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An adjoint data assimilation approach to diagnosis of physical and biological controls on *Pseudocalanus* spp. in the Gulf of Maine–Georges Bank region

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ABSTRACT

The underlying scientific objective here is to determine the mechanisms that control seasonal variations in the abundance of *Pseudocalanus* spp. in the Georges Bank–Gulf of Maine region. It is postulated that the observed distributions result from the interaction of the population dynamics with the climatological circulation. The problem is posed mathematically as a 2-D advection–diffusion–reaction equation for a scalar variable. Given an initial distribution of animals, we seek the population dynamics source term $R(x, y)$ such that integration of the forward model will result in predictions3 that minimize the sum of squares of differences with observed concentrations at a later time. An adjoint data assimilation technique has been designed for these purposes.

This approach has been used to invert for the population dynamics associated with the transition between bimonthly (i.e. for 2 months) climatological *Pseudocalanus* spp. distributions derived from MARMAP data. Vertically averaged velocity and diffusivity fields diagnosed from hydrodynamical simulations of the climatological flow are specified. Solutions converge rapidly, and the procedure reduces the cost function by an order of magnitude within 50 iterations. The resulting population dynamics vary considerably in space and time, as does the balance between local tendency, physical transport and biological source terms. Generally speaking, the patterns in population dynamics are not inconsistent with current knowledge concerning potential controls such as predation and food limitation. Analysis of the solutions indicates that the *Pseudocalanus* spp. population centres located in the western Gulf of Maine and on Georges Bank may be self-sustaining, in contrast to prior studies which characterize the former as a source region for the latter.

Key words: adjoint method, data assimilation, Georges Bank, Gulf of Maine, population dynamics, *Pseudocalanus*, zooplankton.

INTRODUCTION

The interaction of planktonic population dynamics with oceanic circulation can create enormously complex patterns in abundance. Even an ocean at rest could accommodate significant spatial and temporal inhomogeneity through geographic variations in environmental parameters, time-dependent forcing mechanisms, and organism behaviour. Fluid motions tend to amalgamate these effects in addition to introducing yet another source of variability: space–time fluctuations in the flows themselves which impact biological processes. Understanding the mechanisms responsible for observed variations in population abundance is thus a difficult task. Coupled physical–biological models offer a framework for dissection of these manifold contributions to structure in population distributions. However, their utility is predicated on an ability to construct a simulation which is representative of the natural system. One technique for doing so (the 'forward' problem) is to initialize a coupled model with a set of observations, integrate forward in time and then compare with the next set of observations. A successful outcome results in minor discrepancies between observations and predictions, and the model solutions thus can be used as a basis for diagnosis of the processes controlling the observed

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behaviour. Unfortunately, satisfactory completion of the forward problem is not always achievable, owing to limitations in the models, in the observations, or in both. Adjoint data assimilation methods provide an alternative approach which is particularly useful in such cases. These techniques can be used to determine the model inputs (e.g. parameters, forcing functions) that minimize the misfit between observations and predictions, thereby producing an optimal solution from which the underlying dynamics can be gleaned.

Based on classical variational principles and optimal control theory, adjoint data assimilation was introduced into the field of dynamic meteorology in the 1980s (Lewis and Derber, 1985; Le Dimet and Talagrand, 1986). Since then, these methods have become increasingly common in oceanographic applications, beginning with 3-D circulation modelling (Long and Thacker, 1989a,b; Tziperman and Thacker, 1989; Moore, 1991; Seiler, 1993; Schröter *et al.*, 1993; Gunson and Malanotte-Rizzoli, 1996a,b; see also Bennett, 1992). More recently, adjoint techniques have been used for biological problems in the context of parameter estimation in zero-dimensional planktonic ecosystem models (Lawson *et al.*, 1995, 1996). Matear and Holloway (1995) used an adjoint method to examine the biogeochemical cycling of phosphorus in a 3-D model of the North Pacific.

The general approach begins with the definition of a cost function which is a measure of the misfit between model predictions and observations. The goal of the assimilation procedure is to minimize the cost function subject to the constraint that the model equations are obeyed. This is accomplished through adjustment of specified control variables, such as initial conditions, boundary conditions, forcing functions and model parameters. The adjoint method is an efficient iterative technique for solving this minimization problem, which consists of the following steps. Starting with some initial estimate of the control variables, the forward model is integrated to evaluate the cost function. Then the adjoint equations (forced by the model–data misfits) are run backward in time to calculate the gradient of the cost function with respect to the control variables. A descent algorithm is then used to produce a new estimate of the control variables, and the procedure is repeated until convergence to the minimum of the cost function is achieved.

The results of this process provide a variety of means for scientific inquiry into the mechanisms controlling the system of interest. First, the final values of the control variables contain information about the characteristics of the model inputs required for consistency with observations. A solution containing unrealistic values of the control variables would indicate deficiency of the forward model; reasonable values and a good fit to observations form the basis of a solution which is amenable to term-by-term analysis of the dynamics underlying the forward problem. Finally, integration of the adjoint equation facilitates explicit diagnosis of the propagation of information within the system.

The scientific objective here is to determine the mechanisms that control seasonal variations in the abundance of *Pseudocalanus* spp. in the Gulf of Maine–Georges Bank region. It is postulated that the observed distributions result from the interaction of population dynamics with physical transport. A tremendous variety of space and time scales are potentially relevant to this endeavor, ranging from storm-driven advective events to interannual and decadal variations in which the seasonal trends are embedded. Within this broad envelope of scales, a very specific aspect is investigated here: the relationship between seasonal climatologies (long-term means) of both animal abundance and circulation. This is not to say that other scales (or interactions among scales) are not pertinent; rather, in attempting to grapple with an extremely complex coupled problem, it is reasonable to begin by exploring the degree to which the seasonal mean physics and biology are related.

