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Coupling of an individual-based population dynamic model of *Calanus finmarchicus* to a circulation model for the Georges Bank region

CHARLES B. MILLER,[1,*] DANIEL R. LYNCH,[2] FRANÇOIS CARLOTTI,[3] WENDY GENTLEMAN[2] AND CRAIG V. W. LEWIS[2]

[1]*College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis, OR 97331–5503, USA*
[2]*Thayer School of Engineering, Dartmouth College, Hanover, NH 03755, USA*
[3]*Station Zoologique, University of Paris VI, Villefranche-sur-Mer, 06230 France*

ABSTRACT

An individual-based life history and population dynamic model for the winter–spring dominant copepod of the subarctic North Atlantic, *Calanus finmarchicus*, is coupled with a regional model of advection for the Gulf of Maine and Georges Bank. Large numbers of vectors, each representing individual copepods with elements for age, stage, ovarian status and other population dynamic variables, are carried in a computation through hourly time steps. Each vector is updated at each time step according to development rate and reproductive functions derived from experimental data. Newly spawned eggs are each assigned new vectors as needed. All vectors are subject to random mortality. Thus, both life history progression and population dynamics of *C. finmarchicus* are represented for the temperatures in the Gulf of Maine–Georges Bank region in the active season. All vectors include elements representing depth, latitude and longitude. This allows coupling of the population dynamics to the tide- and wind-driven Dartmouth model of New England regional circulation. Summary data from the physical model are used to advance vectors from resting-stock locations in Gulf of Maine basins through two generations to sites of readiness for return to rest. Supply of *Calanus* stock to Georges Bank comes from all of the gulf and from the Scotian Shelf. The top of the bank is stocked from western gulf basins; the North-east Peak is stocked from Georges Basin and the Scotian Shelf. All sources contribute to stock that accumulates in the SCOPEX gyre off the north-west shoulder of Georges Bank, explaining the high abundance recurrently seen in that region. There is some return of resting stock to Wilkinson Basin in the western gulf, but other basins must mostly be restocked from upstream sources to the north-east.

Key words: *Calanus finmarchicus*, Georges Bank, individual-based model, life history, physical–biological coupling

INTRODUCTION

Georges Bank (Fig. 1) is an elongate submarine rise east of Massachusetts, USA, which topographically controls the movement of water into and out of the Gulf of Maine. Historically it has been the site of large fisheries for cod, haddock, yellowtail flounder and other species. *Calanus finmarchicus* (Gunnerus), which is important in the larval diet of these commercial fish (Kane, 1984), dominates the zooplankton over Georges Bank during late winter and early spring (Davis, 1987). However, this 2.5 mm long copepod is absent from the bank top after mid-May and from the flanks after early July, so it must transfer onto and off the bank in the course of its life history. Possible sources of resupply to the bank at the beginning of the *C. finmarchicus* development season are (1) the Gulf of Maine (Bigelow, 1926; Hannah *et al.*, 1998), (2) Scotian Shelf Water to the north-east (Herman *et al.*, 1990; Sameoto and Herman, 1990), and (3) the North-west Atlantic Slopewater to the south (Miller *et al.*, 1991). We have examined the potential of the Gulf of Maine and Scotian Shelf as sources for *C. finmarchicus* winter stock on Georges Bank by coupling an individual-based life history model for the copepod to a three-dimensional, numerical model (Lynch *et al.*, 1996) of water circulation in the region, including the Scotian Shelf, the Gulf of Maine, Georges Bank, and the outflow path to the south-west. In a later study we will examine the potential of North-west Atlantic Slopewater as a source. The approach elaborates that of Hannah *et al.* (1998) by detailing the *C. finmarchicus* developmental schedule, so the model shows where

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*Correspondence. Fax: +1 541 737 2064;
e-mail: cmiller@oce.orst.edu

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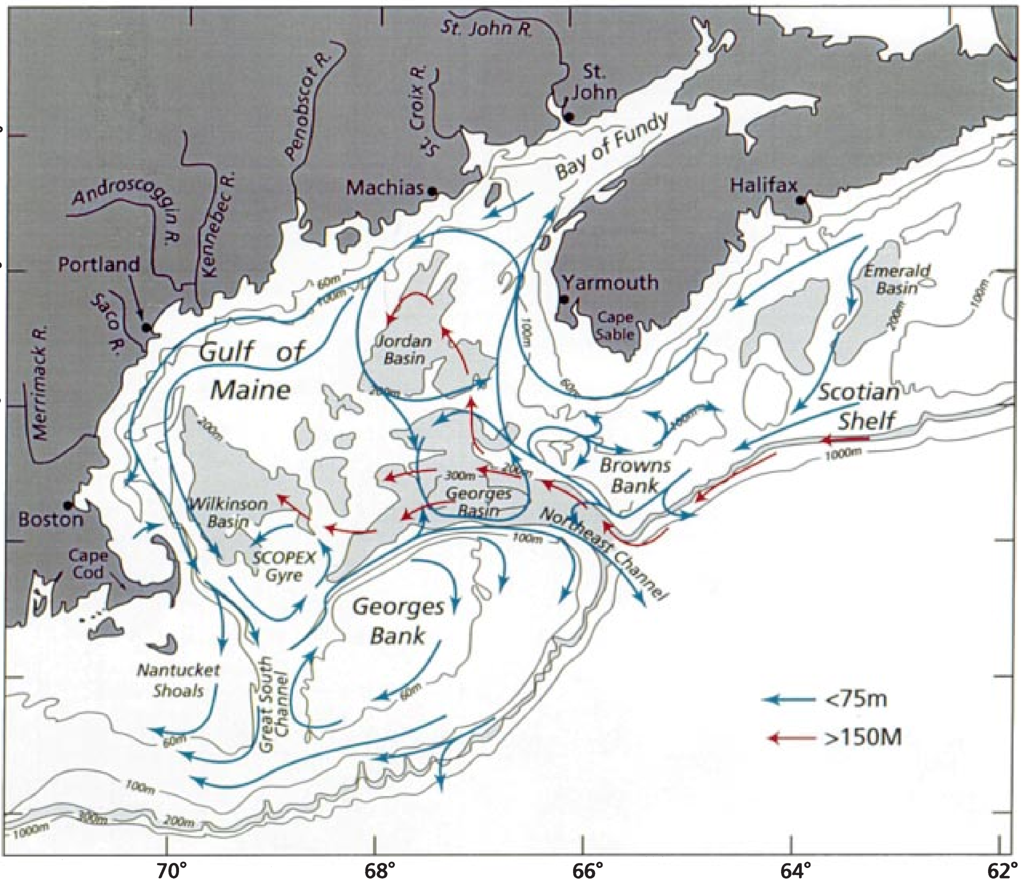
Figure 1. Chart of the Gulf of Maine and Georges Bank, showing the typical water circulation after stratification is established in the spring.



animals originating at a given locale would typically have arrived at each successive life stage.

For this purpose we developed an individual-based model of the life history of *C. finmarchicus* in the spirit of Batchelder and Miller's (1989) model of *Metridia pacifica*, with emphasis on correct timing of developmental events. The basic idea is that a stock of individual animals is represented in a computation by a large number of vectors (up to 5×10^5 as run here), the elements of which represent developmental and reproductive status of individual animals. Elements can include age, stage, age-within-stage, readiness of the ovary for spawning and anything else necessary to represent the likely contribution of the individual to the dynamics of the population. Vector elements are changed at successive time steps according to functions representing developmental progress under habitat conditions provided by data or other submodels. When eggs are produced, each is assigned to a new vector.

The key invention in the model presented here is to add elements to each individual's vector representing its spatial address in a site-specific circulation model. When the model is started, a stock of vector individuals are placed across an interesting zone of origin by assigning corresponding addresses. At suitable time steps, the vector animals are moved by applying velocities specified at each one's spatial address by the physical submodel and also given random moves representing diffusion. Changes in position can also be applied to represent swimming when that is appropriate. Results of the model can be represented as progressive maps (or animations) showing development (as colour change) and movement.

The power of the resulting coupled model to represent the interaction of life history events with circulation is considerable. We have applied the model at present to the following questions.

