Biophysical Simulations of *Calanus finmarchicus*
Population Dynamics in the Gulf of Maine

Daniel R. Lynch¹, Wendy C. Gentleman¹, Dennis McGillicuddy², Cabell S. Davis²

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¹Dartmouth College, Hanover, NH 03755 USA
²Woods Hole Oceanographic Institution, Woods Hole, MA 02543 USA

Abstract

A site-specific, coupled biophysical model is described. The biological portion describes temperature- and food-dependent progression through 17 life stages in an Eulerian (concentration-based) framework. The population is transported in a realistic flow field depicting the climatological mean conditions in terms of 2-month “seasons”. Behavioural assumptions account for depth selection and two limiting cases are contrasted: dispersal throughout the water column, and aggregation in the surface layer. Simulations are inspired by MARMAP and SCOPEX observations, with an emphasis on the mid-winter initiation of the annual bloom by diapausing populations, and their role in supplying reproducing populations to Georges Bank during spring.

Idealized simulations illustrate the role of the circulation. Georges Bank itself is lossy and depends on resupply from external sources. All three deep basins of the Gulf are capable of contributing populations to the Bank. The Scotian Shelf is capable of populating the Southern Flank. In the case where the organisms aggregate in the surface layer, the additional effect of convergence at downwelling fronts is shown to be a significant contributor to population distribution and accounts for some persistent observed features. Baseline simulations are initiated on January 1 by activating a diapausing population of C4 and C5 copepodes, based on 10-year mean abundance and distribution data from the MARMAP program. The simulations provide evidence of behaviour, activation rate, and mortality in this period.
1 Introduction

Calanus finmarchicus is a dominant copepod in the Gulf of Maine. The earliest investigations described the Gulf as a “Calanus community” (Bigelow, 1926) and subsequent investigations confirmed the stable dominance of this copepod (Clark et al. 1943; Davis 1987). More recent field programs continue to highlight the importance of Calanus in the Gulf. The 10-year MARMAP program (Sherman et al. 1996) has refined our description of its year-round abundance and distribution; and the 2-year SCOPEX program (Kenney and Wishner 1995) has revealed important details of the interplay of biological and physical phenomena. Currently, Calanus finmarchicus is a key target species in the USGLOBEC program which seeks to describe the biophysical factors controlling its occurrence on Georges Bank (Wiebe et al. 1996). Because Georges Bank is an open ecosystem, the investigation extends across the Gulf of Maine.

Our study is part of the GLOBEC effort. Current field sampling is dense from a practical standpoint but sparse compared to the biophysical space-time scales. Further, there is no routine sampling in the Gulf of Maine, and the smallest life stages representing at least half of an individual’s development time cannot be effectively sampled. Historical data is in general sparser. Mathematical models are therefore necessary to provide a rigorous framework for inference of the many unobservables which determine site-specific population dynamics. We seek to model the abundance and distribution of Calanus toward these ends.

A unique aspect of this work is the use of a site-specific physical model with comprehensive coverage of the entire Gulf of Maine and reasonable resolution of Georges Bank (Lynch et al. 1996). This model provides us with climatological circulation patterns in 2-month seasons which constitute the best available climatology for the system.

A second unique aspect is the recent publication of a “Calanus climatology” in the form of 10-year seasonal mean abundance and distribution in 2-month bins (Meise and O’Reilly 1996). This study revealed a distinct seasonal cycle with low variance. We hypothesize that the stable outcome can be described by the interaction of population dynamics, behaviour, and the mean physical cycle. Our study is founded on this premise.

We will focus on the initiation phase of the spring bloom, when deep resting populations are exiting diapause and producing a first generation cohort. Variability in this portion of the cycle will be greatly amplified in the second generation, so it is critical to understand the first generation.

