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# Transport and retention of dormant copepods in the Gulf of Maine

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## Abstract

Variability in the availability of dormant copepods to seed productive shelf areas has been hypothesized to influence the abundance of the dominant copepod species *Calanus finmarchicus* in several regions of the North Atlantic. One source of this variability is advection of dormant copepods in deep water. Using Lagrangian particle simulations, we examined the influence of environmental forcing and copepod behavior on transport and retention of dormant *C. finmarchicus* in the deep Gulf of Maine, in the northwestern Atlantic. Retention in the Gulf of Maine was relatively high, >40% over 6 months, under all conditions simulated. Transport within the Gulf of Maine was high, resulting in shifts of eastern copepods into the western Gulf and of upstream copepods, from slope and Scotian Shelf waters, into the eastern Gulf. Copepod behavior during dormancy was a major source of uncertainty, but it is probably not a major source of interannual variability in retention. Retention increased with the initial depth of dormant copepods, and vertical positioning behavior had a strong influence on retention for simulations started at depths greater than 150 m, because copepods that can stay below basin sill depths are retained. Mean cross-shore winds reduced retention slightly (<2% absolute difference), and mean alongshore winds increased retention by 4–8%. Wind-driven interannual variability in retention was low. Variability in Scotian Shelf inflow had a greater influence on retention than did variability in winds, and inflow-driven changes in retention may contribute to interannual variability in copepod abundance associated with changes in deep-water temperature. However, estimates of advective loss are relatively low compared to measured reductions in dormant copepod abundance, and mortality is probably a major factor in this reduction.

*Keywords:* *Calanus finmarchicus*; Copepod; Dormancy; Diapause; Gulf of Maine; Interannual variability; Zooplankton

## 1. Introduction

Quantifying transport of zooplankton is a key element in understanding the zooplankton population dynamics observed in continental shelf regions, and thus understanding the factors that control zooplankton availability as prey for fish and as grazers of phytoplankton. Marine zooplankton have geographical ranges that can span thousands of kilometers, and even the largest zooplankton sampling programs can typically only cover a small fraction of the range of target species. Efforts to understand and model zooplankton population

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dynamics must consider immigration and emigration in addition to reproduction, growth, and mortality. Coupled physical–biological models have made significant progress in comparing the effects of advection and biological processes on near-surface zooplankton population dynamics in many regions, including the Gulf of Maine/Georges Bank region (e.g., Davis, 1984; Lynch et al., 1998; Miller et al., 1998; Werner et al., 2001). However, zooplankton behavior, particularly large-amplitude (100 s of m) seasonal vertical migrations associated with dormancy (i.e. suppressed development) in many dominant copepod species (e.g., *Calanus*, *Neocalanus*, and *Calanoides* species), can move plankton across vertical gradients of horizontal velocity and change the flow velocities to which zooplankton are exposed. Vertical migration associated with dormancy may decrease net advection out of regions favorable for growth and reproduction (Eiane et al., 1998; Johnson and Checkley, 2004; Peterson, 1998). In addition, interactions between behavior, deep flow, and bathymetry influence the horizontal distribution of individuals at emergence from dormancy (Osgood and Checkley, 1997a, b), and can influence the initial conditions for population growth in productive areas (Carlotti and Radach, 1996). In the present study, we use a Lagrangian particle-tracking approach to examine transport, retention, and sources of dormant copepods in deep water of the Gulf of Maine in the northwest Atlantic.

In the Gulf of Maine and Georges Bank region of the northwest Atlantic Ocean (Fig. 1), the copepod *Calanus finmarchicus* is a dominant zooplankton species and an important prey item for larval cod and haddock (Buckley and Lough, 1987; Kane, 1984). *C. finmarchicus* is most abundant in spring on Georges Bank, a productive submarine rise, but it largely disappears from Georges Bank in the fall and winter, when the population is dormant, primarily as fifth copepodid developmental stages, in deep water of the Gulf of Maine, continental slope, and Scotian Shelf basins (Davis, 1987; Meise and O'Reilly, 1996; Miller et al., 1991; Sameoto and Herman, 1990). The Gulf of Maine acts as a source of *C. finmarchicus* repopulating Georges Bank in