1 Because *Calanus* does not rest over the bank, it must be advected there from elsewhere. What are the source areas for the *C. finmarchicus* stock on Georges Bank?

2 Are *C. finmarchicus* resting stocks in Gulf of Maine basins re-populated by offspring that remain

near the basins throughout development? Or, are input from upstream and return from Georges Bank important to restocking of Gulf of Maine basins? Put another way, where do C. *finmarchicus* originating from the basins, some of them growing for extended periods over Georges Bank, arrive when they are ready to enter the resting phase?

3 Do 'hot spots' in the distribution pattern of C. *finmarchicus* have advective explanations?

(a) Is there an advective cause for the great concentrations of late-stage C. *finmarchicus* found at the north end of Great South Channel in spring (Durbin *et al.*, 1995; Kenney and Wishner, 1995; Wishner *et al.*, 1995)?

(b) Do the large numbers of *Calanus* nauplii observed over the North-east Peak in late winter, and apparently supporting the concentration there of cod and haddock spawning, have an advective explanation?

Life history of Calanus finmarchicus

Only a few details have been added since Marshall and Orr (1955) outlined the life cycle of this common copepod of the subarctic North Atlantic (Miller *et al.*, 1991; Tande, 1991). Half or more of the year is spent at depth in a resting or diapause stage (Hirche, 1996). The resting stock is usually dominated by fifth copepodites (C5), but may include fourth copepodites (C4) and adult females (C6F). Emergence from diapause occurs in mid-to-late winter and for C5s is coupled to maturation, males appearing first, then females. These adults are termed the G_0 generation (terminology due to Ian McLaren, Dalhousie University). Females ascend to near-surface layers, mate on the way up (Tsuda and Miller, 1998), feed and soon begin to spawn. Nauplii hatching from the eggs, generation G_1, develop over 2–3 months, then either re-enter diapause or mature immediately to produce a second, spring generation, G_2. Most, but not all (Meise and O'Reilly, 1996; J. Crain and C. Miller, Oregon State University, unpublished Gulf of Maine observations) individuals that develop successfully through G_2 enter diapause.

MECHANICS OF THE MODEL

Population dynamics

There are several models representing the development of C. *finmarchicus* for various purposes. Miller and Tande (1993) modelled developmental timing for a single cohort with prolonged reproduction (as occurs in northern Norwegian fjords) by a very finely divided age-within-stage representation. Their goal was to test the methodological validity of several field techniques for estimating stage duration. Tande and Slagstad (1992), Steele and Henderson (1995), and Carlotti and Radach (1996) have modelled the interaction of C. *finmarchicus* with phytoplankton stock, showing the relative grazing impacts of different developmental stages, the effects of food availability on development rate and the impact of variable predation on population numbers and age structure. Models incorporating phytoplankton production and detailed *Calanus* population structure, such as that of Carlotti and Radach (1996), have been embedded in flow fields in Lagrangian fashion by Heath *et al.* (1997) and as a spatially distributed array of subregional models by Bryant *et al.* (1997). Lynch *et al.* (1998) present results from a spatially distributed array of subregional models for C. *finmarchicus* in the Gulf of Maine. This model is similar in spirit to the study by Bryant *et al.* (1997), but with copepod growth specified by a temperature function rather than a phytoplankton submodel.

In the present model we aim to trace a population of individuals as they develop and as they move in a three-dimensional flow field. We have adapted the modelling strategy of Batchelder and Miller (1989), and of Batchelder and Williams (1995). The model is initiated at the winter solstice, 21 December, by defining a set of 1000 vectors, each representing a single, resting C5. Each vector has six elements.

Resting C5 vector:

1 or 0	Alive or Dead
0 to 10	Inactive to Moult-Ready
X	Latitude
Y	Longitude
Z	Depth
N	Element number

Starting from zero at the solstice (day 1), the probability P_{mat} that any given C5 will begin to emerge from diapause is raised by 0.01 per day. At daily time steps, each inactive C5 is assigned a random number (uniform rectangular distribution, 0.0 to 1.0). If it is less than P_{mat}, its second element is incremented to 1, and it begins a 10 day delay until maturation as a female. Ten days is the time found by C. Svensen (pers. comm., University of Tromsø) from first exposing resting C5 to continuous light until the maturation moult. Continuous light is a disturbance that triggers maturation at any time in the rest interval (Miller *et al.*, 1991). Recurrence of this process generates a distribution of maturation times as shown in Fig. 2. This roughly mimics, or is somewhat slower than, the maturation schedule observed by the GLOBEC Georges Bank Program; winter cruises initiated on 10 January show three quarters of the *Calanus* stock already matured. Planque *et al.* (1997) have shown that at the south-western end of the range, the active season of *C. finmarchicus* starts in February, much earlier than for the Irminger Sea and Norwegian Sea stocks, which mature as late as April.

Next, the stock of matured G_0 females is randomly subsampled, leaving a suitable number of females with roughly the maturation date distribution of the stock as a whole. This number was 250 or 500 in all runs displayed here. Time is rerun from the solstice, and on its maturation date each female is assigned a seven-element vector.

Female vector:

1 or 0	Alive or Dead
Variable	Age Since Maturation, Days
0 to 1	Clutch Readiness Fraction
X	Latitude
Y	Longitude
Z	Depth
N	Element number

Clutch readiness fraction (*CR*) at maturation is set to a random number, 0.0 to 1.0. This forces spreading of egg-laying time around the day, which may not be realistic but smooths the shifting of stage abundances. After activation (vector assignment), 7 days are allowed to pass before reproduction begins, following observations of time of first spawning in mesocosm stocks by C. Rey (pers. comm., Observatoire Océanographique, Villefranche). At 7 days past moulting, *CR* is incremented at each time step by 1/24th of the inverse of the clutch-to-clutch interval in days predicted by a Belehrádek function (Fig. 3) fitted to the clutch interval as a function of temperature data of Hirche *et al.* (1997). This inverse is the fraction of clutch development occurring in the 1 hour time step. When *CR* reaches 1.0, a clutch of 50 eggs (Niehoff and Hirche, 1996) is produced, and *CR* is zeroed. Temperature for this and other purposes in the model is drawn from a seasonal harmonic function developed from MARMAP data by Mountain and Holzwarth (1989). Spatial temperature variation in this region (except at the extreme southern boundary) is very small and ignored in the model. Each day, each female is subjected to a random chance of death (daily survivorship = 0.975) and is moved by the physical submodel.

When a female produces eggs, each is assigned a seven-element vector.

Nauplius/copepodite vector:

1 or 0	Alive or Dead
1 to 12	Stage
0 to 1	Moult Cycle Fraction (MC)
X	Latitude
Y	Longitude
Z	Depth
N	Element Number

Eggs are stage 1, first nauplii are stage 2, and so forth to C5 at stage 12. Durations of each stage at the temperature of the date are calculated from Belehrádek temperature functions (Fig. 4) fitted to full-nutrition stage-duration data (R. Campbell, University of Rhode Island, unpublished data). At each hourly time step, 1/24th of the inverse of the stage duration in days is added to the moult cycle fraction (MC). When MC

Figure 2. Number of female maturations per day from the model resting stock through the first 50 days.

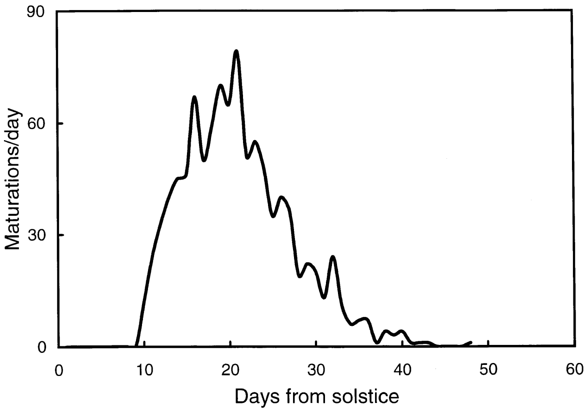


Figure 3. Belehrádek function fitted to data of Hirche *et al.* (1997) for clutch-to-clutch interval at different temperatures.