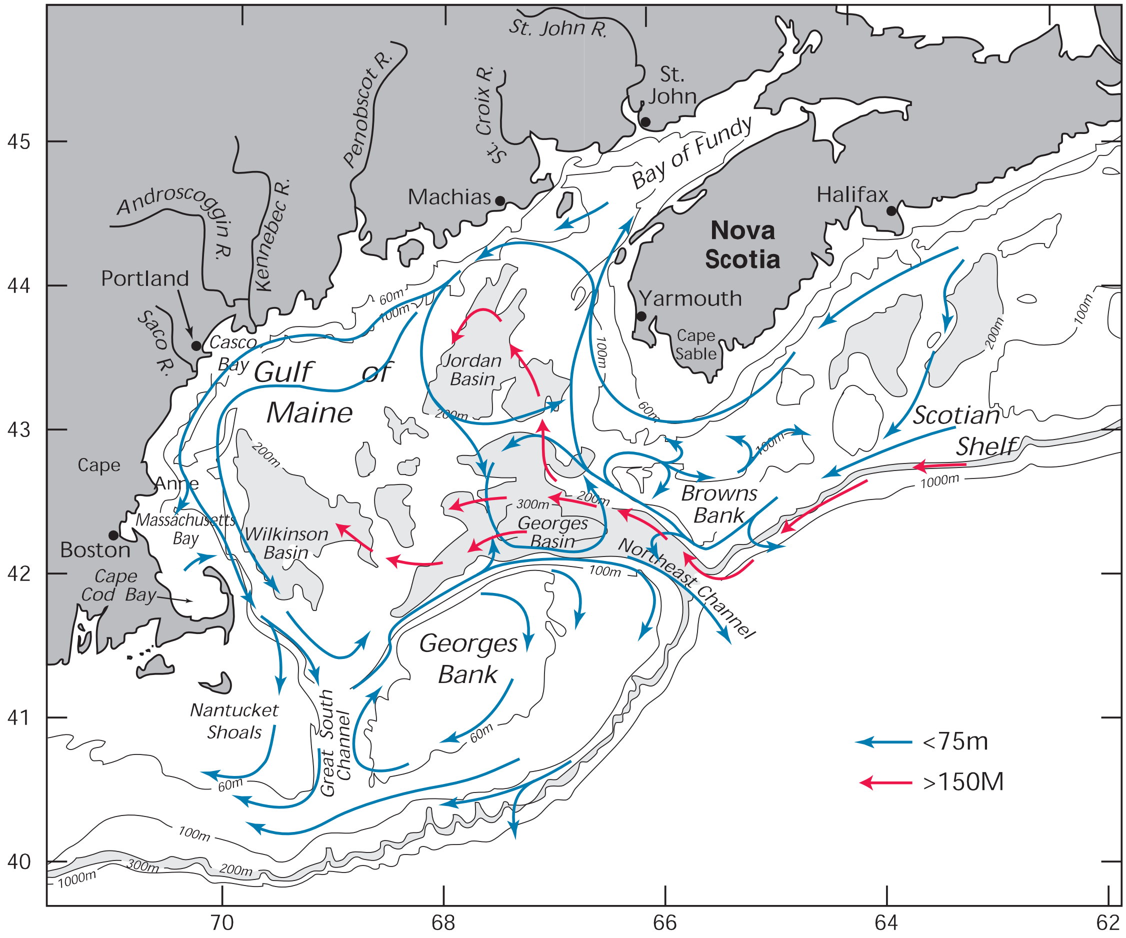
As a starting point for this research, the forward problem is posed as a 2-D (vertically integrated) advection–diffusion–reaction (ADR) equation for copepod concentration, in which the velocity and diffusivity fields are specified from seasonal hydrodynamic simulations of the climatological flow. An adjoint data-assimilation technique is used to invert for the population dynamics (i.e. the reaction term in the 2-D ADR equation) consistent with observed changes in abundance and specified physical transports. Mechanisms controlling the resulting forward model solutions are then diagnosed.

METHODS

Physical oceanographic context

The general circulation in the Gulf of Maine (Fig. 1) tends to be cyclonic (Bigelow, 1927; Beardsley *et al.*, 1997). The near-surface currents are influenced by inflow from the Scotian Shelf, which provides cold, low-salinity water to the north-eastern Gulf. This flow continues past the mouth of the Bay of Fundy and feeds the Maine Coastal Current, with additional input from the St John River and other sources. The coastal current bifurcates near Penobscot Bay, with a portion branching seaward and continuing around the Jordan Basin gyre. The remainder continues down the coast, some of

Figure 1. The general circulation in the Gulf of Maine–Georges Bank region during stratified conditions (May to September). From Beardsley *et al.* (1997).



which feeds the clockwise circulation around Georges Bank. The main channels link the Gulf with adjacent waters on the continental slope: the Great South Channel (sill depth 70 m), the Northeast Channel (depth 230 m), and the Northern Channel (north of Browns Bank, 140 m deep). Thus, planktonic animal populations in the Gulf of Maine–Georges Bank region are interconnected by a fairly complex system of coastal circulation features, and are subject to external inputs from the Scotian Shelf and Slope waters.

Circulation modelling

The circulation in this region has been the subject of intense modelling activity (Lynch *et al.*, 1996). A finite-element approach has been utilized which facilitates realistic representation of the complex geometry in this area. A typical mesh is shown in Fig. 2, which consists of 16749 individual elements. Horizontal resolution in regions of steep topography is as fine as 500 m, so the mesh appears almost solid along the borders of Georges Bank. This 3-D model is hydrostatic, fully non-linear, and incorporates advanced turbulence closure. Published solutions for the climatological mean circulation, broken down into six periods of 2 months each, have been compared with available observations (Naimie, 1996; Lynch *et al.*, 1997). Archived solutions are stored in a form which is available for use in an off-line transport code which solves a depth-integrated form of the 3-D ADR equation on the same grid using the archived hydrodynamic information as input. Biological 'reaction' terms are specified by the user. Boundary conditions consist of (1) no flux through solid boundaries, (2) specification of concentration at inflow, and (3) computation of concentration at outflow assuming no diffusive flux.

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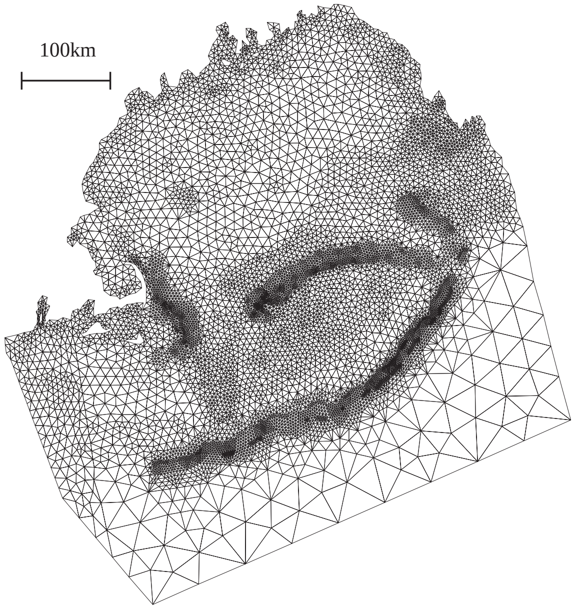
Figure 2. Horizontal finite-element mesh discretizing the Gulf of Maine–Georges Bank region using linear triangles. The mesh is composed of 8563 nodes and 16,749 elements.