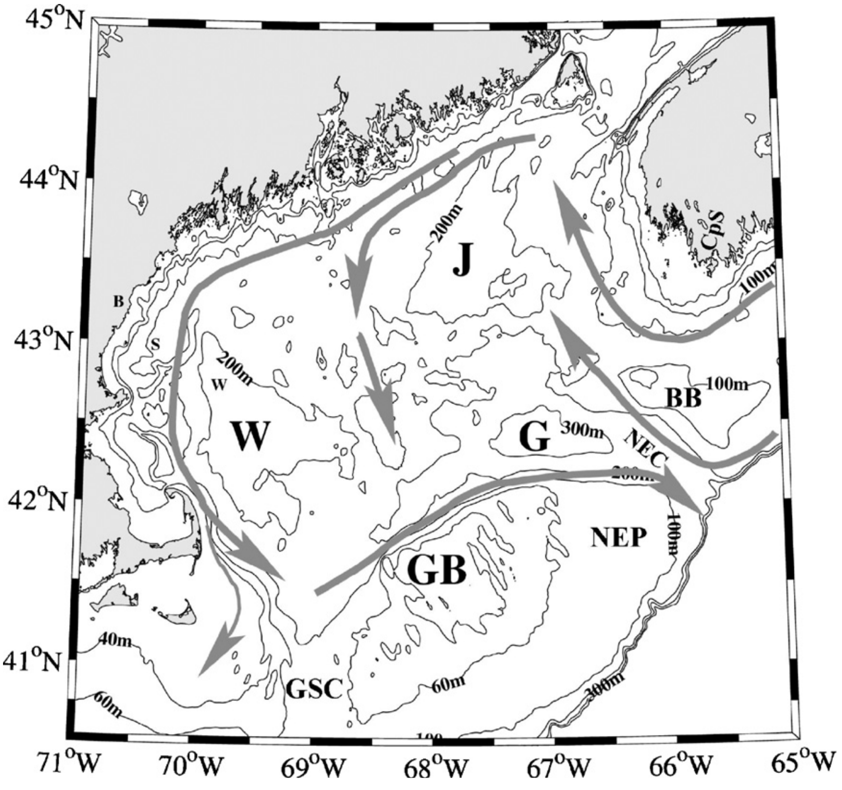

Fig. 1. Circulation in the deep Gulf of Maine. BB—Browns Bank, CpS—Cape Sable G—Georges Basin, GB—Georges Bank, GSC—Great South Channel, J—Jordan Basin, NEC—Northeast Channel, NEP—Northeast Peak, W—Wilkinson Basin.

late winter and spring (Bigelow, 1926; Gentleman, 1999; Hannah et al., 1998; Lynch et al., 1998). When *C. finmarchicus* begins to emerge from dormancy in late December in the deep basins of the Gulf of Maine, individuals molt to the adult stage and migrate to the surface, where they can be transported onto Georges Bank (Hannah et al., 1998; Lynch et al., 1998; Miller et al., 1998). In the Gulf of Maine, *C. finmarchicus* from the first generation to develop after dormancy (G1) begin to enter dormancy and migrate to deep water of the Gulf of Maine starting in May and June (Durbin et al., 2000). A second generation (G2) develops during the summer months, and a small fraction of the population may continue development and enter dormancy in the fall (Fish, 1936). Emergence from dormancy occurs primarily between late December and February; however, copepods also may emerge from dormancy at a low rate during the fall (Durbin et al., 2000).

Surface waters of the Gulf of Maine both supply the deep Gulf of Maine with *C. finmarchicus*, as described above, and in turn are supplied with *C. finmarchicus* from deep water (Figs. 1 and 2). Coupled biological–physical population modeling of *C. finmarchicus* in the Gulf of Maine suggests that endogenous copepods, i.e. offspring of copepods that emerged from dormancy locally, can restock Wilkinson Basin, in the western Gulf of Maine, while self-stocking is minimal at two other major Gulf of Maine basins, Georges Basin and Jordan Basin (Miller et al., 1998). However, retention of active *C. finmarchicus* in the eastern Gulf of Maine may be higher for copepods that stay below the surface Ekman layer (Hannah et al., 1998). The northern and eastern basins of the Gulf of Maine must be re-stocked from upstream sources, either by active *C. finmarchicus* entering the Gulf of Maine in surface waters and subsequently entering dormancy (Lynch et al., 1998), or entering the deep Gulf of Maine through deep channels (Figs. 1 and 2). Surface sources include the western Scotian Shelf and Scotian Slope waters; deep flow into the Gulf of Maine is primarily through the eastern side of the 230-m deep Northeast Channel from the continental slope waters and, to a more limited degree, from the Scotian Shelf through a 130-m deep channel inshore of Browns Bank (Smith et al., 2001). The primary pathways of deep water out of the Gulf of Maine are through the western Northeast Channel or over the Northeast Peak of Georges Bank and out over the southern flank of the bank (Hannah et al., 1998; Hopkins and Garfield, 1979; Smith et al., 2001).