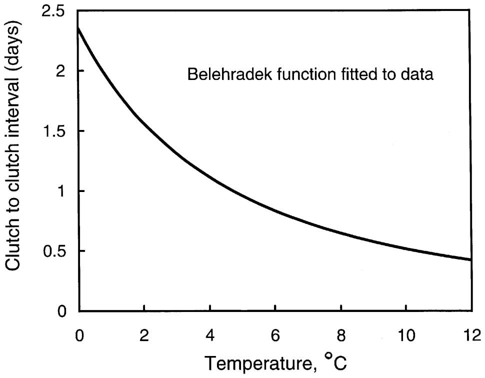
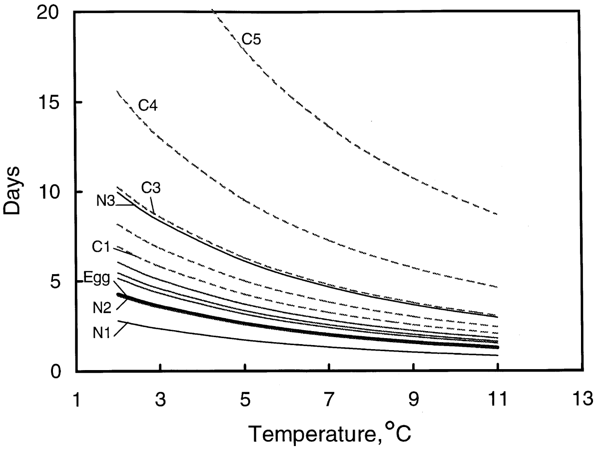


Figure 4. Belehrádek functions fitted to data of R. Campbell (University of Rhode Island, unpublished data) for duration of stages at different temperatures. Eggs, heavy solid line; nauplii, solid lines; copepodites, dashed lines.



reaches 1, it is zeroed and the stage is incremented by one.

At each hourly time step, each individual is subjected to a random chance of dying at a mortality rate set for each stage. For G_1 we have used the *ad hoc*, stagewise survivorship rates from Miller and Tande (1993), while lower survivorship was applied to G_2 (Table 1). The G_2 rates were chosen to produce 50 000–60 000 G_2 resting C5 from 500 G_0 females (after application of the G_2/G_1 generational multiplier, see below). Improved tuning of the mortality scheme should eventually be possible by analysis of the Georges Bank Program Broadscale Survey data. Each vector individual is moved by the physical submodel at each hourly time step. In runs presented here, initiating C5s do not move, females move to a nominal 25 m mixed layer, and all females and developing young are consistently advected at the mean velocity for that mixed layer.

Table 1. Daily survivorship rates applied to generations G_1 and G_2 in the Gulf of Maine / Georges Bank model of *C. finmarchicus* population dynamics. Egg survivorship was reduced by 25% day^{-1}, other stage survivorships by 15% day^{-1} from G_1 to G_2

	Daily survivorship rates[a]	
Stage	Generation G_1	Generation G_2
Egg	0.85	0.6375
N1 to N6	0.92	0.7820
C1	0.95	0.8075
C2	0.96	0.8160
C3	0.97	0.8245
C4	0.98	0.8330
C5	0.99	0.8415

[a] Fraction surviving per day

When a G_1 or G_2 individual completes its C5 development, it either matures or enters diapause by a random process. The fractional rates (mature:diapause) are 50:50 for G_1 and 10:90 for G_2, values based on rough estimates from a seasonal teeth-development study (C. Miller and J. Crain, unpublished observations). Half of maturing individuals are assigned as male (random process) and simply counted; half are female and are stored with maturation date and location. Resting C5 are stored with rest-initiation dates and locations. In runs shown here, we did not subsample G_1 females before they produced G_2, choosing to run very large numbers of vectors during G_2 (just over 5×10^5). For reproduction of G_1 females, time is again rerun from the winter solstice, and G_1 females and their G_2 offspring are treated as were the G_0 females and G_1 offspring in the first run. A further run for G_2 females and G_3 offspring is also possible.

Physics

At each time step, the population model uses output from an advection model to determine the spatial translation of each vector individual. We used archives of hydrodynamic model runs, representing the climatological cycle in six, bimonthly (i.e. every 2 months) realizations. The model itself is a 3-D, nonlinear, finite-element model with advanced turbulence closure. It resolves tidal time scales and is forced by climatological estimates of wind stress and tide plus initial distributions for temperature and salinity. Spatial resolution is variable, with the smallest triangles over steep topography, near shore, and at points of special interest. Details of the model are presented in Lynch *et al.* (1996).

The velocity used here is averaged over the tide to obtain an estimate of the Lagrangian velocity (Eulerian plus Stokes velocities), averaged over a surface layer 25 m thick. Temporal evolution was interpolated linearly among the six climatological archives. The general features of these solutions are displayed in Lynch *et al.* (1996), which used the identical velocities. Figures 10 and 13 of that paper show the several realistic and complex circulation features of the Georges Bank / Gulf of Maine region.

On Georges Bank, most of the motion is tidal flow. The dominant component of long-term, residual flow derives from rectification of this tidal motion into anticyclonic circulation around the bank.

Water-column stratification and seasonal wind changes modify the pattern, with a particularly strong shift in April/May to a summer/autumn pattern. Anticyclonic flow around the bank is generally weaker in winter, and closure northward along the east side of Great South Channel is then at its minimum. Spring stratification and shifting of the wind from strong north-west to weak south-west cause intensification of the gyre and increased recirculation at the south-west end of the bank. Naimie (1995) did a thorough study of these features and their dynamic origin using the present model.

Several cyclonic gyres characterize near-surface flow in the Gulf of Maine, with limbs flowing toward, then along and around, Georges Bank from both the western side and from Jordan and Georges Basins. Generally the intermediate and deep circulation is isolated from Georges Bank (Lynch *et al.*, 1998, Figs 6 and 10). Surface flow into the Gulf of Maine is primarily Scotian Shelf water entering along the eastern side of North-east Channel, turning around Cape Sable and Browns Bank, then joining the cyclonic gyre over Jordan and Georges Basins. Several smaller gyres recur in the flow regime, particularly cyclonic eddies at the north side of Great South Channel (the 'SCOPEX' gyre) and over Georges Basin. The physical model captures these main flow features. Hannah *et al.* (1998) explored the near-surface advective pathways in these solutions linking the gulf to Georges Bank.

Biological-physical interaction

Coupling of the biological and physical models is obtained by linear interpolation between adjacent bimonthly advection fields from the physical model. The advective time step is one day. A copepod at point (x, y, z) at time step i is moved to a new point (x', y', z') at time step $i + 1$ according to the resultant velocity derived from velocities at its finite element apices. The latter are obtained by linear, vector interpolation between mean velocities for the bimonthly periods before and after i. Thus, the velocity for 10 April would be the March/April mean plus 10/61 of the difference between the March/April and May/June means. In addition, a diffusive random (normal) step of 1000 m (root mean square, RMS) was added at each daily time step, equivalent to horizontal diffusivity of the order 1000 m^2 day^{-1}. Trajectories and developmental progress were studied for each of four starting regions: Wilkinson Basin, Jordan Basin, Georges Basin and Emerald Basin. These were chosen as known foci of high resting stock abundance. An objective analysis by Lynch *et al.* (1998) of MARMAP data summarized by Meise and O'Reilly (1996) shows that Jordan and Wilkinson Basins are the zones of highest abundance in the Gulf of Maine for late-stage *C. finmarchicus* from late summer to December. MARMAP data are derived from tows to only 200 m depth, whereas Georges Basin is deeper than that. Sameoto and Herman (1990) and Herman *et al.* (1991) showed that resting *C. finmarchicus* in Scotian Shelf basins are just above the bottom, so it is reasonable to suppose that the bottom of Georges Basin is also a source site, even though it does not show up in the objective analysis of the MARMAP data. Recent autumn GLOBEC observations in Georges Basin (C. Greene, pers. comm., Cornell University) confirm that there is a substantial resting stock in its deep layers. Herman *et al.* (1991) explicitly proposed that Emerald Basin and La Have Basin on the Scotian Shelf are important to regional retention of the *C. finmarchicus* stock between the spring and winter solstices, so we have examined trajectories of lineages from there.