130-40 field stations sampled at 3 depths on Georges Bank, every two weeks.
2 Biophysical Model

2.1 Circulation

We use the finite element hydrodynamic model of Lynch et al (1996). This is a nonlinear 3-D model which transports momentum, heat and salt in tidal time with advanced turbulence closure. The domain of computation includes the Gulf of Maine, Georges Bank, and the Scotian Shelf. A bimonthly climatology has been developed and archived with this model, in six bimonthly realizations. For long-term simulations the Lagrangian mean velocity $V_L$ is approximated as the sum of the Eulerian mean $V_E$ plus a first-order correction $V_S$ (the Stokes velocity). In addition we utilize the time-mean of the modeled temperature and hydrodynamic mixing coefficients.

2.2 Transport

Transport in these circulation fields is represented by the Adveective-Diffusive-Reactive equation

$$\frac{\partial C_i}{\partial t} + \nabla \cdot ([V_L + V_b] C_i - K \nabla C_i) = R_i$$

The term $V_b C_i$ represents behaviour - swimming and/or buoyancy effects. We assume that the horizontal effect is negligible. But the vertical effect is critical. For Calanus, we have essentially no systematic information about younger life stages in the field, either in terms of behaviour or typical depth distribution. For the later stages, reasonable swimming speeds of one body length per second would allow perfect depth regulation, even in the presence of the strong vertical mixing on, for example, Georges Bank. Hence the behavioural portion of the vertical transport dominates and we have very limited ability to describe this. Thus we have simplified the model to a 2-D averaged description reflecting two behavioural extremes.

In the first extreme, we assume the organisms are uniformly distributed over the entire water column. In that case the depth-averaged transport equations apply:

$$\frac{\partial \bar{C}_i}{\partial t} + \bar{V}_L \cdot \nabla \bar{C}_i - \frac{1}{H} \nabla \cdot H \bar{K}_{xx} \nabla \bar{C}_i = \bar{R}_i$$

In the second extreme, we assume the organisms aggregate in a defined surface layer with thickness $h$ - herein 25 meters - irrespective of vertical fluid transports. Behaviour in this case completely negates the hydrodynamic transport (both advective and dispersive parts). In particular, upwelling or downwelling which would normally affect a passive tracer has no impact on the animal count in the layer. In this case, we have $\nabla \cdot (h \bar{V}_L) = w$, the vertical velocity at the bottom of the layer; so the divergence term must be retained:
Divergence (upwelling) has the effect of diluting the layer; while convergence (downwelling) concentrates the organisms.\(^2\) In the absence of diffusion, we have from (3) the evolution of a cohort along a horizontal streamline:

\[
\frac{\partial \bar{C}_i}{\partial t} + \nabla_L \cdot \nabla \bar{C}_i - \frac{1}{h} \nabla \cdot h \bar{K}_{xy} \nabla \bar{C}_i = -D \bar{C}_i + \bar{R}_i \tag{3}
\]

where \(D\) is the layer divergence:

\[
D = \frac{1}{h} \nabla \cdot h \nabla_L = \frac{w}{h} \tag{4}
\]

Divergence (upwelling) has the effect of diluting the layer; while convergence (downwelling) concentrates the organisms.\(^2\) In the absence of diffusion, we have from (3) the evolution of a cohort along a horizontal streamline:

\[
\frac{d \bar{C}_i}{dt} = -D \bar{C}_i + \bar{R}_i \tag{5}
\]

and we obtain the possibility of exponential concentration of a population which is passive biologically but actively swimming in a convergent layer. Clearly, this is a first-order effect on the distribuional pattern which could be mistaken for population dynamics. We find here that values of \(D\) are of order .1 day\(^{-1}\) in certain critical areas of the Gulf; this is comparable to time constants in the population dynamics (e.g. stage durations).

These two limiting cases bracket the extremes of the behavioural uncertainty. Most commonly, Calanus in the Gulf is thought to inhabit the surface layer. However, this is poorly observed in the earlier stages which are hard to capture; and the process of activation from diapause might well involve a period during which the population is effectively sampling a significant portion of the water column. Additionally, Durbin et al (1995c) found strong diel migration in the 1988 SCOPEX campaign, but essentially none in the following year; and that the diel migration was likely to be in response to the presence of predators. Thus it seems that both of our extremes of behaviour have a place in hypothesis testing.