The fate of dormant *C. finmarchicus* in the deep Gulf of Maine is uncertain. Previous transport simulations suggest that dormant *C. finmarchicus* at 175 m are retained in deep basins of the Gulf of Maine for at least 2 months of the approximately 6-month dormancy season (Gentleman, 1999). However, changes in copepod body size over the dormant season suggest that copepods entering dormancy in spring and early summer are removed from the Gulf of Maine, either by advection or mortality, and replaced with copepods that entered dormancy during warmer periods in surface water later in the year (Durbin et al., 2000; Wiebe et al., unpublished results).

The abundance of individuals emerging from dormancy and transported onto the shelf sets the initial conditions for production on the continental shelves in the late winter and spring (Carlotti and Radach, 1996; Slagstad and Tande, 1996). Interannual variability in the abundance of marine zooplankton populations appears to be linked to climatic variability in many regions of the North

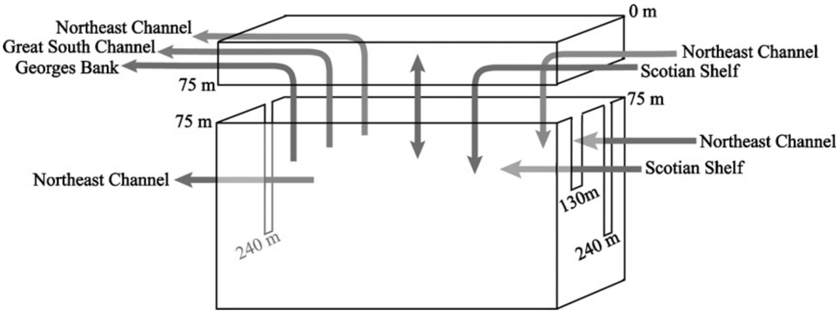

Fig. 2. Conceptual model of dormant copepod transport into and out of the deep Gulf of Maine.

Atlantic (e.g., Beaugrand, 2003; Conversi et al., 2001; Fromentin and Planque, 1996; Greene et al., 2003). Variability in the transport of deep-living, dormant *Calanus* to productive, continental shelf regions, driven remotely by variability in deep-water formation at high latitudes, has been hypothesized to influence the abundance of *Calanus* available to seed population growth on the shelves and to contribute to the observed link between the North Atlantic Oscillation and *Calanus* abundance in the northeast and northwest Atlantic (Greene and Pershing, 2000; Heath et al., 1999; MERCINA, 2001). In the present study, we examine the influence of advection on transport and retention of dormant *Calanus* in the Gulf of Maine, with the primary objective of determining whether dormant *C. finmarchicus* are retained in the Gulf of Maine long enough to seed population growth the following year. We focused on four main questions:

1. How long are dormant copepods retained in the Gulf of Maine, and how does this compare to the timescales of dormancy?
2. How much does uncertainty about copepod behavior influence estimates of retention, and how much can interannual variability in dormant-copepod vertical distribution influence retention?
3. How much does interannual variability in environmental forcing, specifically wind and upstream transport variability, influence retention?
4. How long are dormant copepods retained in individual basins, and what are the dominant sources and fates of copepods in the basins?

## 2. Methods

Copepod paths were simulated using Lagrangian particle tracking in the Finite Volume Coastal Ocean Model (FVCOM). FVCOM is an unstructured-grid, primitive-equation, hydrostatic, numerical model that has been shown to perform well in coastal applications (Chen et al., 2003). The model was initialized with monthly mean hydrographic fields using all available hydrographic data for the Gulf of Maine and Scotian Shelf from the Bedford Institute of Oceanography and National Ocean Data Center databases (Pringle, 2006). Tidal currents in FVCOM are driven by the M2 tide, the dominant tidal constituent in the Gulf of Maine/Georges Bank region. Copepod paths were calculated from tidal residual velocities obtained by tracking Lagrangian particles in the model after the model had been spun up to a quasi-steady-state circulation for a given forcing, as described by Hannah et al. (1998). Lagrangian particle velocities were calculated from the average of the tidal residual Lagrangian velocity calculated over each of four tidal cycles. This averaging reduces the influence of the weak temporal variability in the velocity fields on timescales other than the tidal timescales. The temporal evolution of the flow field was modeled by linearly interpolating the tidal residual velocity fields in time between months.