RESULTS

Population dynamics

Biological aspects of the model output (Fig. 5), without advection, show substantial similarity to Georges Bank Broadscale Survey data on *C. finmarchicus* development in the southern Gulf of Maine and over Georges Bank. Maturation of G_0 out of the resting phase starts in early January and reproduction builds into February. As G_1 completes its development, the long duration of C5 makes it the dominant copepodite stage from day 80 to day 120. There is strong separation between the egg and naupliar pulses of G_1 and G_2. When the model is run with only temperature limitation of development rate, that separation between generations becomes centred (for early nauplii) around day 105, in early April. A corresponding gap in naupliar abundance shows up in field data, but it is a month later. This implies some other limitation on development rate during G_1. Part of the discrepancy could be that the real start of significant spawning, or significant survival to copepodite stages, is later than modelled. That probably is not the full explanation for such a long delay, and the only other likely explanation is short rations slowing G_1 development. We have no strong basis for characterizing this at present, and leave it for future model development. However, there are data, accumulating from GLOBEC process studies, indicating that strong starvation events recur in April and affect *Calanus* fecundity and growth. Despite the apparently early start of G_2 in the model, it finishes up at about the same time as the field population, about the middle of July, after which *Calanus* is a much-

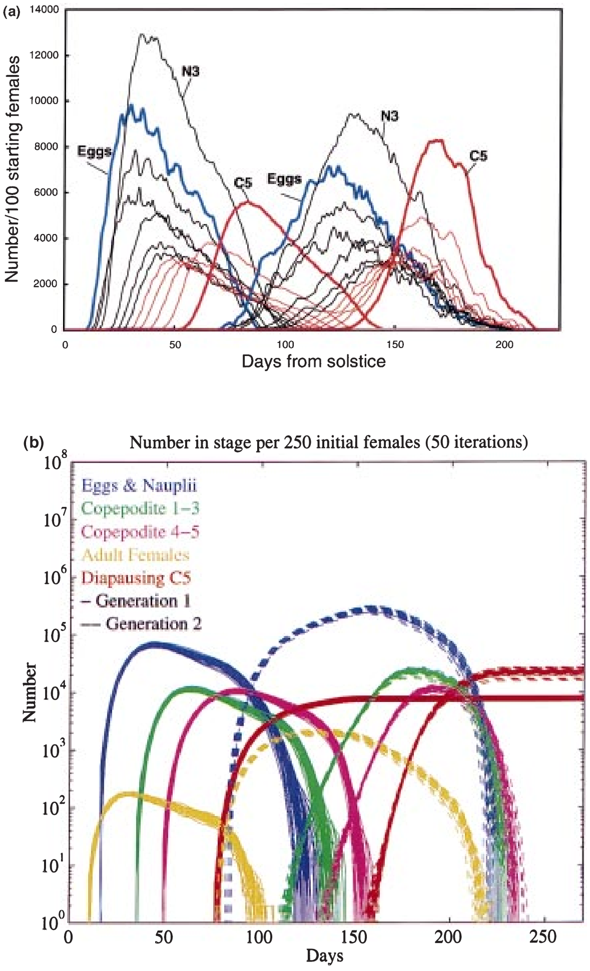


Figure 5. (a) Number of surviving offspring of 100 females of the G_0 and G_1 generations, model output. Generations shown are G_1, left, and G_2, right. Survivorship was reduced for G_2 (Table 1). Blue lines-eggs; black lines-naupliar stages; red lines-copepodite stages. (b) Model estimates of the number of individuals in grouped stages surviving from 250 females starting G_0 for each day following the winter solstice. In these runs, all G_1 females and their offspring were retained without subsampling. Results of 50 separate runs are plotted together to show the effects of stochastic processes.

reduced component of the regional, near-surface plankton (Meise and O'Reilly, 1996).

As survivorship is currently set and starting with 250 G_0 females, the model produces a mean near 8000 resting C5 from G_1 (plus half that many females) and about 22 500 from G_2 (plus about 1125 females). These 'output' values are subject to modest stochastic variation, due to the random mortality process. Over 50 runs, the G_1 output ranged from 7101 to 8805 (CV = 5.4%). The G_2 output was more variable, from 15 856 to 27 392 (CV = 10%). Increased variability of G_2 appears to result from its higher mortality rates. Output values of G_1 and G_2 were positively correlated ($r = 0.72$), simply because more females produce more offspring. The relative contributions of G_1 and G_2 to the resting stock over the 50 runs ranged from 1:2.2 to 1:3.3.

Trajectories

The most effective presentation of the interaction of development with flow is by animation, showing movement over a map of individuals initially spread across an interesting subregion, such as Wilkinson Basin in the Gulf of Maine. Life stage is shown by changing the colour of dots locating each individual in the cohort. Computer animation files can be obtained from the archival World Wide Web site: http://www-nml.dartmouth.edu/Publications/internal_reports/NML-98-7/. Here we present a few successive frames for launches of groups of resting C5s from four different sites in the region (Fig. 6). The spread of individuals is shown at days 40, 70, 100, 130, 160 and 190 days from the winter solstice.

From Wilkinson Basin in the western Gulf of Maine, the newly matured stock shifts south, producing G_1 nauplii. These divide. One group (A) travels along the west side of Great South Channel (GSC), turns west around Narragansett Shoals and heads off to the Mid-Atlantic Bight. A second group (B) moves up against the north-west shoulder of the bank and circulates there for many weeks. A third group (C) crosses onto the shallow centre of the bank at about 68°W. No Wilkinson Basin G_1 nauplii reach the North-east Peak. By day 100, group B is recirculating in the small, cyclonic, SCOPEX gyre, found over the bathymetric funnel at the entrance to the GSC, while group C is scattered over the end of the bank west from 68°W to the edge of the GSC. The G_2 nauplii from group C become the most widespread and occupy the whole western end of the bank by day 120. In the course of the second generation, the Wilkinson Basin stock circulates around the entire bank, many of them returning in the intensified northward recirculation of spring along the west end of the bank (up the east side of the GSC). By day 160, the shallow sections of the bank begin to clear of *Calanus*, and the stock becomes strongly annular in the gyral flow between the 50 and 100 m isobaths. Fates of stock found late in the growing season over the eastern end of Georges Bank are about evenly split between northward delivery to the SCOPEX gyre and transfer south-west into the Mid-Atlantic Bight. Large numbers of G_2 C5 reach diapause readiness in the SCOPEX gyre, and from there presumably have ready access back to Wilkinson

Basin, so that it is partly self-stocking. Others reach diapause all the way around the bank. A small remnant slides off the bank to the east and seaward after day 200. They might reach the North-west Atlantic Slopewater for their rest phase.

From Jordan Basin in the north-eastern Gulf of Maine, newly matured stock moves south-west, eventually spreading south to Wilkinson Basin. One group breaks off, joins group C from Wilkinson Basin and crosses onto the bank at 68°W. The bulk of G_1 is over Wilkinson Basin in early copepodite stages, and a majority pass around Narragansett Shoals to the Mid-Atlantic Bight. Offspring of the very latest G_0 females to mature get caught up with Wilkinson Basin group B and either remain against the north-west shoulder of Georges Bank or become scattered along the peripheral current. As G_2 reaches diapause readiness, they are distributed in much the same pattern as the Wilkinson Basin stock, some in the SCOPEX gyre, some along the flanks of the bank. None of the progeny of *C. finmarchicus* that rested during summer/autumn in Jordan Basin are returned there; it is not self-stocking.

