each cruise, a cast was done with a conductivity-temperature-depth (CTD) probe to characterize the water column hydrography (Horner et al. 2005). On the first night of each cruise, depth-stratified vertical net tows were conducted with a 1-m-diameter Puget Sound net (Miller et al. 1984) fitted with $209\text{-}\mu\text{m}$ mesh (Pierson et al. 2005b). Egg production measurements for *C. pacificus* were also taken on the first night of each cruise by collecting female copepods just after dusk, and incubating individuals in tissue culture plates containing ~ 35 mL of ambient seawater (Pierson et al. 2005a).

We linearly interpolated the following data between cruises to estimate daily values for the inter-cruise periods: copepod abundance, depth integrated (0–30 m) stock of Chl *a* (Pierson et al. 2005b), measured values of egg production rate and naupliar viability (Pierson et al. 2005a), phytoplankton carbon (Horner et al. 2005), layer depth (described below), and mean salinity and temperature in different layers (Horner et al. 2005; Pierson 2006). In addition, the calculated sill cross-sectional area and volume of different layers were linearly interpolated between cruise dates (see below).

We defined the upper layer (UL) as the water in Dabob Bay found above the layer depth (LD—the depth of the 22.5 isopycnal), and the lower layer (LL) as the water below the LD. The 22.5 isopycnal occurs between 7 m and 20 m and corresponds closely to the depth of the 29 isohaline (Horner et al. 2005), and we assumed this to be the level of no net horizontal motion in the bay (Pierson 2006). The volume and sill cross-sectional area of Dabob Bay were calculated in Matlab (The MathWorks, Inc.) using bathymetry data provided by David Finlayson (1 : 24,000 scale, Finlayson 2005). Volume of the LL was determined by calculating the volume of the region that falls below the LD, and the volume of the UL was calculated as the difference between the LL volume and the total volume. The cross-sectional area at the sill was determined at the narrowest point at the mouth of Dabob Bay at mean lower-low water (MLLW, from Finlayson 2005).

Advective loss of Dabob Bay surface layer—Advective loss in Dabob Bay was estimated based on the semi-empirical relationship between wind speed and surface currents: surface current speed is $\sim 3\%$ of wind speed (Knauss 1997). Daily averaged wind speed and direction data were gathered from the National Climate Data Center (<http://www.ncdc.noaa.gov/oa/ncdc.html>) for the Olympia airport in Olympia, Washington, U.S.A. ($46^{\circ}58'N$, $122^{\circ}54'W$). Northward velocities were multiplied by 0.03 to estimate surface current speeds, and the absolute values of these current speeds were then multiplied by the cross-sectional area of the sill for the UL to get volume flux out of the bay. Advective loss rate (d^{-1}) was calculated by dividing the daily volume flux by the upper layer volume. These estimates of advective loss are likely an overestimate because they are applied to the entire layer, but the wind generally applies only to currents in the upper 5 m in Hood Canal (C. Sarason pers. comm.). It was assumed that there is no upstream source of copepods, so that advection always resulted in a loss to the copepod population (out of the bay to the south and losses due to subduction of the surface waters to the north), further overestimating advective loss rates. An advective coefficient (AC) ranging from 1.0 to 0.1 times the advective loss rate was employed in the model runs to span the likely range of the overestimated advective losses.

Copepod recruitment model—We developed a simple model to describe the survival of cohorts of spawned *C. pacificus* eggs developing into stage I (CI) copepodites in Dabob Bay, based on a modified version of eq. 3 in Aksnes et al. (1997):

$$\frac{dN}{dt} = N(bv - m - a), \quad (1)$$

where N is the copepod population size, t is time, b is the egg production rate, v is the naupliar viability, m is the natural mortality (e.g., predation), and a is the advection loss term. This model differs from the original model (Aksnes et al. 1997) in that it includes a naupliar viability term and disregards the immigration term. Again, we assume there is no upstream source of copepods in the model, and thus advection induces a simple loss from the system. Young stages of *C. pacificus* are found in the near-surface waters (Huntley and Brooks 1982; Osgood and Frost 1994b; Pierson et al. 2005b), and here we assume that all egg-CI stages are found in the UL. Eggs and nauplii of *C. pacificus* are found primarily in the upper 10 m of the water column in Dabob Bay (C. Miller pers. comm.), and the median depth of CI copepodites is ~ 5 m (Pierson et al. 2005b).