Copepod behavior associated with dormancy was simulated as a vertical velocity added to the vertical component of passive particle velocity. Only vertical velocity was used, because copepods are assumed to respond primarily to vertical gradients, and because copepod swimming ability is weak compared with horizontal current velocities. Behavior was broken into two components, a choice of initial depth distribution and depth-adjustment behavior during the period of dormancy. The initial depth simulates the depth to which copepods migrate at the onset of dormancy. The factors that control copepods' choice of depth at the onset of dormancy are not known. Typical depths occupied by dormant *C. finmarchicus* in slope waters of the western North Atlantic are greater than the maximum bottom depth of the Gulf of Maine (Miller et al., 1991; Wiebe et al., unpublished results). Dormant *C. finmarchicus* in slope waters also occupy lower-temperature water than dormant *C. finmarchicus* in the deep Gulf of Maine, where deep water is warmer than cold intermediate layer water (Wiebe et al., unpublished results; E.J.H. Head, unpubl. data). Initial particle depths in the simulations were set empirically based on vertical distribution data available for *C. finmarchicus* in the Gulf of Maine (Durbin et al., 1997; Wiebe et al., unpublished results). The vertical distribution of *C. finmarchicus* fifth copepodid stages, the primary developmental stage that enters dormancy in this area, is often bimodal in the Gulf of Maine in fall and winter, and the deep mode, assumed to be dormant, is typically distributed over a broad depth range from 75 m or slightly deeper to near the bottom. The depth of highest abundance in the deep mode is variable and shows no clear relationship with temperature, salinity, or density, but median depths of the deep mode are typically close to 150 m (Durbin et al., 1997; Wiebe et al., unpublished results).

Swimming behavior during dormancy is not understood and appears to vary among regions and/or seasons. Dormant copepods may either respond to mechanical disturbance with a jump (Miller et al., 1991) or be unresponsive to poking (Hirche, 1983), suggesting that, at least in some regions or time periods, active swimming is not used for depth-correction during dormancy. Body composition and resulting buoyancy control also influence the vertical distribution of dormant copepods (Campbell and Dower, 2003; Heath et al., 2004; Visser and Jónasdóttir, 1999). Copepod lipid content plays a key role in buoyancy control, but dormant copepods also appear to adjust their buoyancy on timescales of hours (Campbell, 2004). The behavioral parameters chosen for simulations were intended to encompass the broad range of uncertainty about behavior. Simulations were run at initial depths of 75, 100, 150, 200, and 250 m to evaluate retention over the depth range that dormant copepods are known to occupy. Two simple depth-adjustment behavior formulations, return to the initial depth after each time step and return to the initial density surface after each time step, were compared with simulations in which copepods were advected as passive particles with no behavior. In the passive particle simulations, the particles followed the path of the fluid, with no random vertical motion added. In FVCOM in the stratified interior of the Gulf of Maine, vertical mixing was weak, less than $10^{-4}\,\mathrm{m}^2\,\mathrm{s}^{-1}$, about an order of magnitude higher than observed values in well-stratified waters (Oakey, 1985; Oakey and Elliott, 1982). At this level of vertical mixing, passive particles would spread ±27 m (±1 s.d.) over 6 months, so adding random vertical motion to the simulations would have a relatively minor effect on estimates of retention. Depth-adjustment behavior would override the influence of vertical diffusivity on vertical position. In all simulations, particles whose trajectories intersected the bottom were moved vertically to a position slightly above the bottom.