Control volume simulations

In order to develop an interpretive framework in which to gauge the impact of the circulation on passively drifting organisms, control volume experiments of two types were performed. The first set was designed to address an important issue which arises in regional studies of this type: the impact of boundary conditions. This matter is of particular concern in the present study because animal abundance is not well sampled in some of the critical inflow regions (see below). Quantitative assessment of the influence of inflow boundaries is facilitated by initializing the concentration to be equal to 1.0 everywhere in the domain, prescribing the concentration at inflow to be 0.0 and integrating forward in time. An example of this type of calculation is shown in Fig. 3 for the January–February time period. After two months of integration, inflow from the Scotian Shelf has spread along two separate branches, one along the south-western tip of Nova Scotia, and the other across Browns Bank and then north-west into the interior of the Gulf of Maine. Water from the Bay of Fundy flows south-westward along the New England coast, bifurcating to some degree offshore of Penobscot Bay. Another area of significant inflow is located at the south-western boundary, just seaward of the 100 m isobath. By the end of the integration, north-eastward flow in this area reaches the southern entrance of the Great South Channel. Significant penetration of low-concentration water is also evident along the south-eastern border of the domain, but the boundary effect stops short of the southern flank of Georges Bank.

Results similar to the January–February case were obtained for simulations performed using each of the five remaining 2 month periods (not shown). Although each period is somewhat different in detail, the overall conclusion of these experiments is that much of this domain is unaffected by boundary conditions in a two-month integration. For the purposes of this study, the 'region of interest' is operationally defined as the intersection of the areas in which (1) observations are available and (2) boundary effects are minimal on two-monthly time scales (Fig. 3).

One of the most salient features of the region of interest identified here is Georges Bank, an area which has been the subject of intensive study. Key issues with respect to understanding population distributions on the bank include (1) transport pathways on and off the bank, and (2) the degree to which the circulation retains organisms on the bank. The second set of control volume experiments was designed to quantify these characteristics by performing integrations in which the initial concentration is set to 1.0 on the bank, and 0.0 elsewhere. Figure 4 shows the initial conditions and the results after 2 months of integration using three different bimonthly flow fields. In the January–February case, there is significant transport onto the bank across

Figure 3. Concentration after 2 months of integration in the basin-wide control volume experiment using January–February transport fields in the domain shown in Fig. 2. Locations of the tiles onto which the MARMAP observations were binned are indicated by plus signs. The region of interest for this study (see text) is also identified.

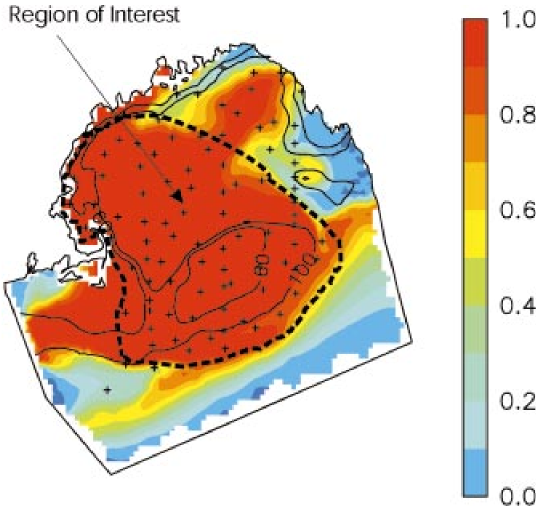


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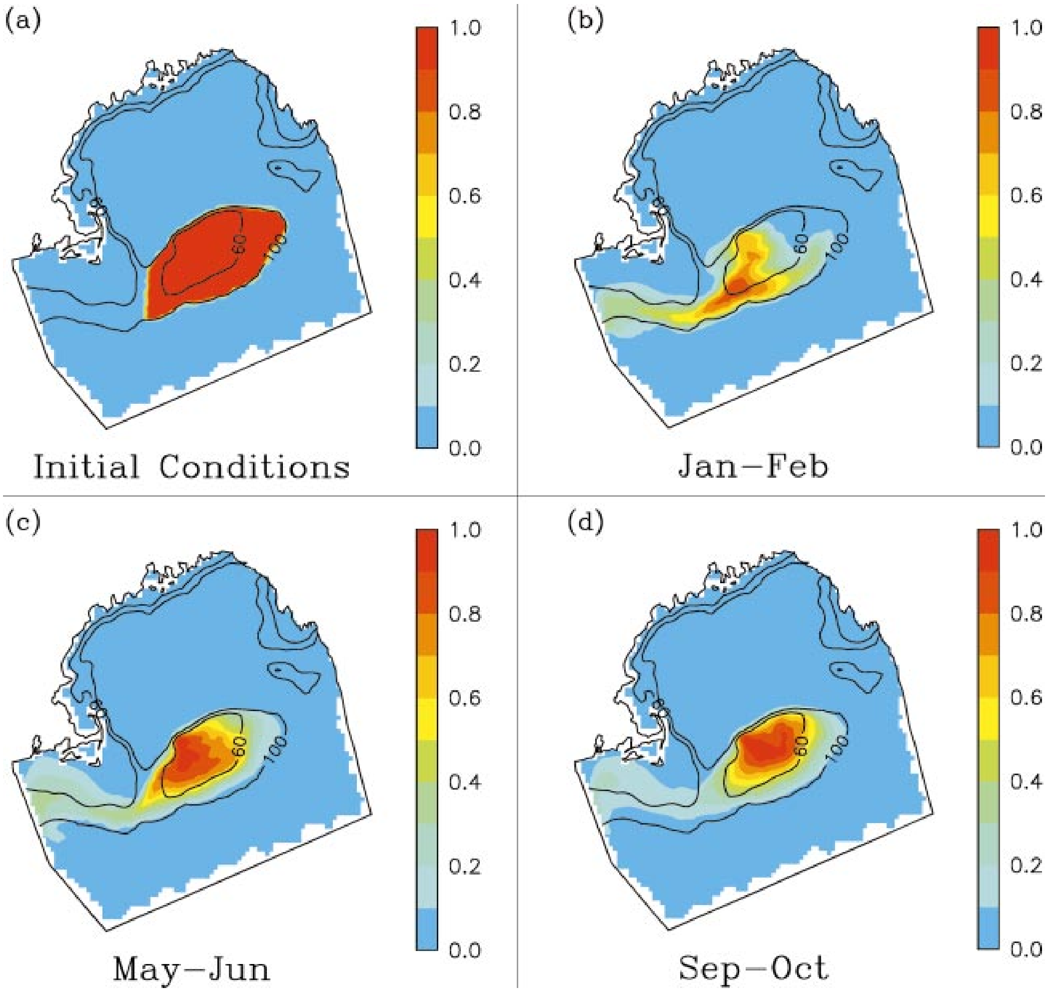
Figure 4. Georges Bank control volume experiments. (a) Initial conditions, in which the concentration is set to 1.0 on the bank, and 0.0 elsewhere. The boundaries of Georges Bank are defined to be the 100 m isobath and 69°W meridian. (b–d) Results after 2 months of integration using climatological transport fields for January–February, May–June and September–October, respectively.