The model was run with three different parameterizations of EPR (b): measured EPR from cruises (b_m), estimated EPR based on an Ivlev fit between depth-integrated (0–30 m) stock of Chl a and the measured EPR data (b_{chl}), and estimated EPR based on an Ivlev fit between microplankton carbon concentration (determined from carbon:volume relationships; Menden-Deuer and Lessard 2000) and the measured EPR data (b_c). For

information on these Ivlev fits, see Pierson et al. (2005b). Values for b_c were calculated by dividing the depth-integrated Chl a by 30 m (to convert units to $\mu\text{g L}^{-1}$), and then multiplying those values by the carbon:chlorophyll ratios (Horner et al. 2005). The total number of eggs ($b \times$ female abundance) input each day into the model for each method is shown in Fig. 2.

Three different schemes for naupliar viability (v) were also included in separate model runs: 100% survival (v_{100}), measured naupliar viability (v_m), and measured naupliar viability with the low values observed in February of each year (Pierson et al. 2005a) replaced with average naupliar viability values from the rest of the year (v_a). Fig. 2 shows the time distribution used in the model for each of these variables. The v_a naupliar viability data were used to test whether the short-term decrease in naupliar viability that occurred in February of each year significantly affected the population dynamics in the model, compared with the v_m naupliar viability, and the v_{100} naupliar viability data were used to test how sensitive the model was to inclusion of naupliar viability at all. Loss rates from naupliar viability were converted to units of d^{-1} as $(1.0 - \text{naupliar viability})$ to compare these rates to calculated advected and estimated natural mortality rates.

The duration of each model run was from the first sampling day in February each year to the final sampling day in April of the same year, using a 5-min time step. Cohorts of eggs were input into the model daily at midnight using one of the three egg production estimates described previously. A temperature-dependent development rate was applied to the individuals in each cohort, based on the development time for egg-CI (DT_{CI}) and egg-stage II (CII) (DT_{CII}) for the congener *C. finmarchicus* (Campbell et al. 2001), using the equation $Dt_i = \alpha(T + 9.11)^{-2.05}$, where $\alpha = 5267$ for DT_{CI} and $\alpha = 6233$ for DT_{CII} . There are no published development times for *C. pacificus* eggs and nauplii, but measured development rates for copepodite stages (Vidal 1980) were compared to those for *C. finmarchicus* (Campbell et al. 2001) at 8°C and 12°C , and found to be nearly identical ($r^2 = 0.98$). At the in situ temperatures observed in Dabob Bay, development times were 13–14 d, and the variability in development time over that duration was less than 6 h.

Daily natural mortality (m) in the model ranged from 0– $0.7 d^{-1}$, with a single mortality rate applied to the entire duration of the cohort for each model run, from egg to CII. Naupliar viability (v) was applied immediately to each cohort at the time of spawning, as the product of the egg production estimate and v_m , v_a , or v_{100} naupliar survival.

Mortality estimates—Population loss rates for each cohort were calculated using two approaches: an inverse model and a vertical life table. For the inverse model, observed CI abundances on sampling dates were linearly interpolated between sampling dates, and the temperature-dependent development times were calculated to determine when CIs from a particular date would have been spawned. As with the model described above, we used the development times to both CI and CII to estimate a range of time in which the CIs would have been spawned. The