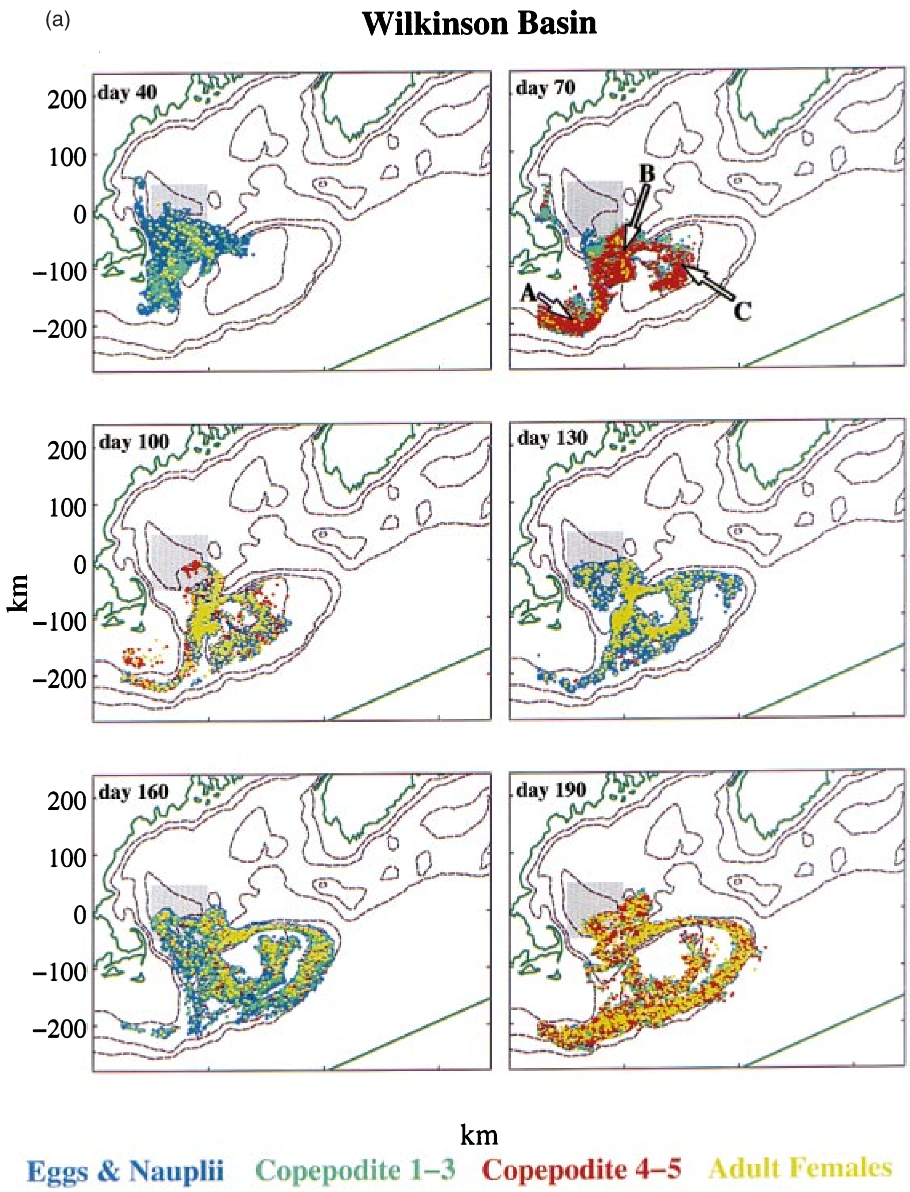
From Georges Basin just north of the east end of Georges Bank, the newly matured females are moved south, into the eastward current jet along the north edge of the bank, then down across North-east Peak. By day 50 some have moved around the peak, turned south-west and reached as far as 67°W below Great South Channel. However, later maturers are spread all over North-east Peak by that date and have produced high naupliar concentrations there. Thus, Georges Basin appears to be the source of females producing the nauplii that attract cod and haddock spawning at the peak (Smith, 1983; Lough and Bolz, 1989). Large numbers of Georges Basin nauplii remain over the peak until day 90. The bulk of the G_1 are eventually carried west into the Mid-Atlantic Bight, very few of them passing west at a high enough latitude to turn north in the recirculation around the west end of the bank. Around day 70, a number of G_1 *Calanus* diverge from the south flank of Georges Bank at about 68°W and are thereafter carried east. They become a separate, slowly moving, offshore stock producing resting C5 in both G_1 and G_2. The reality of this transfer will need review in models with more reliable representation of the interaction of flow over the south slope of Georges Bank with North-west Atlantic Slopewater. The model shows only a small contribution of new diapause stock from G_2 returned to the vicinity of Georges Basin, the product of the very small fraction carried north in the recirculation at the west end of Georges Bank. Thus, the model suggests that Georges Basin is mostly not self-stocking.

The Scotian Shelf simulation is initiated over, and inshore of, Emerald Basin. Initial movement is to the south-west, with a small portion of the females advecting directly to the south and leaving the shelf. The balance of the cohort moves south-west, experiencing some additional off-shelf losses, and divides into three groups at North-east Channel. The earliest maturers and their offspring are carried south and west, cross North-east Channel, then circulate around Georges Bank above the 100 m isobath. Already by day 40 (end of January) this narrow projection reaches past 68°W. Some later starters also follow that route, but more are carried north-west into the Gulf of Maine. Some turn toward Jordan Basin. More are carried out over Georges Basin, gradually entraining in the eastward jet along the bank. At adulthood, the G_1 of this last group are split between the 'Jordan–Georges gyre' and the North-east Peak. The G_2 offspring of those groups that have been carried into the gulf spread all around Georges Bank and across the southern gulf, contributing C5 to resting stocks over both Wilkinson and Georges Basins. There was no self-restocking of the Emerald Basin area evident in the simulation; it is most probably restocked from upstream to the north-east.

Abundance on Georges Bank

Figure 7 shows the time histories of abundance on Georges Bank, defined here as east of 69°W and within the 100 m isobath. With no advection, these plots would be stochastic equivalents of Fig. 5. The addition of motion introduces distortion owing to the limited scope of the sampling. There are systematic effects. The delay in reaching the bank results in an apparently late G_1; at the end of the simulations, a premature termination of G_2 occurs as the stock drains from the bank with no further inputs. Overall, the apparent abundance is reduced because the bank does not capture all individuals and retention is imperfect. Georges Basin is the earliest and most efficient contributor in G_1, followed by Wilkinson and Jordan Basins. During G_2, the order is reversed: Wilkinson and Jordan contribute with comparable efficiency, while the cohort from Georges Basin is eroded by advection even in the naupliar stages. The Scotian Shelf cohort arrives at about the same time as the Wilkinson cohort; but it is inefficient, with abundances of G_1 and G_2 reduced by a factor of 10. These systematic effects illustrate the importance of the openness of Georges Bank, which needs to be accounted for in any ecosystem analysis.

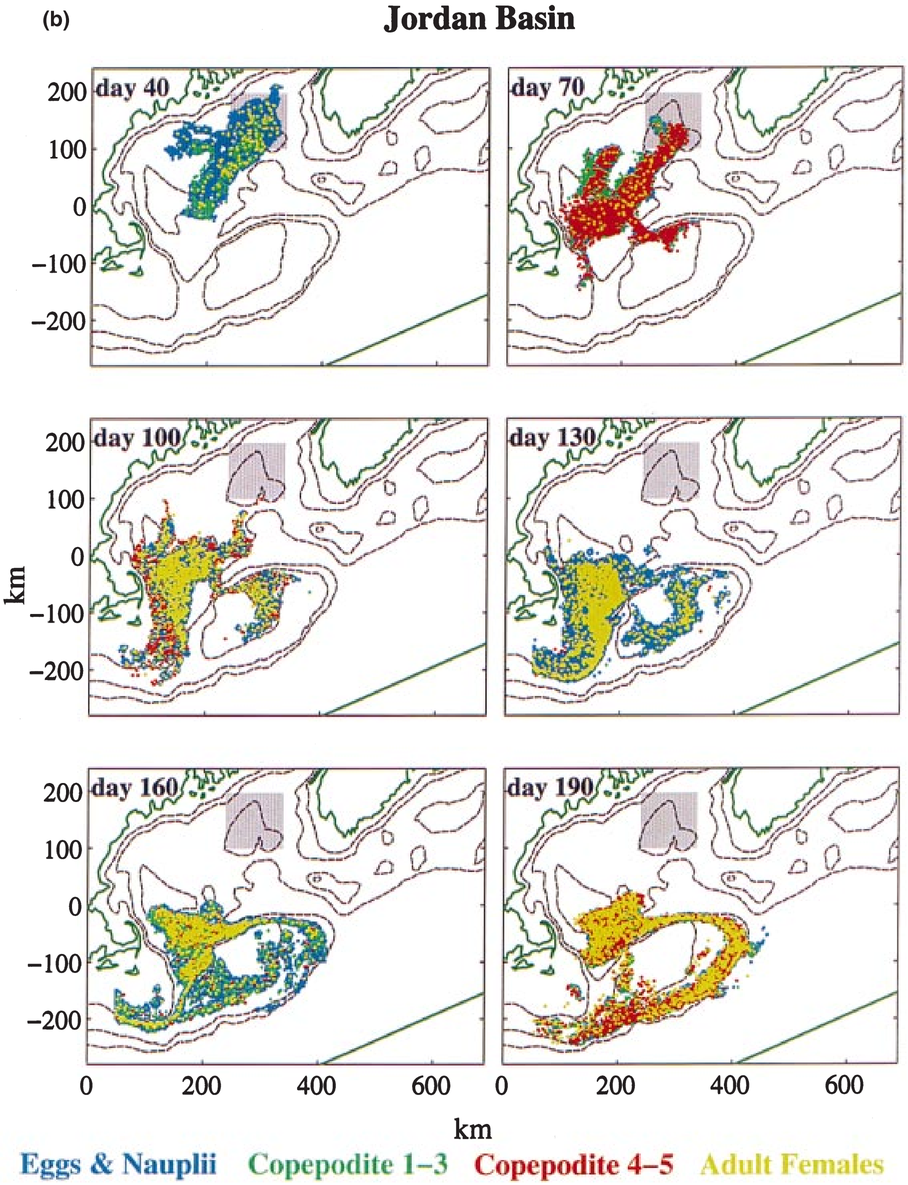
Figure 6. (a) Spatial distribution at successive intervals of *C. finmarchicus* maturing from diapause at four different 'launch' sites in the Gulf of Maine / Scotian Shelf area: (a) Wilkinson Basin; (b) Jordan Basin; (c) Georges Basin; (d) Scotian Shelf. All launches were of 500 G_0 females. Each panel shows progressively later distributions with different life stages distinguished by colour. Distributions are shown for 40, 70, 100, 130, 160 and 190 days after the winter solstice. Groups A, B and C at day 70 for the Wilkinson Basin launch are discussed in the text. (continued on following 3 pages)