Copepod tracks were forced by the surface winds and by inflow from the Scotian Shelf. Wind data were obtained from the NCEP climate reanalysis (Kalnay et al., 1996), and the statistics of the Scotian Shelf inflow were defined by Loder et al. (2003), cf. Pringle (2006). Winds were divided into alongshore and cross-shore components. The alongshore component corresponds to the Maine coast, 55° from north, and is the direction of maximum ocean response to winds in the Gulf of Maine (Greenberg et al., 1997). The particles were tracked in velocity fields formed by the linear superposition of model runs made with each forcing alone. This technique allowed the relative contribution of each source of variability to be distinguished and quantified, and was several orders of magnitude more efficient than running the model many times with all observed combinations of forcing. Comparison of model runs made with different forcing find that the flow field varies very nearly linearly with variations in wind stress and Scotian Shelf inflow (errors of less than 5% on timescale of a week). These errors are discussed in greater detail by Pringle (2006). However, this linearization misses the feedback between inflow, winds, and the internal density field of the model on timescales of weeks or longer. These interactions between the wind and Scotian Shelf inflow and the circulation driven by gradients in the density field are poorly understood, may not be linear, and are significant on timescales longer than several months (Pringle, 2006). On those timescales, inflow from Scotian Shelf and Slope and other large-scale forcings are probably dominant. These processes are not captured in the present generation of models because currently available data are insufficient. The implications of this uncertainty for estimating retention are discussed further below. Relationships between wind forcing and retention were tested using analysis of variance. One-tailed *t*-tests were used to test whether retention was enhanced or reduced in simulations with alongshore or cross-shore wind forcing compared to simulations forced by mean hydrography alone.

Characterization of retention in a region is sensitive both to the size of the region and the time period of interest. Here, retention was defined specifically for the biological questions addressed. To address the effect of behavior and environmental forcing on overall retention in the Gulf of Maine, retention was defined as the percentage of particles remaining in the Gulf of Maine (Fig. 3 legend, including Georges, Jordan, and Wilkinson basins and the Northeast Channel) for a given period. Retention of copepods entering dormancy after the first generation, second generation, and in the fall was estimated and compared by simulating particle pathways from May 1, July 1, and September 1, respectively, until January 1. The effect of initial depth, depth-correcting behavior, and wind and upstream transport variability were compared in simulations from July