the northern flank, such that much of the north-east quadrant of the bank has been completely diluted by the end of 2 months. The main exit pathway is in the strong south-westward flow across the southern portion of the Great South Channel, which then turns westward, guided by the bathymetry. During the period of integration, significant tracer mass transits this pathway all the way to the western boundary where it exits the model domain. Seasonal development of stratification strengthens the clockwise circulation around the bank in May–June, reducing exchange with surrounding water masses. This is clearly evident in the vastly diminished on-bank transport across the northern flank, and to a somewhat lesser extent in the south-western exit pathway. The net effect is to make the Georges Bank system much more retentive. This characteristic reaches its peak with the stratification in September–October. The centre of mass in the tracer distribution stays centred on the bank, rather than being shifted to the south-west as in previous cases. Thus, seasonal variations in circulation have substantial ramifications in terms of the transport of organisms into and out of this area. These solutions are consistent with analysis of the circulation features themselves, conducted by Naimie (1996).

Biological observations

Pseudocalanus is a calanoid copepod which inhabits a wide variety of boreal and temperate environments. Its distribution and life history characteristics have been reviewed extensively by Corkett and McLaren (1978). Laboratory rearing experiments document

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temperature-dependent development times ranging from 2 weeks to 2 months (McLaren *et al.*, 1989). A preferred prey item for larval cod and haddock, *Pseudocalanus* is one of the most abundant (in terms of number per unit volume) zooplankton on Georges Bank and in the Gulf of Maine (Davis, 1987).

Eleven years of sampling in the MARMAP programme provide a substantial database from which to derive climatological biological distributions in this region (Sherman, 1980; Sherman *et al.*, 1988, 1996). Extensive overviews of seasonal patterns derived from these data have been presented for *Calanus finmarchicus* (Meise and O'Reilly, 1996), invertebrate predators of zooplankton (Sullivan and Meise, 1996) and chlorophyll *a* (O'Reilly and Zetlin, 1996). Bimonthly abundance data for the adult stage of *Pseudocalanus* spp. were binned onto the same tiles used in the Meise and O'Reilly (1996) analysis, and then objectively analysed using the OAX software package (see http://www.tuns.ca/~hey/ocean/oview. html).

The resulting abundance patterns for the six bimonthly periods are shown in the top row of Fig. 5. Although *Pseudocalanus* spp. concentration is mapped throughout the entire model domain, interpretation must be confined to the subregion in which data are present (Fig. 3). Elsewhere, the concentration is simply an extrapolation based on the objective analysis. In the January–February period, there are two population centres within the region of interest: one in the coastal waters of the western Gulf of Main (from here forward, 'western Gulf of Maine" refers specifically to the coastal waters therein) from Casco Bay extending southward into Massachusetts and Cape Cod Bays, and one on the crest of Georges Bank. Between January–February and March–April, abundance increases in both areas. The western Gulf population, previously confined to waters landward of the 100 m isobath, begins to extend into the interior of the Gulf of Maine, impinging on the western portion of Wilkinson Basin. The Georges Bank population has expanded significantly, with highest concentrations still on the crest. These trends continue through the May–June period, when abundance reaches its annual maximum in both areas. Highest concentrations in the western Gulf are still located within Massachusetts and Cape Cod Bays, yet significant numbers of organisms are present all the way to the Bay of Fundy. Between May–June and July–August, abundance begins to decline. The overall pattern is quite similar to the preceding period, but the peak concentrations within the population centres is reduced significantly. The downward trend continues to September–October. During this time, the decline in the Georges Bank population appears to have accelerated to the point that a population centre is no longer visible on the crest of the bank. This trend ceases in November–December, when concentrations stabilize on the crest of Georges Bank, as well as in Massachusetts and Cape Cod Bays.

It is important to point out that these distributional patterns may not reflect a single species. On the basis of molecular genetic techniques, Bucklin *et al.* (1998) document the relative abundance patterns of the two species of *Pseudocalanus* inhabiting this region (*P. moultoni* and *P. newmani*). Furthermore, they suggest the two could differ in important aspects of their ecology (e.g. distribution and reproductive timing) despite their morphological similarity. Unfortunately the MARMAP data do not resolve *Pseudocalanus* distributions to species level, so for the purposes of this study, the two species will be considered functionally equivalent. Species-specific investigations of this general type will be the subject of future research.

An adjoint data-assimilation technique

The coupled problem is formulated in terms of the 2-D advection–diffusion–reaction equation for the positive definite depth-averaged copepod concentration $C\ (x,\ y,\ t)$:

$$\frac{\partial C}{\partial t} + \mathbf{v} \cdot \nabla C - \frac{1}{H} \nabla \cdot (HK\nabla C) = R(x, y), \qquad (1)$$

where $\mathbf{v}$ is the velocity, K the diffusivity, and H is the bottom depth. The reaction term $R(x,\ y)$ represents a highly idealized parameterization of population dynamics which varies in space only. Positive R implies net growth, while negative R implies net mortality.

A cost function J is defined which is a measure of the misfit between predicted and observed concentrations C_{obs}:

$$J = \int_{-L_x}^{L_x} \int_{-L_y}^{L_y} \int_{t_0}^{t_1} \delta_{\mathrm{M}} (C - C_{\mathrm{obs}})^2 \, dx dy dt, \qquad (2)$$

where L_x and L_y define the extent of the domain of interest, and δ_{M} is a measurement functional which is equal to 1 where observations exist in space-time and 0 elsewhere.

The variational problem of interest here is: given initial conditions $C_{\mathrm{obs}}\ (t_0)$, find $R(x,\ y)$ which minimizes the cost function at time t_1 when the next set of observations $C_{\mathrm{obs}}\ (t_1)$ is available, subject to the constraint that the forward model equations are obeyed. That is, we seek to invert for the population dynamics implied by the observed changes in abundance together with the transport imposed by the circulation. Satisfactory solution of this problem will yield an $R(x, y)$ such that a model initialized with the observations from one period and integrated forward in time will come as close as possible to the distribution observed in the subsequent period. This can be articulated as the minimization of a Lagrange function $\mathscr{L}$ given by:

$$\mathscr{L} = J + \int_{-L_x}^{L_x} \int_{-L_y}^{L_y} \int_{t_0}^{t_1} \lambda \left(\frac{\partial C}{\partial t} + \mathbf{v} \cdot \nabla C - \frac{1}{H} \nabla \cdot (HK\nabla C) - R \right) dxdydt, \quad (3)$$