Produced resting stock

The present model does not track C5 after they are assigned to diapause. However, ranges of points of diapause entry for G_1 and G_2 individuals (Fig. 8) that are offspring of G_0 parents allow some reasonable inferences. Only the Wilkinson Basin resting stock is significantly self-sustaining, with both generations contributing some return of resting stock. Most of the individuals of Wilkinson parentage reach rest-readiness somewhere around Georges Bank or are carried alongshore to the Mid-Atlantic Bight. However, many individuals, considerably more than the initial starting group of G_0 adults, were retained by the cyclonic gyre that recirculates in the topographic funnel just north of Great South Channel. This relative increase depends upon approximate mortality rates that are very

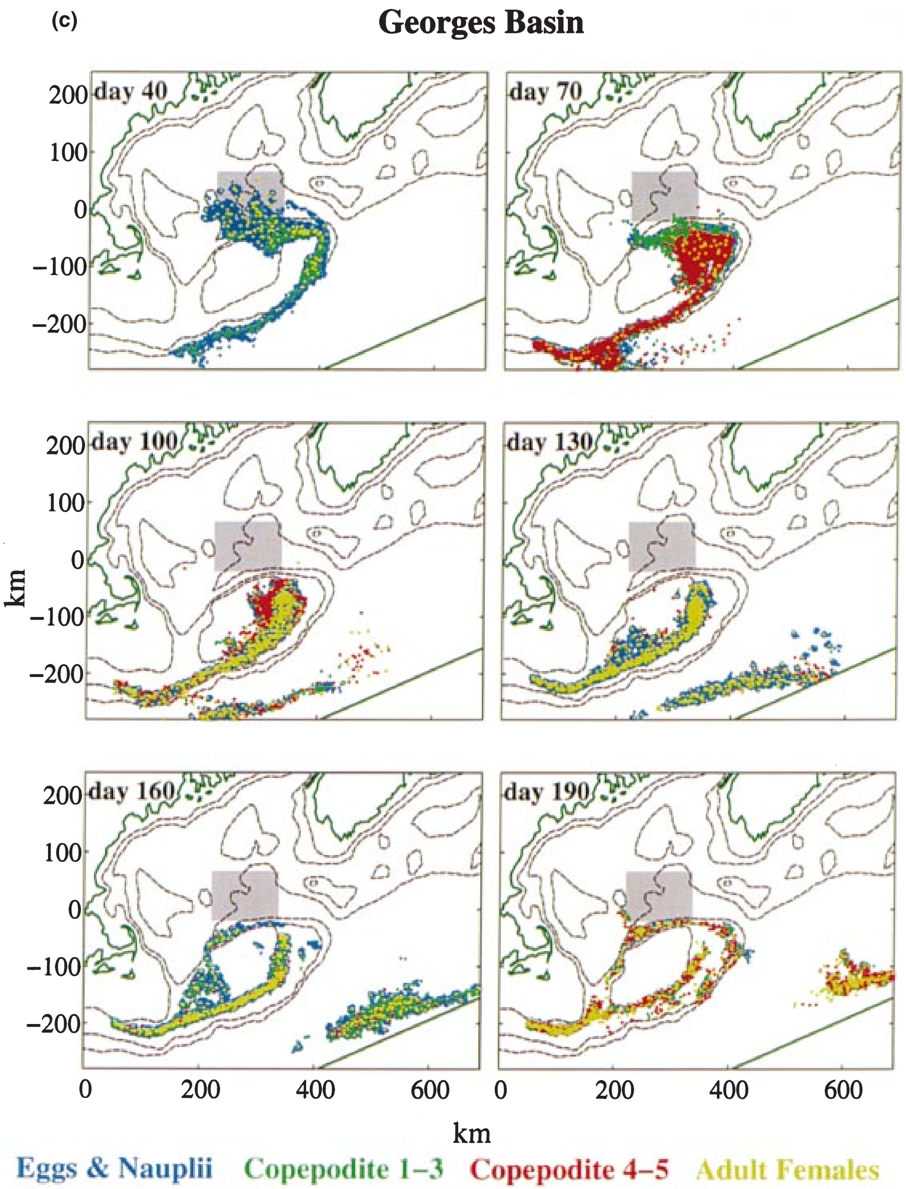
Figure 6. (b)



uncertain. These C5 are likely to make their way back down toward the basin bottom through the summer and autumn. This Wilkinson restocking is reinforced by accumulations in the same gyre of new resting stock derived from G_0 parents originating throughout the gulf and farther to the east, with an especially strong contribution from the Jordan Basin area in both G_1 and G_2.

The model shows that Georges Basin might receive a few resting stock produced by G_2 that move off the bank from the north limb of the peripheral current. Some resting stock may also be carried east into Georges Basin as they settle from the accumulation in the SCOPEX gyre. However, Georges Basin must mostly receive resting stock from lineages starting the growing season upstream. Likewise, Jordan and Emerald Basins are not self-stocking. Some of the G_1 C5 that were offspring of females in the northernmost branch of the flow around Nova Scotia into the gulf, and that cycled during development between Georges and Jordan Basins, came to rest in Jordan Basin. The model suggests that Scotian Shelf basins must receive new resting stock primarily from upstream sources. Future development of coupled IBM/physical models will allow us to trace the deposition of resting C5 after they descend to near-bottom layers.