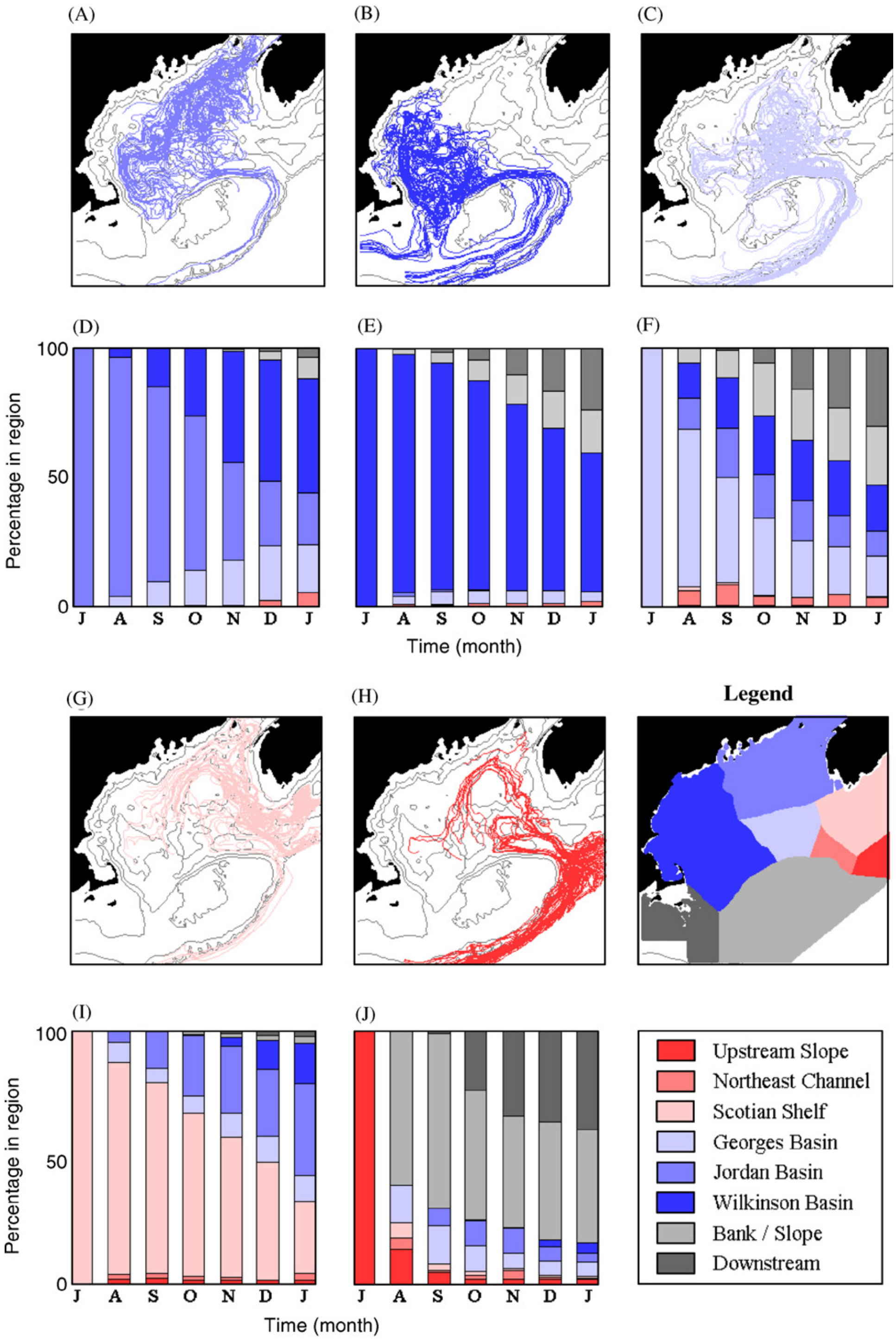

Fig. 3. Particle pathways and fates in and around the Gulf of Maine. Passive particles were seeded at 150 m in transport simulations forced by monthly mean hydrography and running from July 1 to January 1. Paths of 100 particles from each region are shown. Particle fates were plotted for the first day of each month.

1 until January 1. To evaluate the sources and fates of copepods, retention in sub-regions of the Gulf of Maine and upstream regions (Fig. 3) was defined as the percentage of particles remaining in a sub-region from July 1 until January 1. Table 1 summarizes the simulations presented here.

Table 1
Lagrangian particle simulations

| Forcing | Initial depth (m) | Depth-adjustment | Time period |
|---|---|---|---|
| Mean hydrography | 75, 100, 150, 200, 250 | Passive, depth-seeking, density-seeking | 1 July–1 January |
| Mean hydrography | 100, 150, 200 | Passive, depth-seeking | 1 May–1 January |
| Mean hydrography | 100, 150, 200 | Passive, depth-seeking | 1 September–1 January |
| Mean hydrography + alongshore wind (1990–2000) | 150 | Passive, depth-seeking, density-seeking | 1 July–1 January |
| Mean hydrography + crossshore wind (1990–2000) | 150 | Passive, depth-seeking, density-seeking | 1 July–1 January |
| Mean hydrography + Scotian Shelf inflow (1990–2000) | 150 | Passive, depth-seeking, density-seeking | 1 July–1 January |

## 3. Results

### 3.1. *Passive particle pathways in the deep Gulf of Maine*

Passive particles seeded in transport simulations at intermediate depths in the Gulf of Maine followed generally cyclonic pathways around the Gulf. Flow bifurcates in the northern Gulf of Maine, and particles either moved southwest toward Massachusetts Bay or southward across the central Gulf of Maine. The primary pathways of particles out of the Gulf of Maine were through the western Northeast Channel, across the Northeast Peak of Georges Bank, and through the Great South Channel. Particles seeded above and around the three deepest Gulf of Maine basins followed these general pathways, leading to distinct fates of particles from each basin. This is illustrated by the fates of passive particles seeded at an initial depth of 150 m, the median depth of dormant copepods in Gulf of Maine basins, on July 1 and tracked until January 1 (Fig. 3).

Particles seeded in the northeastern Gulf of Maine above and around Jordan Basin followed two main paths out of the sub-region, either west into Wilkinson Basin or south across the central Gulf of Maine into Georges Basin (Fig. 3A). Those that left the Gulf of Maine within 6 months followed two major pathways, either along the northern flank of Georges Bank and then across the Northeast Peak or through the Great South Channel via the Wilkinson Basin region. About five times as many particles from Jordan Basin left the Gulf of Maine via the Northeast Peak as left via the Great South Channel. It took approximately 4 months before passive particles seeded at 150 m in the Jordan Basin region began to leave the Gulf of Maine (Fig. 3D). Passive particles seeded at 150 m in and around Wilkinson Basin followed two main pathways out of the Gulf of Maine, either along the northern flank and across the Northeast Peak or through the Great South Channel (Fig. 3B), with about twice as many leaving via the Northeast Peak. Very few particles moved from Wilkinson Basin into the eastern half of the Gulf of Maine. The primary pathway of passive particles out of Georges Basin was through the western Northeast Channel and across the Northeast Peak of Georges Bank (Fig. 3C). Particles from Georges Basin also moved both into the Jordan Basin/northeast Gulf of Maine and into Wilkinson Basin during 6-month simulations.