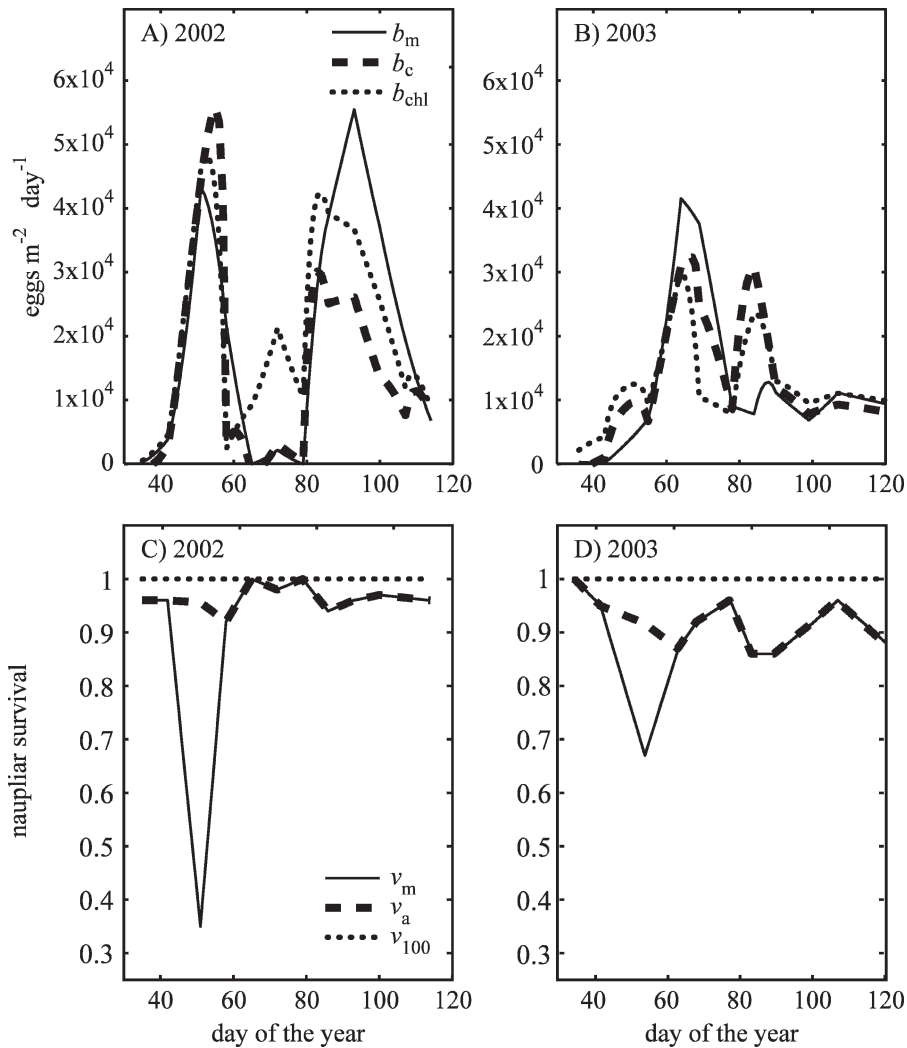


Fig. 2. Egg and naupliar viability input schemes used in the model for each year. (A–B) Daily abundance of eggs input into the model (eggs m⁻² d⁻¹) in (A) 2002 and (B) 2003, with different lines for different schemes: observed egg production rate (b_m , solid line), estimated egg production using carbon to EPR Ivlev fit (b_c , dashed line), and estimated egg production using Chl *a* to EPR Ivlev fit (b_{chl} , dotted line). (C–D) Naupliar viability parameterization schemes used in the model runs for (C) 2002 and (D) 2003: measured naupliar viability (v_m , solid line), averaged naupliar viability (v_a , dashed line), and assuming 100% naupliar viability (v_{100} , dotted line).

abundance of eggs on each day was then calculated as the product of the egg production rate, egg viability, and female abundance. These data were then applied to an exponential growth equation (for each cohort using both development times) to estimate the population loss rate. Calculations were made for all pairs of cohorts and eggs that would have developed within the sampling period. The inverse model estimated a range of mortality rates that could account for the observed egg production rate and CI copepodite abundances. For the vertical life table estimates of mortality, we used eq. 7a in Aksnes and Ohman (1996) to calculate mortality for the combined egg-CI stages on each sampling date on which there were sufficient data. The

estimates of mortality rate from both the inverse model and vertical life table were compared with the mortality rates used in the recruitment model.

Analysis of results—The model was run with all combinations of the four parameters: egg input, b_i ; naupliar viability, v_j ; advection coefficient, AC ; and natural mortality, m , to determine the sensitivity of the time distribution of CI copepodites to changes in each of the parameters. The time series of daily CI abundances from individual model runs for each year were compared with the observed data, and the cumulative abundances of CI copepodites for each model run were used to determine the sensitivity of the

Table 1. Descriptive statistics for the volume and area of each layer of Dabob Bay calculated for the copepod recruitment model. LL—lower layer; UL—upper layer.