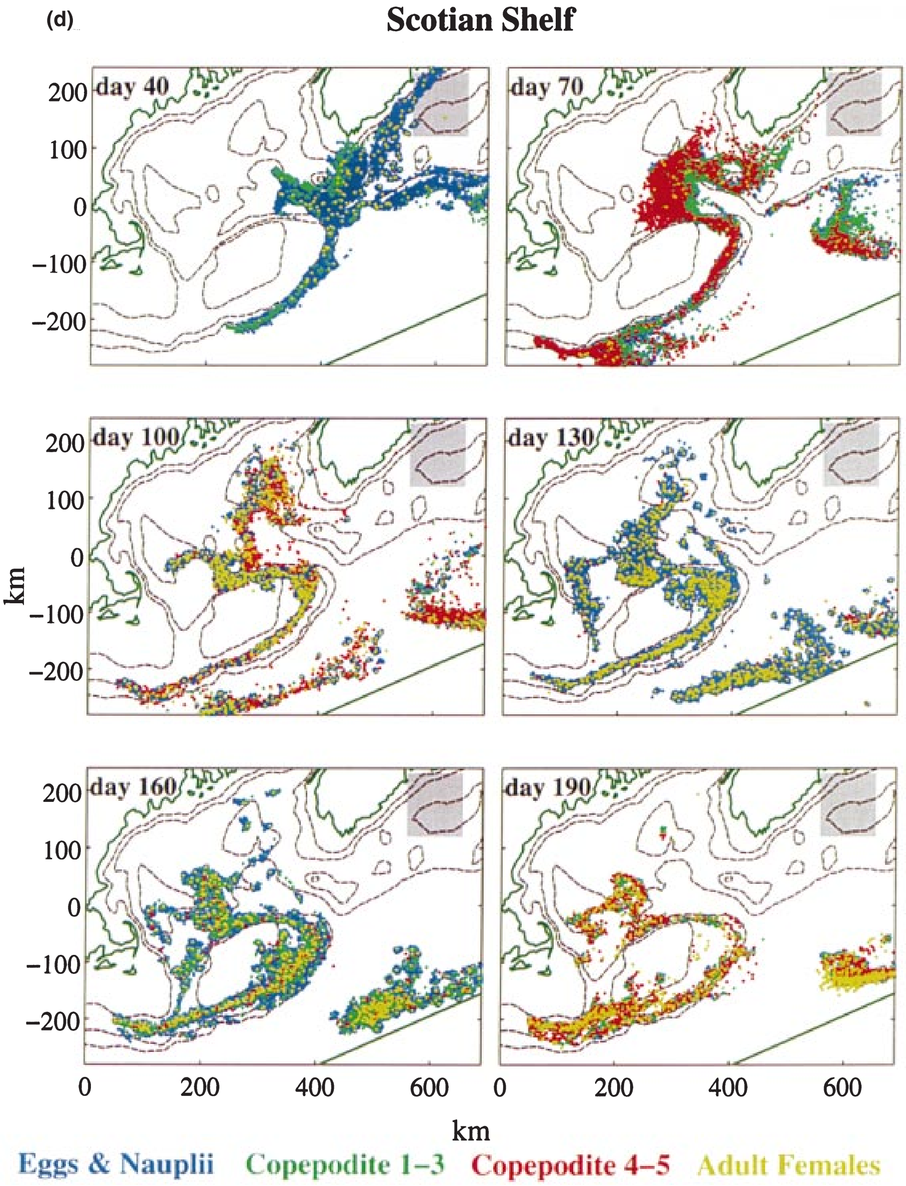
Figure 6. (c)



DISCUSSION

Coupling of the individual-based life history model to a numerical flow simulation has allowed us to address a number of classic questions about the *C. finmarchicus* stock of the Gulf of Maine / Georges Bank region. First, because the bank inside the 200 m isobath has virtually no *Calanus* stock during late summer and autumn (Davis, 1987), it must be restocked as the resting generation emerges from diapause and begins to reproduce. Bigelow (1926) suggested that the winter/spring stock moves to the bank from the Gulf of Maine, and the present simulation confirms that flow from the gulf should restock the bank, supplemented by *Calanus* moving across North-east Channel from the Scotian Shelf. Crossing North-east channel is direct early in the active season, G_0 females and G_1 nauplii moving with transfers during winter of Scotian Shelf water across the mouth of the channel and directly onto the eastern tip of the bank (Bisagni *et al.*, 1996). Few of these early starters cross inside the 100 m isobath on Georges Bank, and most are eventually lost seaward. Later starters mostly turn northwest around Browns Bank, then follow a cyclonic turn in the flow out over Georges Basin. The main points of

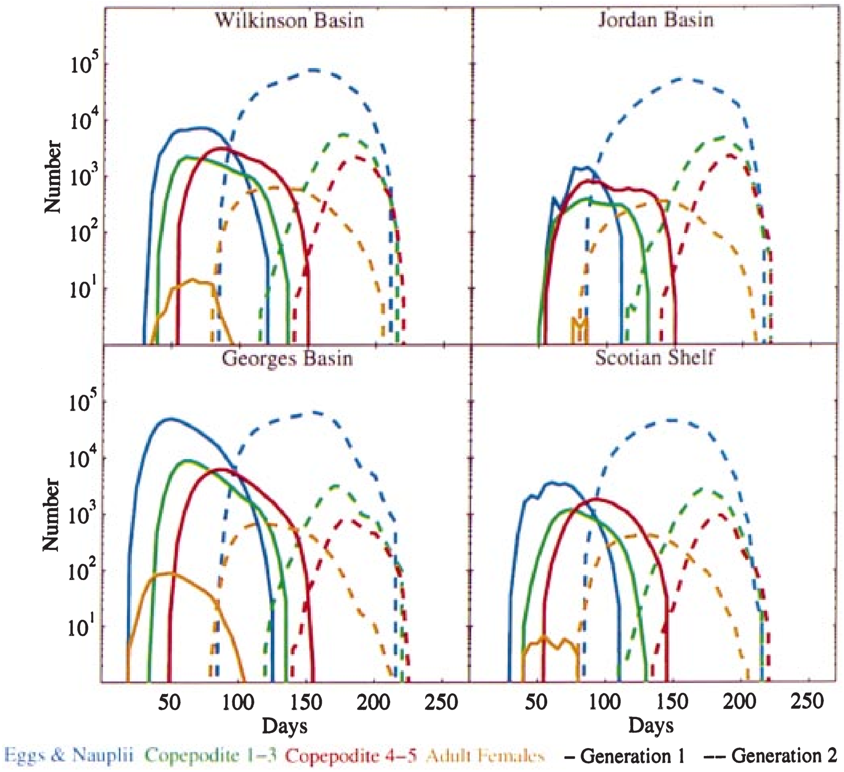
Figure 6. (d)



crossing the 100 m isobath onto the bank are scattered along the north edge. They join in this transfer at the west with Wilkinson Basin stock, crossing at about 68°N, and at the east with Georges Basin stock crossing onto the North-east Peak.

Second, the sources of late-stage C. *finmarchicus* for restocking of the resting populations in the bottom waters of the basins need to be identified. The model suggests that Wilkinson Basin should be significantly self-restocking, some of the population having circumnavigated the bank once (G_1) or twice (G_2) before returning in the northward recirculation at the western edge of the bank. Some Wilkinson Basin *Calanus* simply complete their life history in the SCOPEX gyre at the north end of the Great South Channel. The model strongly suggests that other basins in the system must be restocked from upstream sources. Flow enters the Gulf of Maine region along the Scotian Shelf and slope. Sources of origin of this water include the Gulf of St Lawrence and Labrador Sea, both of which sustain large stocks of C. *finmarchicus*.