Retention of passive particles in the Gulf of Maine as a whole was higher for particles seeded in and around Jordan Basin (88% over 6 months for passive particles started at 150 m on July 1) than for particles seeded in the Wilkinson (59%) or Georges Basin (47%) regions (Fig. 3D–F). This is probably because particles originating in Jordan Basin must travel the farthest before leaving the Gulf. The percentage of particles retained in and around Jordan Basin itself was low (20%), and many particles originating in this region moved into the Wilkinson Basin region (Fig. 3A) between July and January. Particle retention over 6 months in Georges Basin was similarly low, but in contrast to Jordan Basin, particles exported from the Georges Basin region mainly left the Gulf of Maine (Fig. 3F). Particle retention in the Wilkinson Basin itself was high, 54%, compared to the other basin regions and was nearly as high as retention of particles from this region in the Gulf of Maine as a whole (Fig. 3D).

Particles were transported into the deep Gulf of Maine from the Scotian Shelf and upstream slope waters. A relatively high percentage of passive particles (65%) seeded at 150 m on the western Scotian Shelf moved into the Gulf of Maine after 6 months, either moving directly into the Gulf of Maine or moving off the shelf into the slope water region and entering the Gulf of Maine through the Northeast Channel (Fig. 3G and H). Particles from the deep western Scotian Shelf moved primarily into the Jordan and Georges Basin region during the first 2 months of the simulation and were later transported from the Jordan Basin region into both the Wilkinson and Georges Basin regions. Particle retention was low in the slope water region upstream of the Northeast Channel, and nearly all passive particles seeded at 150 m left the upstream slope water region within 3 months (Fig. 3I and J). Particles seeded close to the slope were transported into the Gulf of Maine through the eastern side of the Northeast Channel and into the Georges Basin region. From Georges Basin, these particles either moved into the Jordan Basin region or were transported out of the Gulf of Maine through the western Northeast Channel.

### 3.2. Effects of behavior on retention and transport in the deep Gulf of Maine

Retention of simulated copepods in the deep Gulf of Maine over 6 months, from July 1 to January 1, ranged from 41%, for depth-seeking particles started at 75 m to 100%, for depth-seeking particles started at 250 m in simulations forced by monthly mean hydrography (Fig. 4). Both initial depth and depth-adjustment behavior influenced retention in simulations. Retention increased monotonically with initial depth in particles with depth-adjustment behavior. For passive particles, retention was highest for particles seeded at 200 m. Initial depth influenced retention of passive particles less than it influenced retention in depth-adjusting particles. The difference between the lowest and highest retention was 17% for passive particles, while the difference was 58–59% in particles with depth-correcting behavior (differences in retention are reported as the difference between the percent retained under each condition throughout this paper). Retention was similar for passive, depth-seeking, and density-seeking copepods that started at 75 and 100 m. At deeper initial depths, both depth-adjustment behaviors enhanced retention compared to passive behavior. This is probably because depth-adjustment behavior at greater initial depths allows particles to remain at depths near or below the sill depth of the Northeast Channel, decreasing their probability of transport out of the Gulf of Maine. The difference in retention between depth-adjusting and passive particles increased with initial depth to 42% in particles started at 250 m. Because loss of particles from the Gulf of Maine