2.3 Population Dynamics

The terms \(R_i\) [\(#m^{-3}d^{-1}\)] represents the local rate of change in the concentration due to population dynamics: reproduction, development and mortality. These vital rates are dependent upon local environmental parameters (e.g. temperature, food and predators).

Stages

A stage-based approach is used. The “natural” staging involves 13 morphologically distinct stages: egg, six naupliar stages, five copepodite stages, and adult (Marshall and Orr 1955). We have expanded these basic stages into 17 states to account for different environmental influences and behaviour. Two of the extra states distinguish between active and

\(^{2}\)Note that the case of net vertical migration to the surface layer, e.g. of animals exiting diapause, would be accounted for as a net source and would contribute to \(R\).
Table 1: Vital Rates for *Calanus finmarchicus* (days), at 5°C. Development times are given by the Belaradek form $D(T) = \alpha(T - \beta)^\alpha$ with $\alpha = -2.05$ and $\beta = -9.11°C$.

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<th>D(10°C)</th>
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<th>Mortality, %/day</th>
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Table 2: Miscellaneous Coefficients.

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<td>Male fraction</td>
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<td>Diapause fraction, C4</td>
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<tr>
<td>Diapause fraction, C5</td>
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<tr>
<td>Male Mortality Multiplier</td>
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<td>Carbon/Chlorophyll ratio</td>
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diapauing C4s and C5s. A fraction (50%) of the molting C5's are diverted to C5 diapause rather than becoming adults. C4's are treated similarly except the diapause fraction is less (10%). This allows differential mortality and development during diapause, as well as differential depth preference which is critical to the physical coupling. Three additional states account for sexual development following C5. Knowing that males have a higher mortality in the field, new adults are divided evenly into males and females as they molt from C5. To account for the time lag between molting to adulthood and the completion of the final stages of oogenesis, we distinguish between prereproductive (or immature) females and those which are able to reproduce. Female fertilization is ignored as a non-limiting phenomenon.

Development

Average development times $D_i$ are sensitive to both temperature and food availability. Generally, increasing temperature $T$ decreases the stage durations, $D_m$. These are traditionally related through Belaradek equations as indicated in table 1.

*Food Effects* are less precisely known. For stages other than Egg, N1 and N2, which do not feed, we expect that stage durations will increase as food concentrations are reduced. We model this by decreasing development rate ($\frac{1}{D_i(T)}$) linearly toward zero when food is below a satiation value. (Equivalently, development time varies inversely with food availability.) The baseline parameters used are summarized in table 1.

Egg Production

Spawning is modeled as a continuous process with constant clutch size of 50 eggs per female. The interclutch interval $d$ is considered to be sensitive to variations in the environment. Both laboratory and field experiments have found temperature and egg production to be positively correlated. We model this by making the interclutch interval a Belaradek function of temperature.

*Food Effects.* The above relation holds for superabundant food levels ($>400 \mu gC/l$). As food concentration is reduced, egg production decreases with a few days time lag before the effect is seen. Laboratory experiments at low levels ($<300 \mu gC/l$) show both a tendency for increased interclutch interval and decreased clutch size. Reduced egg production in the field is also observed for ambient levels $<25 mg Chl/m^2$. We characterize this effect in the same way as development rate: decreasing the egg production rate linearly to zero when food is below a satiation value.

Mortality

Stage-dependent mortality is represented. Generally, it is assumed highest for earlier life-stages stages. Male mortality is assumed higher than female mortality (a factor of 5 herein), reflecting observations of behavior and relative abundance in the field.
Predation is likely to be the dominant source of mortality. Unfortunately, the details of predator abundance and distribution must await a fuller understanding. In the meantime, we have adopted baseline mortality estimates in table 1 as lower limits. Additional detail must be inferred at present.