where $\lambda = \lambda(x, y, t)$ are unknown Lagrange multipliers. We require R that minimizes $\mathscr{L}$ (and hence J) at which point $\partial\mathscr{L}/\partial C = \partial\mathscr{L}/\partial R = \partial\mathscr{L}/\partial\lambda = 0$. Introducing small perturbations to $\mathscr{L}, C$ and R into the Lagrange function facilitates derivation of the adjoint model, which turns out to be:

$$-\frac{\partial \lambda}{\partial t} - \nabla \cdot (\lambda \mathbf{v}) - \frac{1}{H} \nabla \cdot (HK\nabla\lambda) = -2\delta_{\mathrm{M}}(C - C_{\mathrm{obs}}) \quad (4)$$

subject to homogeneous boundary conditions. Dynamically analogous to the forward model, the adjoint system is an advection–diffusion–reaction equation for the Lagrange multipliers forced by the misfit between modelled and observed values of C. It can be shown that:

$$\frac{\partial J}{\partial R(x,y)} = \int_{t_0}^{t_1} \lambda(x,y,t)dt. \quad (5)$$

Thus the gradient of the cost function with respect to the control variable R can be evaluated through integration of the adjoint model. This provides the basis for an iterative assimilation procedure which consists of the following steps.

1 Starting from some initial guess of R (e.g. $R = 0$), integrate the model equation forward in time and evaluate the cost function J which is a measure of the misfit between the model and observations.
2 Integrate the adjoint model backward in time (forced by differences in predicted and observed concentrations) to evaluate the gradient of the cost function with respect to the unknown biological reaction term R.
3 Having determined J and $\partial J/\partial R$, we need to choose perturbations to the reaction term δR which will minimise J in the direction defined by $\partial J/\partial R$. The value of δR is determined using the method of steepest descent, and the optimal step size can be computed via an additional integration of the forward model as in Derber (1985).
4 By repeating steps (1)–(3) we can iteratively converge on the values of $R(x, y)$ that minimize the cost function, thus providing the best fit to the observations of C at t_0 and t_1, subject to the constraint that the forward model equation is satisfied exactly.

It has been asserted that the efficacy of iterative assimilation schemes such as this can be compromised if the computational effort characteristics of the forward and adjoint models are not consistent. Thus it is prudent to construct the adjoint of the discrete representation of the forward model rather than to discretize the continuous from of the adjoint. Fortunately this task can be reduced to a set of relatively simple recipes for which automated software has been developed to produce the adjoint of the discrete model directly from the forward model source code (Giering and Kaminski, 1996). A straightforward test of the resultant code is provided by the fact that for linear models, the adjoint operator is simply the transpose of the forward model operator. It is a simple matter to construct the $N \times N$ matrix operators for the forward and adjoint systems in an idealized case of reduced dimension by perturbing the N state variables one at a time and taking one time step with each. The results of this exercise were used to verify that the transpose relationship exists to within round-off error, thereby validating the adjoint model.

RESULTS

This investigation of the climatological mean seasonal cycle of *Pseudocalanus* spp. abundance consists of six separate 2 month cases. In each assimilation experiment, initial conditions from a particular period are specified, and $R(x, y)$ is sought such that integration of the forward model will fit observations from the subsequent period. The procedure converges rapidly in the first 10 iterations, and by the 50th iteration the cost function (normalized to the initial value in each case) has been reduced by approximately an order of magnitude (Fig. 6). Although it is not possible to demonstrate *a priori* that the assimilation procedure results in a global minimum of the Lagrange function, the existence of local minima can be investigated by starting from different initial guesses of the control variables. A suit of additional experiments was conducted using different random distributions to initialize R, and each case converged on the same solution.

Figure 5. Top row: bimonthly climatological *Pseudocalanus* spp. distributions (adults only) derived from the MARMAP data (number of animals m^{-3}). Second row: source terms $R(x, y)$ resulting from each of the six inversions. Each $R(x, y)$ is located directly below the observations used to initialize the experiment. That is, the JF–MA source term results in a forward model integration which matches the March–April observations. Third to fifth rows: the remaining terms in the ADR equation averaged over the period of integration: advective flux divergence, diffusive flux divergence, and overall tendency. Fields in the bottom four rows have been normalized to the bottom depth, so the units are number of animals $m^{-4}\ s^{-1}$. The sign convention is such that the overall tendency equals the sum of advection, diffusion and source terms.