		LL volume (m ³)	UL volume (m ³)	LL sill area (m ²)	UL sill area (m ²)
2002	Mean	3.66×10 ⁹	5.43×10 ⁸	3.17×10 ⁵	4.19×10 ⁴
	Minimum	3.41×10 ⁹	3.73×10 ⁸	2.96×10 ⁵	2.80×10 ⁴
	Maximum	3.83×10 ⁹	7.92×10 ⁸	3.31×10 ⁵	6.26×10 ⁴
2003	Mean	3.68×10 ⁹	5.25×10 ⁸	3.18×10 ⁵	4.05×10 ⁴
	Minimum	3.52×10 ⁹	3.12×10 ⁸	3.05×10 ⁵	2.31×10 ⁴
	Maximum	3.89×10 ⁹	6.81×10 ⁸	3.36×10 ⁵	5.33×10 ⁴
Total volume:		4.16×10 ⁹ m ³			
Total sill area:		3.57×10 ⁵ m ²			

model to the EPR and naupliar viability schemes. Sensitivity of the model to EPR was calculated as the percent difference between cumulative CI abundance using the measured (b_m) and either the b_c or b_{chl} egg inputs. Sensitivity to naupliar viability was calculated as the percent difference between model runs using 100% naupliar viability (v_{100}) and either the v_m and v_a viability schemes.

Results

Volume, area, hydrography, and advection in Dabob Bay—

The total volume and the total sill area of Dabob Bay are given in Table 1 as is the percent of total for the mean, minimum, and maximum of each layer. In general, the UL comprised 7–19% of the total volume and 6–18% of the total sill area. Mean temperature in the UL was 7.6–11.0°C in 2002 and 8.6–10.9°C in 2003 (Horner et al. 2005; Pierson 2006). Temperature was higher in 2003 than in 2002, and maximum surface temperatures in late April were at least 2°C greater in 2003 than in 2002 (Horner et al. 2005; Pierson 2006). The values for the advection coefficient (AC) used in the copepod recruitment model ranged from 1.0 to 0.1, and fell within the wide range of daily loss rates estimated for the population using the inverse model (Fig. 3). Daily advective loss rates (d^{-1}) were highly variable, with values ranging 0–0.65 d^{-1} for all values of AC . Mean advective loss rates ranged 0.02–0.16 d^{-1} and 0.01–0.13 d^{-1} (for $AC = 1$ to 0.1) for 2002 and 2003, respectively.

Mortality estimates—Mortality estimates from the inverse model generally increased throughout the duration of the model runs (Fig. 3). In 2002 the population loss rate increased from $\sim 0.25 d^{-1}$ to $0.70 d^{-1}$, with a peak on day 90 of $0.95 d^{-1}$. In 2003, loss rates at the start of sampling were $\sim 0.1 d^{-1}$, then peaked at $0.8 d^{-1}$ on day 67, and were $0.4 d^{-1}$ by the end of sampling. Vertical life table estimates generally tracked the inverse model estimates, although for both 2002 and 2003 peak values occurred on the last sampling date (Fig. 3). Mean values (\pm standard deviation) for 2002 and 2003 were $0.51 (0.34) d^{-1}$ and $0.54 (0.13) d^{-1}$, respectively.

Copepod reproduction and recruitment—Examples of the abundance of CIs from selected model runs are shown in

Fig. 4. The observed data are shown for comparison, with 95% confidence intervals calculated from triplicate samples collected on each sampling date. There was nearly an order of magnitude difference in CI abundance between the two years, with 2002 having a larger abundance; this pattern is also reflected in the model output.

For 2002, the model results had two peaks of CI abundance over the three-month period for the b_m egg input term (Fig. 4). Results were similar when the b_c egg input was used, but three peaks often occurred when the