Base Model

A ‘best case scenario’ will be assumed: food satiation and no mortality, with active response to temperature. There is good support for these necessary model elements; in effect they become the “passive tracer” for the reproducing system. Properly initialized, the base model will be systematically biased to overestimate abundance (low mortality), reproduce too early (no food limitation), and continue reproducing too long (infinite female lifetime.)

The impacts of food limitation and more detailed mortality can then be explored. The impact of food-limited development time and interclutch interval will be approximated as above, using bi-monthly MARMAP Chlorophyll-a data and a Chlorophyll to Carbon conversion factor of 100 (see below). Narrowing the gap between base model results and observations, should yield insight into the role of these effects.

2.4 Coupled Model Summary

Summarizing the main features of the coupled model:

• a detailed circulation model describes the climatology in 2-month Lagrangian means;

• behavioural assumptions lead to two 2-D limits which bracket the possibilities: surface only and full-depth transport;

• a 17-stage population dynamics focuses on the initiation of the growing season through the first generation;

• the base model is idealistic with low mortality and abundant food; its elements are well-supported.

3 Observations

Meise and O’Reilly (1995) analyzed 10-year mean abundance of Cf from the MARMAP program (1977-1987). The data include stages C3 through adult (females + males) combined in six bimonthly snapshots, and distributed across 97 spatial tiles covering the Gulf of Maine and Georges Bank. Sampling depth was limited to the upper 200m. These data were interpolated onto the finite element mesh using objective analysis. Additional snapshots
were prepared in the same way to provide resolution at monthly intervals (Meise, personal communication). The resulting sequence from Dec. 1 to April 1 appears in figure 1. The data are dominated by C5's, with some C4 and adults, occupying the central Gulf and decaying through the fall, consistent with a diapausing population. There are well-defined population centers over Jordan and Wilkinson basin. After Jan. 1, there adults increase and C5's decrease, indicative of activation of the resting stock with adults increasing and C5's and C4's decreasing. New copepodites C3 and above emerge in March and by April 1 are well-established.

Based on these observations, we initiate our simulations on January 1. This puts us at the start of the growing season. The data provide initial conditions for C4, C5, and adults. The unobserved smaller stages are assumed to be zero. This assumption would be inappropriate later in the year and would confound any interpretation.

O'Reilly and Zetlin (1997) Provide a similar decadal average of Chlorophyll abundance in the upper 75m. This data has been processed in the same way (not shown). Peak abundance occurs in March-April, well after the initiation of the C5 cycle apparent in the data. Clearly the emergence of generation 1 C3 and older in by March would indicate that spawning and development of eggs and nauplii is occurring prior to the phytoplankton bloom. Food abundance appears to limit three critical rates during generation 1: female maturation, egg production, and development.

4 Results

We made several simulations with the goal of building inference about the dynamics as represented in the MARMAP data. Generally, all simulations are started on Jan 1 and run for 90 days, with the physical fields interpolated linearly within the climatology.

- How retentive is Georges Bank? Results of a passive tracer initially occupying Georges Bank \((C = 1\) within the 100m isobath) but absent from the rest of the system (not shown) clearly show the washout effect of the circulation. The initial population advects to the southwest and the bank is restocking from the north and west. In the surface layer there is an additional loss to the south due to the Ekman transport. These clearly confirm the inability of an insitu population to sustain itself on-bank, and the necessity of continuous resupply from off-bank.

- How do the deep basins affect the Bank? Figures 2 (vertically averaged flow) and 3 (surface layer) show the fate of passive tracers released as Gaussian bumps over the three deep basins of the Gulf. Recalling that Jordan and Wilkinson basins are clearly population centers for resting stock in late fall; and due to incomplete
sampling, Georges Basin may also be a center. Generally, all three basins contribute populations to the bank. The vertically averaged flow provides slower and smoother distributions, being steered by the deep topography in the Gulf and tending to go around the Bank rather than over it. The surface layer is faster and more directed by Ekman transport; and shows the effect of the convergence structure in this layer.