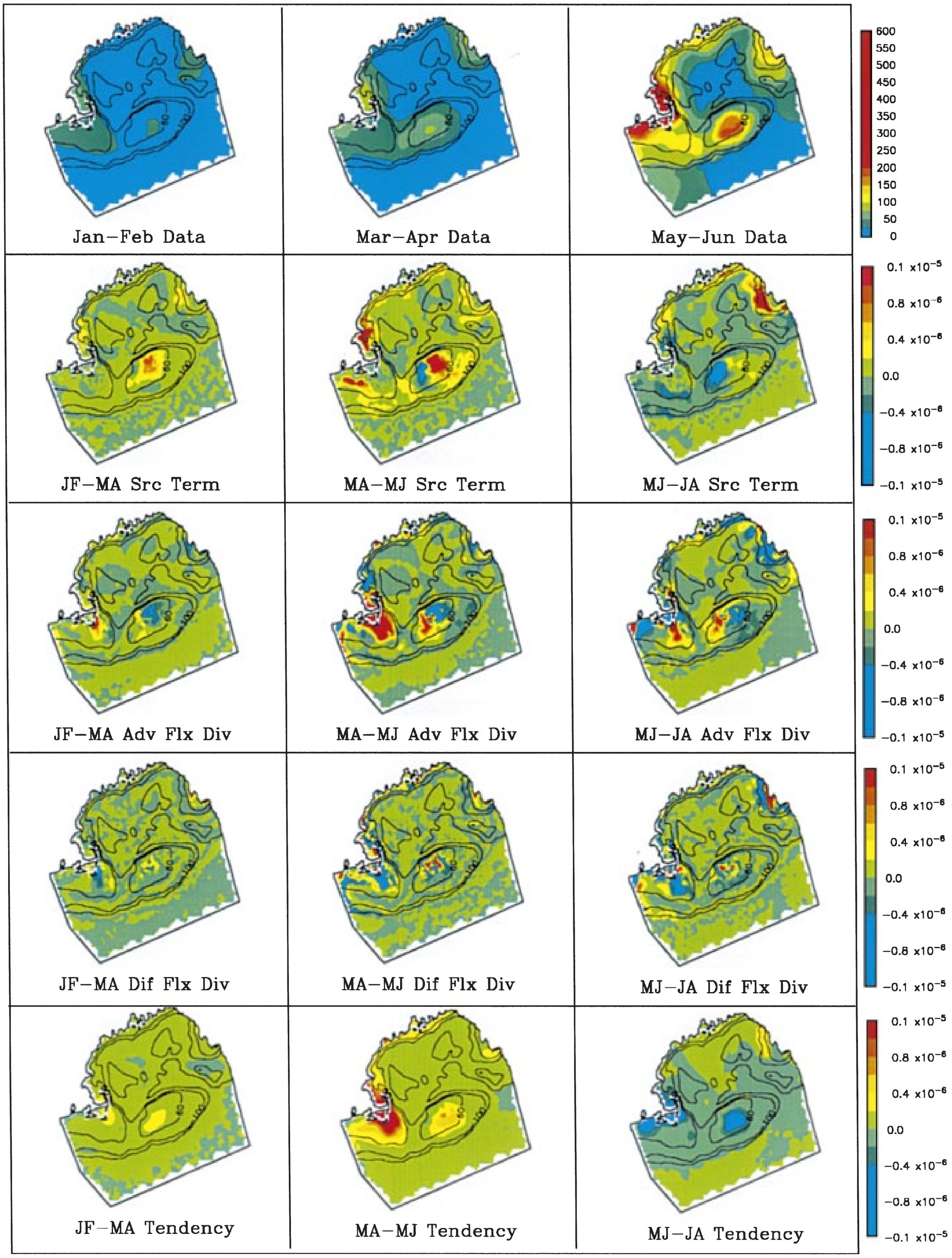

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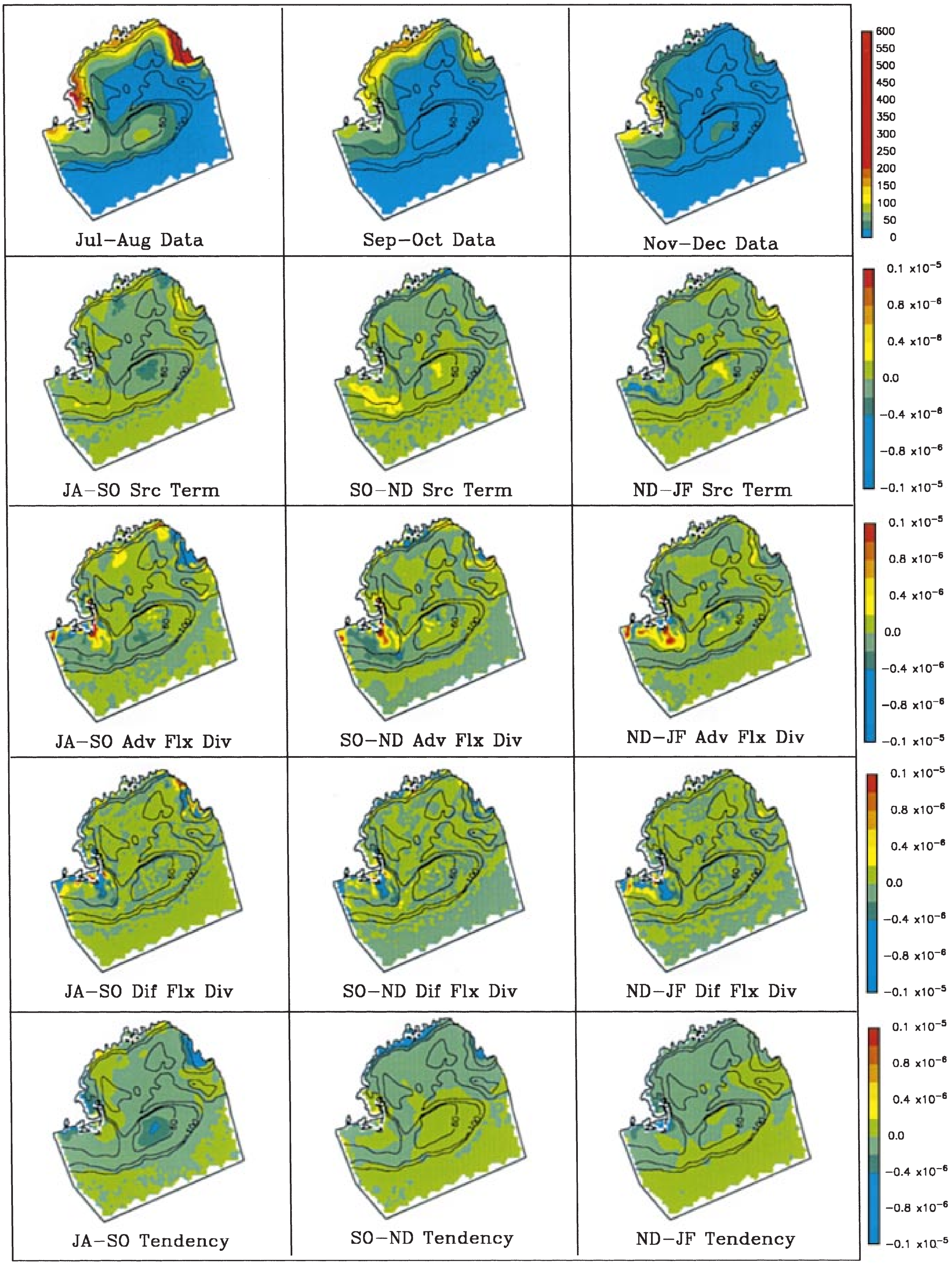
Figure 5. (*continued*)



This, together with the fact that the resulting forward model predictions are nearly identical to the data, attests to satisfactory solution of the minimization problem.

The results of the inversions are shown in Fig. 5. Observations are plotted in the top row. Corresponding source term maps are located directly below the observations used to initialize each experiment (e.g.

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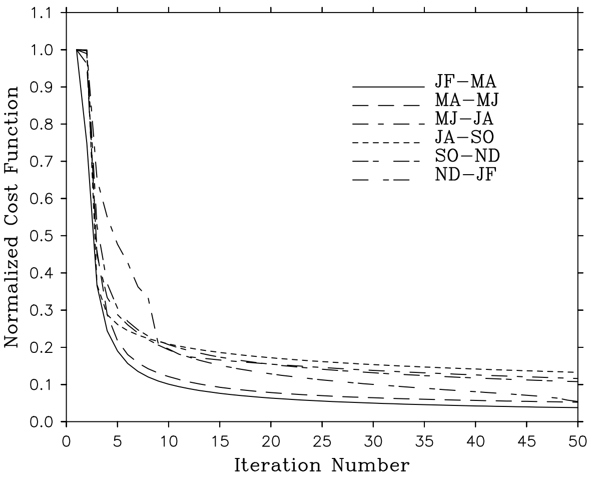
Figure 6. Cost function for each iteration of the six assimilation experiments normalized to the initial value in each case.



the source term below January–February is that which results in a forward model integration which matches the March–April data). Results of the final forward model integrations are not displayed here because they so closely resemble the observations. Also included in each column are maps of the remaining terms in the ADR equation, averaged over the period of integration. The sign convention is such that the mean tendency is equal to the sum of advection, diffusion and source terms.