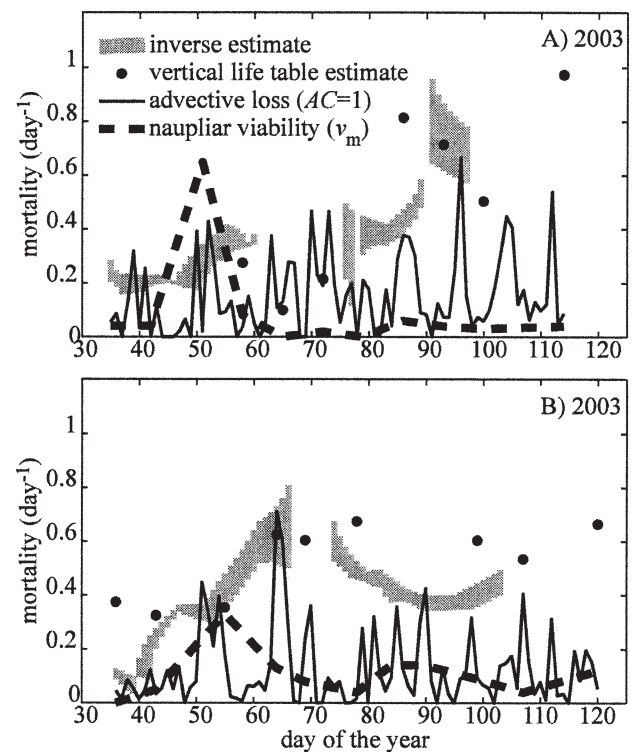


Fig. 3. Comparison of estimates of two of the population loss terms used in the recruitment model, advection (solid line) and naupliar viability (dashed line), with loss implied by vertical life table (filled circles) and the inverse model calculations (gray boxes) for (A) 2002 and (B) 2003. The results of the inverse model are shown as gray boxes representing the minimum and maximum estimates of mortality for each cohort on the day of spawning.

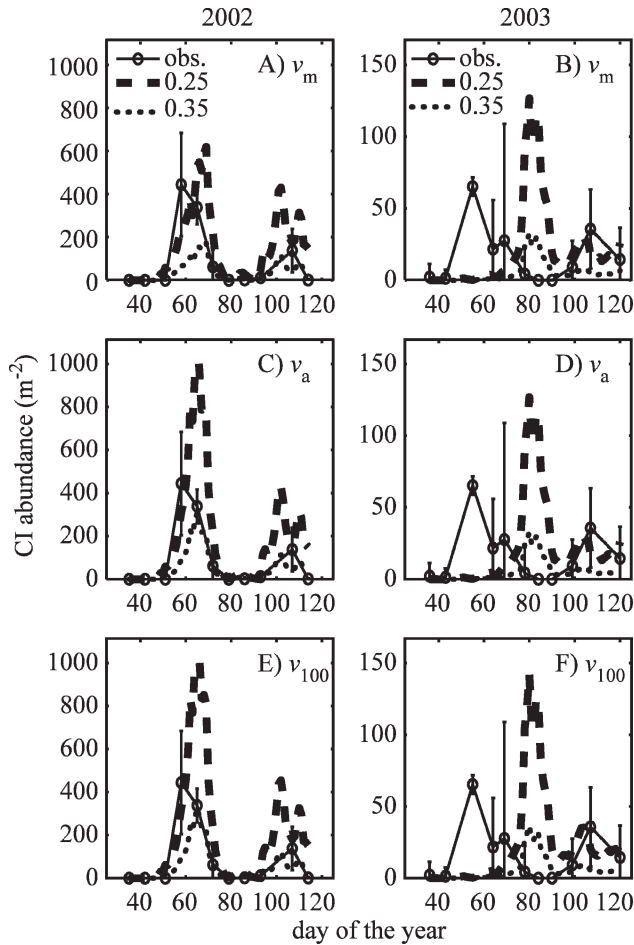


Fig. 4. An example of model output for (A, C, E) 2002 and (B, D, F) 2003 for each of the different naupliar viability schemes: v_m (panels A and B), v_a (panels C and D), and v_{100} (panels E and F). The solid lines with open circles symbols show the observed abundance of CI copepodites on field sampling dates in each year (Pierson et al. 2005b), and error bars shows the 95% confidence intervals from the mean of triplicate samples taken on each date. Dashed and dotted lines show the model results using different estimates of mortality. All model results shown here were generated using the observed egg production rate (b_m) and an advection coefficient $AC = 1$.

b_{chl} egg input term was used, with a middle peak that was similar in magnitude to the other two. Good agreement between modeled and observed data occurred when $AC = 1$ (corresponding to a mean advective loss of 0.16 d^{-1} over the whole modeled period) and $m \approx 0.30 \text{ d}^{-1}$, using the b_c and b_m egg input terms. Decreasing advective losses ($AC < 1$) did not change the overall pattern.