From Jordan Basin, the average flow is first to the southwest, with the center of the plume situated after 60 days over the sill between Georges and Wilkinson Basins. The leading edge of the plume branches southeast toward the Northern Flank of Georges. The surface flow is faster, with the 30 day result resembling the 60 day average result. At 60 days the plume has bifurcated with downstream branches over Wilkinson basin and Georges Bank, the latter spilling over the N. flank and populating the central shoal area.

From Georges Basin the average flow is to and around Georges Bank. At 60 days the center of mass is still over the basin. The surface flow at 30 days is further downstream, and concentrated on the NE Peak of the bank. Later at 60 days the surface flow shows an elongated plume along the southern flank; but retains the concentration on the NE Peak, shifted south by the advection.

From Wilkinson Basin the average flow retains the population center in the Basin, shifted slightly to the southeast. The basin is lossy, with a well-defined exit path southward through Great South Channel. As in the other basins, the surface layer pattern at 30 days resembles the average pattern at 60 days; but the convergence zones have concentrated the retained population and also narrowed the exit lane along the western side of GSC. At 60 days the retained population has moved onto the western end of GB with significant presence in the recirculation zone between the 100 and 60m isobaths.

These results confirm the ability of the deep basins to deliver populations to the Bank during at the initiation of the growing season. The behavioural limits - average versus surface layer - matters. The surface transport is significantly faster and more directly connected to the bank over 60 days. The deeper circulation is more retentive.

- What will be the influence of inflow from unmodeled upstream sources? Simulations will be initialized with MARMAP data; implied is the dependence of subsequent distributions on initial conditions. However there are three points of entry in this limited domain: the Scotian Shelf, the Bay of Fundy, and the slope water. We have no simple way to specify the population structure entering at these points, since the first generation will not be visible until it has matured to stage C3. What is the impact of zero inputs on these boundaries?
Figures 2 and 3 show 90-day passive results with $C = 0$ everywhere but $C = 1$ maintained continuously on inflow boundaries. Clearly the influence of all three “sources” can be seen. In the surface layer we see the Maine Coastal Current entering from the Bay of Fundy and meandering offshore south of Penobscot Bay. From the Scotian Shelf inflow invades Browns Bank and eastern Georges Basin, with a branch crossing to GB. On GB there is a convergence on the NE Peak, as well as an exit lane between the 100 and 200m isobaths. Finally, the offshore eastward-flowing currents are entering the model but remain uninvolved with the Bank and the basins. The deeper, average circulation is a muted version, with similar patterns but less penetration on this time scale.

For our purposes, two of the influences (Bay of Fundy and offshore) appear to be benign but the Scotian Shelf is a concern, especially with the surface circulation. We will have to either remain agnostic about model/data comparisons in the regions of its influence, or reach beyond the data to formulate credible boundary conditions.

- **Is total abundance consistent with circulation?** Here we initialize with the Jan.1 population totals (C3-C6) and treat as a single conservative tracer. The results appear in figure 4 for the vertically averaged case. Comparable results for the surface layer examined but not shown. Generally:

  - At least for the first month, the data favor the vertical average over the surface layer results; indicating that exit from diapause is likely to be distributed in time and the animals are occurring throughout the depth.
  - Overall abundance is too high without loss; reasonable loss rates come out about right.
  - The dominance of C5's in these simulations means that 2 params govern mortality estimation: the molt rate to adult, and female mortality (assuming male mortality is elevated by a factor of 5). These features are being explored now through additional simulations.

5 Acknowledgements

We thank Carol Meise, Jay O'Reilly, Ken Sherman, Jack Jossi, and Jack Greene for help us with the MARMAP data.
References


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<th>April 1</th>
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MAP TOTALS SIMULATIONS IN DP