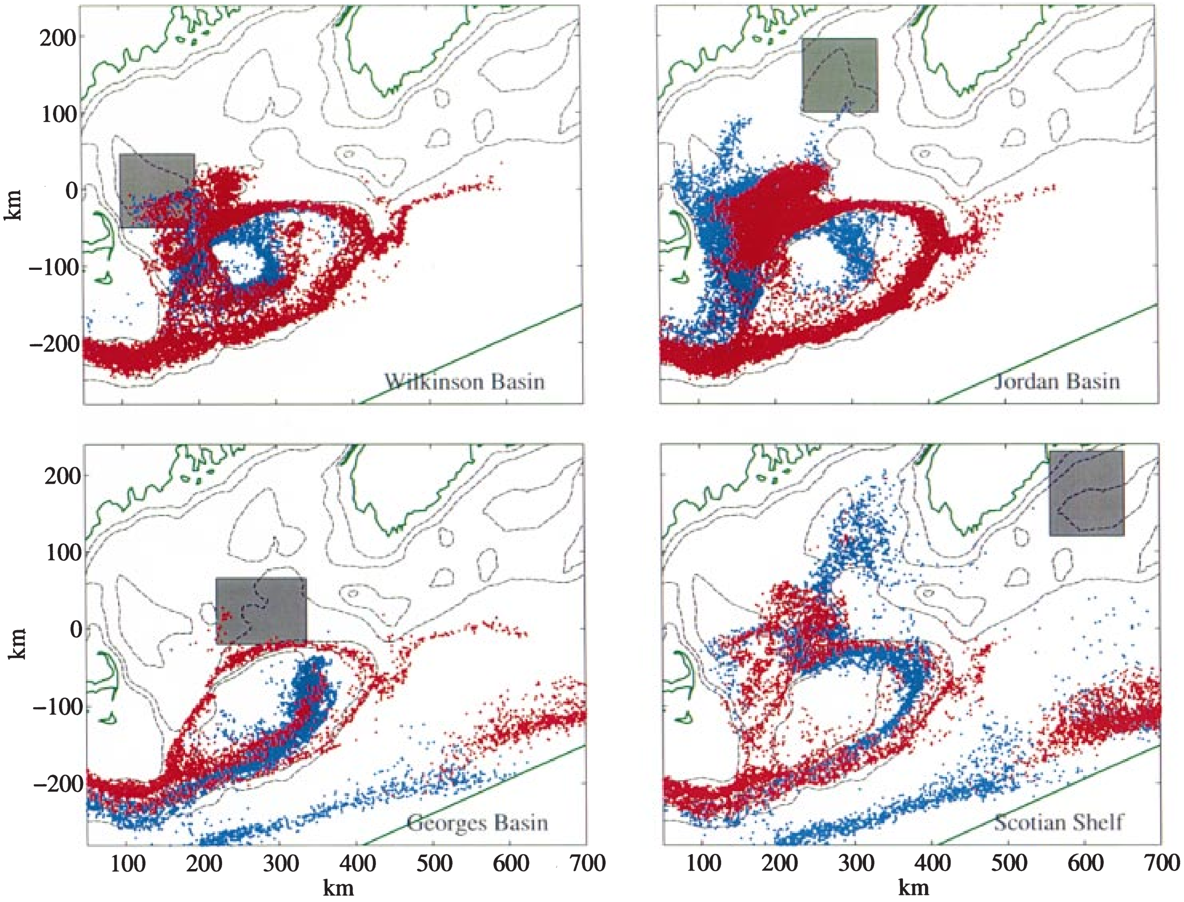
Figure 7. Time series of abundance of various groups of *C. finmarchicus* life stages on Georges Bank inside the 100 m isobath from each of the four launch points shown in Fig. 6.



Third, why are there 'hot spots' in the *C. finmarchicus* distribution on and around the bank? The best-studied of these is the strong accumulation of late-stage *Calanus* at the north entrance to Great South Channel (Durbin *et al.*, 1995; Kenney and Wishner, 1995; Wishner *et al.*, 1995), which is the recurring site of active feeding on *Calanus* by northern right whales (Kenney *et al.*, 1995). While 'curtains' and other dense patches of *Calanus* at this site (Wishner *et al.*, 1988; Macauley *et al.*, 1995) may result from details of behaviour, the model suggests that the overall high densities there result from accumulation of late copepodites finishing diapause preparation in a recurring current gyre. Sources of these late-stage *Calanus* spread along an extended upstream region, including Georges Bank, much of the Gulf of Maine and Scotian Shelf waters. Sampling in the SCOPEX gyre region in May (Durbin *et al.*, 1995; C. Miller, unpublished observations made during 1994) often shows two distinct groups of *C. finmarchicus* C5, one deep and nearly colourless, the other near the surface and dark purple-red when seen in bulk. The colour difference is one of integumental pigmentation. The model makes it reasonable to suggest that the deep group came to rest after G_1, while the surface group are G_2 C5s preparing for rest. Arrival of these groups in the area is separated by a mean of about 3 months in the model, perhaps by a little less than that in the field if G_1 is delayed by an April starvation interval. Contrary to this interpretation, however, Durbin *et al.* (1995) found that the deep group had full guts, and supposed that they were feeding on phyto-detritus above the bottom. Perhaps they were not fully at rest, and possibly the 'diapause rules' for *C. finmarchicus* allow some feeding. Feeding *Calanus* have been observed near the surface in the Gulf of Maine in November (Durbin *et al.*, 1997), none of which showed progress of tooth formation in anticipation of maturation (C. Miller, unpublished observations).

Another hot spot is the accumulation of *C. finmarchicus* nauplii over the North-east Peak in February/March. The peak is a principal area of cod and haddock spawning over this 2 month interval (Smith, 1983; Lough and Bolz, 1989). The matching of larval fish to naupliar stocks seasonally and regionally is part of the explanation (Lough, 1984), because *Calanus* nauplii are a principal diet component for the fish larvae (Kane, 1984). The model

Figure 8. Sites at which C5 of *C. finmarchicus* reached readiness for diapause from different 'launch' areas. Panels (a) to (d) represent G_1 (blue) and G_2 (red) offspring of G_0 females that terminated diapause in five different 'launch' areas (shaded rectangles).



shows the peak receiving newly matured females in very large numbers during this interval, primarily from the Georges Basin area. There is also a contribution from the Scotian Shelf, but only after a turn into Georges Basin. The area of outflow from the peak along the south flank receives developing *Calanus* and is the site of continued copepod reproduction. Thus, the cod and haddock are in the midst of active production of suitable food throughout their transit along the bank. This has been well understood for a long time (Lough, 1984); the model supports this widely held view.

The coupled model in its present state is by no means a finished product. Improvements are needed on both the biological and physical sides. Better information about *C. finmarchicus* from the GLOBEC Georges Bank sampling programmes will be incorporated as it becomes available. This should include a more accurate maturation schedule for G_0, a more exact estimate of reproductive rates, characterization of starvation delays which seem to occur in G_1, and better data on relative numbers entering diapause as the growing season advances. Thorough analysis of survivorship on a stage-by-stage basis will improve the depiction of stage composition through the active season. For now, the relative mortality of G_1 and G_2 has been set by the observed ratio between resting-stage standing stocks in July and stocks of C5 and adults in early January, about 100:1. This reduction is due to mortality, and it must on average be replaced by a 1:100 increase over the active season. More detailed characterization of the vertical distribution of *C. finmarchicus* and its changes with stage and season will allow better tracing of trajectories. It is likely, for example, that Wilkinson Basin stocks can in fact make their way to the North-east Peak of Georges

Bank and contribute to the naupliar concentration there, following current trajectories deeper than the 25 m layer to which we restricted transport (Lynch *et al.*, 1998).

In future studies we can apply more precision and individual variation in vertical positioning and follow C5 at depth for a time after they enter diapause. As the model is now formulated, the positions of newly resting C5 are simply recorded and plotted (Fig. 8). Addition of a period of transport at depth after the onset of diapause will allow us to trace the fate of the large numbers of individuals that come to rest in the model inside the 200 m isobath. There is reason to suspect this may produce more restocking of Gulf of Maine basins that we see at present. Lynch *et al.* (1996, their Fig. 13) show a vertically averaged inflow of about 0.8 Sverdrups through North-east Channel in July/August, which may carry G_2 resting stock back to the gulf basins after they descend to sufficient depth.

Better physical information and more detail in modelling advection along the southern side of the region should allow better evaluation of stock removal from the southern flank of Georges Bank now occurring in the model. That removal seems likely to be an artefact. Better flow modelling at the south edge should also allow us to model the movement onto Georges Bank of *Calanus* stocks maturing in early winter from the resting stock offshore in North-west Atlantic Slopewater (Miller *et al.*, 1991). Better modelling along the Scotian Shelf should allow an estimate of where the two preceding generations of *Calanus* resting in the Gulf of Maine basins during summer must have started the active season in the winter.

Individual-based models of life history are easy to understand and modify because the units manipulated by the model are individual animals, the unit which biologists know and can characterize most effectively. This allows substantial biological realism. Because a population of individuals is represented in the computer, these models also have the properties and power of Monte Carlo statistical models. A wide range of sampling observations and 'field experiments' can be simulated readily. Adding spatial addresses to the individual vectors of the model makes coupling to physical models straightforward, so that both a stock's movement in the flow and its biological progress can be traced in parallel. While the present model needs more work, as outlined above, adaptation to new biological and physical facts should be simple. We predict that models of this type will find very broad application in biological oceanography.

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