January–February to March–April

From January–February to March–April, the source term consists of strong growth (red shading) on the crest of the bank and moderate growth (yellow shading) in a coastal strip just offshore of Cape Ann. In the latter location, physical transport has little impact, resulting in a modest accumulation of animals in an area coincident with the patch of local growth. Note that this accumulation is clearly evident in the data, but is obscured by the shading used in the tendency maps. The situation on Georges Bank is quite different, where a balance exists between the advection and source terms. Flow onto the crest across the northern flank of the bank (clearly shown in the control volume experiments) imports low concentrations of animals from the interior of the Gulf of Maine. This results in a strong negative contribution from the divergence of the advective flux. Similar in pattern, of opposite sign, and stronger in magnitude, the source term overshadows advection such that the tendency is for concentration on the bank to increase. Notice that the peak in the source term is slightly 'upstream' of the resulting maximum in animal abundance.

March–April to May–June

During the March–April to May–June period, the net growth along the coast east of Cape Ann intensifies. This is partially balanced by advective and diffusive flux divergences. In particular, the pattern of advection is organized into an area of loss north of Cape Cod Bay and gain within it. The overall tendency for net growth throughout this area can thus be interpreted as a moderate source in the vicinity of Cape Ann which feeds accumulation in Massachusetts and Cape Cod Bays via transport by the coastal current following through these bays in late spring (Lynch *et al.*, 1997).

The source term on the crest of the bank consists of a dipole structure during this interval. As in the January–February to March–April situation, advection of low concentration water from the interior of the Gulf of Maine onto the crest of the bank is balanced by net growth in the region of inflow. However, in contrast to the previous period, there is a significant flux of organisms advected from the crest toward the Great South Channel driven by the south-westward current present at that time (Fig. 4). This positive advective contribution on the south-western quadrant of the crest is balanced by net mortality in the source term. The divergence of the diffusive flux, although stronger than in the previous period, is not organized with respect to the main features of the animal distribution. Diffusion therefore does not appear to have a systematic effect other than to smooth out the peaks in concentration. Again, the overall balance of terms leads to significant accumulation of organisms on the crest of the bank.

May–June to July–August

The general trend in *Pseudocalanus* spp. abundance reverses in May–June to July–August, such that its abundance decreases substantially on the crest of Georges Bank. This tendency is created by a two-component process: south-westward advection of the population centre on the crest in combination with net mortality on its south-western flank. Note that the northern extent of the area of advective dilution is no longer coincident with the north flank of the bank, which was the primary inflow location during the winter months. Summertime stratification reinforces the clockwise circulation around the bank, resulting in strong along-isobath flow which is particularly intense on the north flank. Evidence of this newly imposed isolation from the Gulf of Maine can be seen in the tendril of positive advective flux divergence along the northern edge of the crest: the high concentration of animals present in the north-west quadrant of the crest is being swept east-northeast by the current. The large area of positive advective flux divergence on the western half of the crest (caused by net south-westward transport of the population centre) is overshadowed by net mortality in that region. The aggregate impact of these complex patterns is to induce a significant decrease in the peak animal concentration on the crest of the bank.

There is little change in the western Gulf population during this time period.

July–August to September–October

In late summer, seasonal stratification causes a peak in the clockwise flow around Georges Bank, thereby maximizing its retentive character. The decrease in abundance during this time period is therefore largely controlled by the source term in an area of net mortality on the crest. However, a weak dipole pattern in the advective flux divergence serves to displace the centroid of negative tendency slightly toward the south-west.

Generally speaking, the population in the western Gulf of Maine decreases slightly during this time period. Although the signals are weak, it appears this decline in abundance is a result of net mortality just south of Cape Ann in combination with advection of low-concentration water southward into Cape Cod Bay.

September–October to November–December to January–February

During the period from September–October to November–December, the downward trend in abundance characteristic of the prior two bimonthly periods reverses. A small population centre is maintained on the crest of the bank through a balance between local growth and advective loss. This situation persists in a similar balance of terms through January–February.

In the western Gulf of Maine, the decrease in *Pseudocalanus* spp. concentration which began in July–August to September–October, accelerates somewhat. The decline begins in earnest in the coastal waters to the north of Cape Ann during September–October to November–December. Subsequently, it continues more toward the south in November–December to January–February, such that significant concentrations are present only in Massachusetts and Cape Cod Bays by the end of this period. The population appears to be maintained by a small area of net growth just south-east of Cape Ann.

DISCUSSION

Climatological abundance patterns of *Pseudocalanus* spp. in the Georges Bank–Gulf of Maine Region derived from the MARMAP data exhibit strong seasonal signals with significant geographic variation. Two population centres reside in the region, one on Georges Bank and the other in the western Gulf of Maine. Generally speaking, their temporal evolution is synchronous and consists of three phases: a ‘growing season’ from January–February to May–June, a period of decline from May–June through to September–October, and a relatively stable interval from September–October to January–February.

Numerical experiments using the vertically integrated advection–diffusion–reaction equation show that these tendencies are primarily controlled by a balance between advection and source terms. Both of these contributions include strong seasonal variations. During the first part of the growing season (January–February to March–April), growth on the crest of Georges Bank barely overcomes the dilution caused by southward flow of Gulf of Maine water across the northern flank. As the bank becomes more isolated from the surrounding waters by intensification of the clockwise circulation resulting from seasonal baroclinic effects, this influx has less effect. However, south-westward advection persists across the crest, causing the displacement of the population centre in that direction. An increasing population centred on the crest thus requires net growth in the north-east quadrant and net mortality in the south-west, in order to counterbalance advective effects. In other words, growth is required slightly upstream of the area where the animals are observed, and mortality is needed slightly upstream of where they are not.

When the population begins its decline (May–June to July–August), the advective contribution to the balance on Georges Bank remains much the same. So too does the mortality component of the source term; however, net growth no longer takes place in the north-east quadrant of the crest. Thus the initial decrease in abundance on the crest results from a combination of advection and mortality. Later in the period of decline (July–August to September–October), the around-bank circulation reaches its maximum, which serves to increase retention of organisms on the bank. This reduces the role of advection, and the decrease in the population on the crest is largely controlled by net mortality. This scenario is consistent with the idea of predatory control set forth by Davis (1984c).

The period of population maintenance on the bank (September–October to January–February) is characterized by a balance of weak contributions from both advection and source terms. Growth on the crest is just sufficient to compensate for dispersal by the currents. This results in a stable pattern of relatively low abundance during these 4 months.