For 2003, the model results did not look similar to the observed CI time series in most cases (Fig. 4). Although two peaks often occurred, they were not at the same time as the peaks in the observed CI abundances. For all egg input terms and $AC = 1$, the model results showed a peak in mid-March, between the two observed peaks, followed by a smaller peak at the end of the time series that occurred before the observed peak. As AC decreased, two peaks were

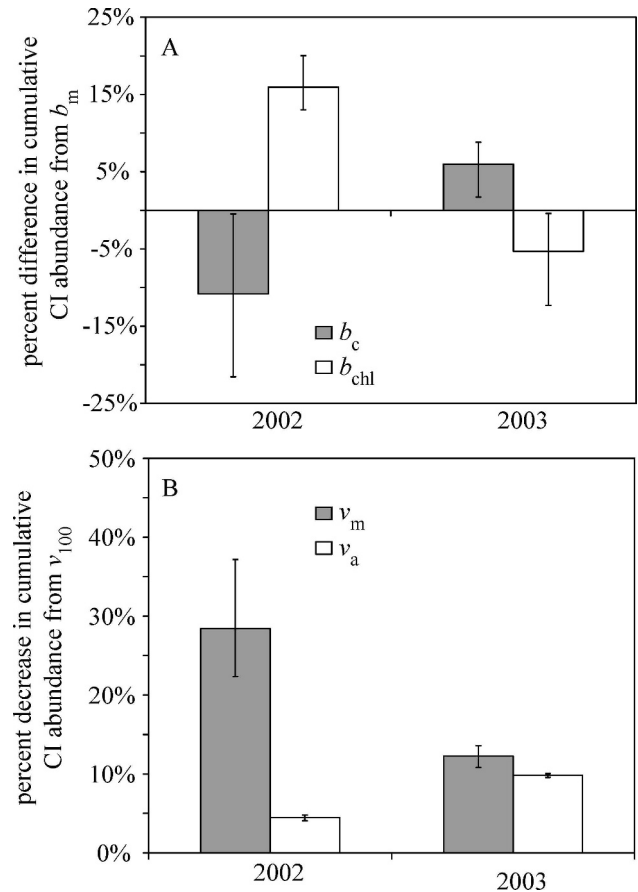


Fig. 5. Sensitivity of the model results to different parameterizations of (A) egg input and (B) naupliar viability for both years. Comparisons were made by taking the percent difference in the cumulative abundance of CI copepodites from model runs using different parameterizations; bars show the mean of the comparisons and error bars show the range of values. Model results from all runs using b_c or b_{chl} egg input schemes were compared to model results from runs using b_m egg input schemes (panel A), and model results from all runs using v_m or v_a naupliar viability were compared to model results from all runs assuming v_{100} naupliar viability (panel B).

more distinct, but the first modeled peak occurs after the first observed peak, and the second modeled peak occurs before the second observed peak.

Unique problems with the 2003 data must be considered when accounting for many of the differences we observed between the years. Due to an oil leak, we were only able to obtain water samples and electronic data from a CTD cast on the one cruise at the height of the February bloom (day 50) in 2003. It is possible that we missed a low naupliar survival event, based on diatom abundance during that cruise (Horner et al. 2005); however, we lack the samples to test that hypothesis. In addition, CI copepodites were present on our first sampling date in 2003, suggesting that egg production likely commenced at least two weeks prior to our first cruise, and in the model, egg production necessarily begins with the first cruise. Unfortunately, there is no way to correct for the problems in the data, and

results from 2003 must be considered in light of these issues. The inferences from this study are based chiefly on the model results from the 2002 data, but comparisons between years are noted where appropriate in the discussion below.

Sensitivity analysis—Abundance of CI copepodites in the model was sensitive to both the parameterization of egg production rate and of naupliar viability, and the sensitivity varied between years (Fig. 5). For 2002, model runs using the b_c parameterization resulted in lower cumulative CI abundance than the observed b_m , whereas the b_{chl} parameterization resulted in higher abundances. In 2003, the results were reversed with b_c resulting in higher cumulative CI abundance and b_{chl} lower. The magnitude of the differences between parameterization schemes was lower in 2003 than in 2002. In the sensitivity analysis of the naupliar viability, the v_m parameterization induced a greater decrease in the cumulative abundance than the v_a parameterization in both years, but the magnitude of the difference between the parameterizations differed between years (Fig. 5). For 2002, the v_m viability resulted in a 22–37% decrease in cumulative abundance while the v_a naupliar viability induced a less than 5% decrease. In 2003, the v_m naupliar viability induced a 10–13% decrease in cumulative CI abundance and the v_a naupliar viability induced a nearly 10% decrease.