For the most part, advection plays less of a role in the dynamics of the western Gulf of Maine population centre. In general, changes in abundance are driven directly by local growth or mortality in the source term. A notable exception occurs during the March–April to May–June period, when the spring freshet intensifies the southward-flowing coastal current in this region (Fong *et al.*, 1997; Lynch *et al.*, 1997). During this time, strong southward advection is evident from the waters east of Cape Ann down into Cape Cod and Massachusetts Bays, as well as the coastal waters east of Cape Cod. Accumulation of organisms throughout this area is thus a result of strong growth east of Cape Ann and southward transport of animals by the coastal current.

Considering interpretation of the source term, some aspects of the population dynamics are attributable to reasonable ecological factors, while others remain problematic. For example, these results seem compatible with what is known about the influence of food availability of this animal. Laboratory rearing experiments conducted by Davis (1984a) document a threshold for food limitation in the survival of *Pseudocalanus* spp. between 0.6 and 1.2 mg chl a m^{-3}. Given these parameters, analysis of the MARMAP chlorophyll data (O'Reilly and Zetlin, 1996) reveals that from a climatological point of view, food concentration is always limiting in the interior of the Gulf of Maine, never limiting on Georges Bank, and sometimes limiting in the coastal waters of the western Gulf of Maine (only during the late summer). The numerical solutions presented here are thus consistent in that growth in never predicted in situations where food concentrations are limiting. However, it is important to point out that in food-saturated conditions, (1) net growth does not always occur, and (2) net mortality is often present.

These findings therefore suggest significant predatory influence on the two main population centres. Climatological distributions of invertebrate predators of zooplankton have been compiled by Sullivan and Meise (1996) using the MARMAP data. Their analysis shows that the most numerically abundant potential consumers of *Pseudocalanus* spp. are chaetognaths in the case of Georges Bank and euphausiids in the coastal waters of the western Gulf of Maine. It is interesting to note that the period of decline of *Pseudocalanus* spp. on Georges Bank (May–June to September–October) overlaps the time during which chaetognath abundance is at its maximum. However, there is little evidence in the chaetognath distributions themselves which would suggest higher predation on the south-western quadrant of the crest, which is a persistent feature of the solutions during the period of decline. The relationship between euphausiid abundance and trends in *Pseudocalanus* spp. in the western Gulf of Maine is even less clear. The highest concentration of euphausiids in this area actually occurs during the middle of the *Pseudocalanus* spp. growing season. However, the lack of rate information coincident with the distributional data makes inference of grazing pressure based on predator abundance patterns difficult.

CONCLUSIONS

Inversion of the vertically integrated advection–diffusion–reaction equation has revealed geographically specific patterns in the population dynamics of *Pseudocalanus* spp. in the Georges Bank–Gulf of Maine region. These spatial patterns vary seasonally according to the animal distributions, the climatological currents, and their orientation with respect to each other. In cases when the flow is either weak or aligned with gradients in organism abundance, changes in concentration over time are dominated by local population dynamics. In situations where the currents are normal to these gradients, complex three-way balances arise between the local tendency, advective transport, and the population dynamics source term. Diffusion does not appear to play a major role in these simulations. With some notable exceptions, the inferred population dynamics appears generally consistent with what is known about ecological controls such as food limitation and predatory consumption. However, it is important to point out that current knowledge of these aspects, particularly the latter, is incomplete.

Based on this analysis, it is possible to distill a conceptual model of the oceanographic ecology of *Pseudocalanus* spp. in this region. The scenario that emerges consists of two self-sustaining populations in the western Gulf of Maine and Georges Bank, separated by a stretch of ocean in which food concentrations are too low for the organism to thrive. This working hypothesis of separate populations is consistent with a cluster analysis of the MARMAP *Pseudocalanus* spp. data (Meise *et al.*, unpublished data, 1995). However, it differs from that suggested by the population dynamics model of Davis (1984b, 1987) in which the Gulf of Maine provided a source of low concentrations of adult females to Georges Bank.

There are three important caveats to the interpretation of the resulting patterns in population dynamics. First of all, it is possible that the solutions obtained here are sensitive to the formulation of the coupled problem. For example, the 'geographic' specification of the source term $R(x, y)$ used here, which varies only as a function of space, is not necessarily the most appropriate representation of the underlying biological processes. However, preliminary results using a density-dependent formulation in which the population dynamics is expressed as the product $R(x, y)\ C(x, y, t)$ do not appear to be drastically different with respect to the overall conclusions. Nevertheless, a more sophisticated treatment of the population dynamics is clearly warranted, and is a central focus of future research. Application of the density-dependent term represents a first step toward more complex formulations, which will eventually include multiple life stages and explicit inclusion of behaviour. Equally important is the need to recognize that the data are imperfect, and to relax the strong conditions on model–data agreement (both initial and terminal conditions). This will require knowledge of the covariance structure of these errors and that of the population dynamics themselves, within a more general weighted least-squares approach.

Secondly, it is possible that aspects of the resulting population dynamics could represent deficiencies in the physical model rather than biological processes. If changes in animal abundance were incompatible with the prescribed circulation, the inversion technique used here would make up for that discrepancy by inventing the necessary $R(x, y)$. However, the most salient characteristics of the solutions presented here are associated with robust features of the circulation that are well documented in the literature. This is not to say that the vertically integrated transport model used here is completely sufficient, especially in stratified conditions. Furthermore, the potential for non-linear impacts of time-dependent flows (such as storm events) on the mean behaviour of the system remains to be investigated. Explicit treatment of these effects is another priority in this ongoing effort.

Finally, it is important to note that this analysis is based solely on a genus-level distribution of adults. Because the younger stages of *Pseudocalanus* spp. were not sampled by the MARMAP protocols, their abundance patterns are not available to constrain spatial and temporal variations in the population dynamics. There is at least one scenario which could compromise the interpretation of separate populations presented here: if the transit between the western Gulf of Maine and Georges Bank population centres were made by non-feeding early stages of the animal. Also, the possible effects arising from differences in autecological characteristics between the two species cannot be discounted.

Newly emerging data sets and assimilation methodologies may help sort out these issues. Monthly stage-based distribution patterns of *Pseudocalanus* spp. are being measured routinely in the broadscale survey component of the US Globec Georges Bank programme. In addition, population genetics are being used to refine these distributions down to the species level (Bucklin *et al.*, 1998). Incorporation of these data into realistic circulation hindcasts which can now be constructed for specific time periods (Lynch *et al.*, 1998) will facilitate direct analysis of quasi-synoptic snapshots of animal abundance. Synthesis of such observations through both forward and inverse modelling techniques should lead to a better understanding of the controls on spatial and temporal fluctuations of *Pseudocalanus* abundance in this region.

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