Discussion

Estimates of predation and advective losses from the copepod recruitment model, as well as estimates of overall mortality from the inverse model, suggest that sources of mortality other than decreased naupliar viability are the primary causes for recruitment failure in *C. pacificus* in Dabob Bay during spring. Thus, the diatom effect is not likely the primary agent for the lost generation; instead predation was found to be the main source of mortality to the *C. pacificus* population in Dabob Bay. The model results suggested that the observed decrease in naupliar viability that occurred in February 2002 may have reduced the recruitment of *C. pacificus* eggs to CI copepodites by nearly 30%, compared to estimates of recruitment based on an assumption of high naupliar viability. This result was not strongly supported by the 2003 data, mainly due to a combination of issues described previously. The model results also showed that the parameterization of egg production rate based on either Chl *a* or microplankton carbon concentration had variable but distinct effects on recruitment results between years, although the problems with the 2003 data should be taken into account.

Advection in Dabob Bay—Advective losses in Dabob Bay are difficult to estimate because of the paucity of data. However, for the purposes of this study, order of magnitude estimates allow comparison with results from an inverse model and the measured losses due to decreased naupliar viability. Generally, advective losses were likely lower than predation mortality losses in the surface layers of the bay, although advective losses may have reached

0.65 d^{-1} during strong wind events. There was no trend in advective losses throughout the period, and because the inverse model showed that overall loss rates increased throughout the sampling period, the observed population decline was likely due to increasing predation mortality during the sampling period.

Flow out of Dabob Bay in the upper mixed layer is small compared to the volume of the bay (Table 1) due to the low river inputs, low tidal exchange rates, and stratification in the upper layer (Kollmeyer 1965; Ebbesmeyer 1973; Barnes and Ebbesmeyer 1978), but the few studies of advection in Dabob Bay were done in late summer or autumn (Kollmeyer 1965). Circulation has been described as generally estuarine (outflow in surface waters, inflow at depth), but strong northward winds caused three layer flow (inflow at the surface and at depth, outflow in the middle depths) that relaxed shortly after the wind ceased (Kollmeyer 1965). Estimates of maximum along-axis current velocities using combined tidal current and hypothesized wind stress never exceeded 5 cm s^{-1} (Barnes and Ebbesmeyer 1978). Although a more rigorous exploration of the temporal and spatial circulation patterns in Dabob Bay is needed for a more complete understanding of how advection affects the plankton community there, our model results suggest that predation mortality is likely to have a greater impact on the *C. pacificus* population in the bay.

Predation mortality—In this study we tested a range of predation mortalities pooled for the entire egg-CI period, and found good agreement with modeled and observed populations when predation mortality was $>0.25\text{ d}^{-1}$. However, because advection was probably overestimated, actual rates of predation mortality were likely $>0.4\text{ d}^{-1}$ in most cases, which is greater than both naupliar viability and advective loss rates. Mortality rate of zooplankton is notoriously difficult to measure in the sea, and stage-specific estimates of mortality rates for *Calanus* spp. eggs and nauplii range $0.182\text{--}2.0\text{ d}^{-1}$ (Ohman and Hirche 2001; Eiane et al. 2002). Unfortunately, we cannot make stage-specific estimates of mortality with our data. We estimated total loss rates for the entire egg-CI developmental period using both a simple inverse modeling approach and a vertical life table, and found that both calculations showed mortality increased between early February and late April. Comparisons between the model output and the observed data supported this finding (Fig. 4).

The causative agent of most plankton mortality is likely interspecific predation, although there is laboratory evidence of egg cannibalism by female copepods (see Bonnet et al. 2004 and reference therein), supported by field evidence of density-dependent mortality rates (Ohman and Hirche 2001). However, in our study the egg-CI mortality estimates from the inverse model and vertical life table calculations were negatively correlated with abundances of CV copepodites and adult females (J. Pierson, unpubl.). This negative relationship is due to decreasing abundances of stage V (CV) copepodites and adult females (Pierson et al. 2005b) during a period in which mortality is increasing. Density-dependent mortality due to cannibalism may still

occur for this species at other times of the year, however there is no evidence for it in the winter-spring period.

The increasing predation mortality between February and April in Dabob Bay is seemingly contradicted by the patterns of abundance of two potential predators on *C. pacificus* eggs and nauplii, the chaetognath *Sagitta elegans* and larval Pacific hake, *Merluccius productus* (Fulmer and Bollens 2005). However, the abundance of numerous other potential predators were not analyzed, including the carnivorous copepod *Euchaeta norvegica* and the euphausiid *Euphausia pacifica*, as well as larvae of other fish species; predation on *C. pacificus* by these organisms may account for the discrepancy (Bollens and Frost 1989; Bollens et al. 1993).

Reproduction and recruitment—We used the copepod recruitment model to test the response of copepod recruitment to different parameterizations of egg production and naupliar viability. For 2002, the b_c parameterization resulted in fewer CI copepodites recruited to the population and b_{chl} parameterization resulted in more (when compared to b_m), but in 2003 the outcomes were reversed, probably due to the problems with the 2003 data (Fig. 5). The difference in species composition of the microplankton between years may have had an effect. In late April 2002, the microplankton community was dominated by *Phaeocystis* spp., and high chlorophyll values did not support high EPR during that time (Pierson et al. 2005a), similar to previous observations of copepod egg production during *Phaeocystis* spp. blooms (Turner et al. 2002). Also, *C. pacificus* egg production rate has a steep response curve to low but increasing Chl *a* and carbon values (Bunker and Hirst 2004; Pierson et al. 2005a), and this may have affected the egg production rates during periods of low Chl *a* in Dabob Bay. Generally, the relationship between egg production rate and either Chl *a* (Niehoff 2004; Bunker and Hirst 2004; Plourde et al. 2005) or carbon concentration (Park and Landry 1993) is well established. In our study, varying the parameterization of egg production using these relationships resulted in less than a 15% change in copepod recruitment (Fig. 5).

Naupliar viability parameterization had a greater impact on the model output than the egg production parameterization. For 2002, there was an ~30% difference between the cumulative CI recruitment using v_m versus v_{100} naupliar viability schemes, but only a 5% difference between v_a and v_{100} naupliar viability schemes, suggesting that v_m naupliar viability had a more significant effect on CI recruitment. For 2003, the differences in cumulative CI recruitment between v_{100} and the other two parameterizations were smaller, but concerns about the 2003 data described above should be heeded in interpreting this result: if we had measured an instance of lowered naupliar survival in 2003 concomitant with the *Thalassiosira* spp. bloom, the v_{100} and v_a may have been more similar, as they were for 2002. The presence of CI copepodites on the first sampling dates in 2003 may have also contributed to the differences in model sensitivity to naupliar viability between the years.

As noted above, there was also a nearly order of magnitude decrease in observed CI abundance between

2002 and 2003 (Pierson et al. 2005b). The lower abundance in 2003 likely made the model more sensitive to the loss parameters in that year than in 2002, and this may also account for some of the differences between the model results and the observed data for 2003. The winter-spring abundance is directly related to the overwintered stock of copepods in Dabob Bay (Colebrook 1985), and this stock is the result of the overwintering mortality as well as the growth and mortality conditions that affected the copepods in the previous autumn when they entered the dormant phase. Although not addressed in this study, a clearer understanding of the factors controlling the onset, maintenance, and release from overwintering is imperative to a better understanding of copepod population dynamics.

Many modeling approaches have been used to analyze copepod population dynamics in both idealized and natural systems (Carlotti et al. 2000). Here we used a simple model to determine the sensitivity of the population abundance to changes in reproductive parameters, but Mazzocchi et al. (2006) used different methods and applied them to a vastly different system than Dabob Bay, yet reached similar conclusions. Using an individual based model (IBM) that tracked individual copepods throughout their life history under different prey conditions, they found that prey-type effects on reproduction significantly affected the potential recruitment of copepods in the system, but that other factors were determined to be more important in shaping the seasonal cycle of the population. On Georges Bank *C. finmarchicus* abundance increases throughout the winter and spring and an inverse modeling study found that advective inputs to the population were less important than biological factors in driving population increases (Li et al. 2006).

In this study, the effect of naupliar viability on copepod recruitment was most apparent when comparing the cumulative recruitment of CI copepodites between model runs using different parameterizations of naupliar viability, and less apparent when comparing the time distribution of CI copepodites from the same model runs. Comparison of our estimates of population loss terms indicates that predation mortality is greater than combined losses due to decreased naupliar viability and advection, and thus the lost generation phenomenon in Dabob Bay is likely to be primarily the result of predation mortality, not the diatom effect. Advective losses and depressed naupliar viability are lesser contributors to the phenomenon. While this work highlights the importance of considerations of naupliar viability in copepod recruitment studies, it also indicates that greater understanding of the effects of predation mortality in the sea is necessary.

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