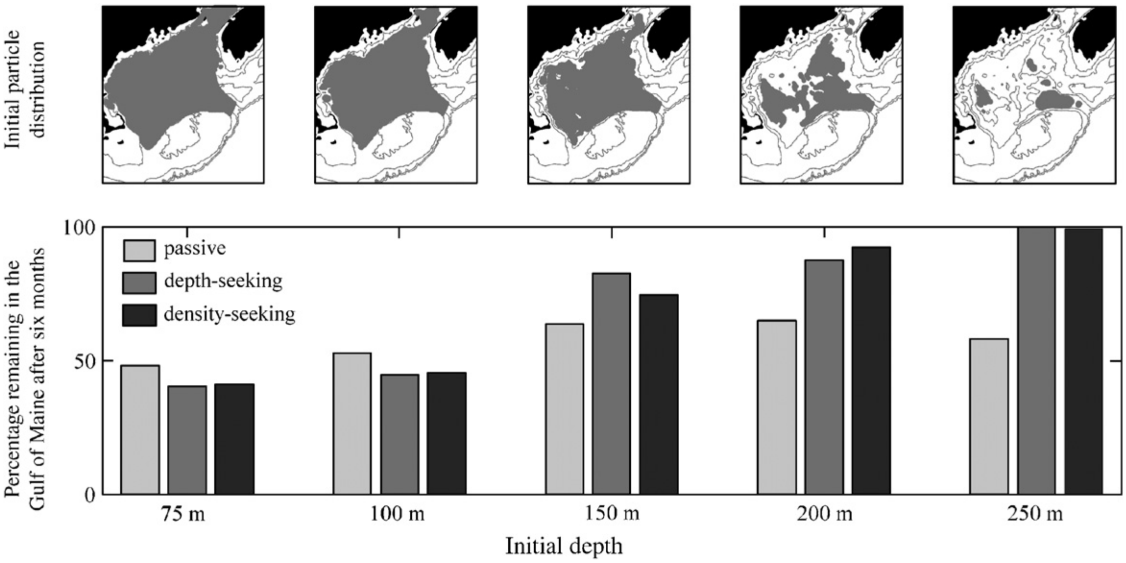

Fig. 4. Retention of deep particles in the Gulf of Maine after 6 months, July 1–January 1. Initial horizontal positions of particles are in upper row panels, above corresponding initial depth.

region is restricted to several distinct regions, retention is related to the initial particle distribution, which changes for different initial depths in the simulations (Fig. 4). Passive particle retention is probably highest at 200 m rather than at 250 m, in part because the mean distance of particles from the Northeast Channel is shortest when particles are seeded at 250 m. Passive particles, whose vertical distribution broadens over the course of the simulations, are thus more likely to be transported out of the Gulf of Maine when seeded at 250 m, while depth-adjusting particles remain below the sill depth and are retained, despite their proximity to the Northeast Channel.

The effect of the timing of onset of dormancy on retention was evaluated by estimating the retention of particles released on May 1, July 1, and September 1 and left to advect until January 1. Particles were seeded at 100, 150, and 200 m and were either passive or depth-seeking. In most simulations, retention of particles from the start date until January 1 increased as the period of dormancy decreased (Table 2). The greatest difference between retention of particles seeded in May and in September was 20%, for depth-seeking particles started at 100 m (Table 2). The difference between the retention of passive particles seeded in May and September was similar for all initial depths examined, ranging from 15% to 18% (Table 2). For depth-seeking particles seeded at 150 and 200 m, retention was slightly greater from May 1 to January 1 than for September 1 to January 1 (Table 2). This may be due to greater transport of these particles from Georges Basin to Jordan Basin, where retention of depth-seeking particles is very high, in May than in later months.

The fate of passive particles after six-month simulations was influenced less by their initial depth distribution than was the fate of depth-correcting particles. Passive particles seeded at 100, 150, and 200 m in upstream slope water and Georges, Jordan, and Wilkinson basins had similar fates at the end of six months (Fig. 5A–D), but at deeper initial depths, more particles remained in the initial region, and a greater proportion of particles left the Gulf of Maine via the Northeast Peak/Northeast Channel rather than the Great South Channel. The fates of particles seeded at 100 m were similar for both passive and depth-correcting particles, although depth-correction reduced both retention in the Gulf of Maine as a whole (Fig. 5A–E) and transport from the western Scotian Shelf into the Gulf of Maine (Fig. 5F). At greater initial depths, depth-correction behavior reduced transport out of Jordan, Wilkinson, and Georges basins (Fig. 5A–C, 150 and 200 m, with the greatest enhancement of retention in the Jordan Basin region (Fig. 5A). Depth-correction behavior reduced transport out of Jordan Basin more than density-correction behavior (Fig. 6). Retention in the initial region was greatest in 200 m, depth-correcting particle simulations in Jordan and Wilkinson basins (Fig. 5A, B). This is likely due to the reduced probability of transport out of basins for particles that maintain their depth below the basin sill depth, 188 m in Wilkinson Basin and 190 m in Jordan Basin (Uchupi, 1965). Depth-correction behavior reduced transport of particles from upstream slope water into Jordan and Wilkinson basins, although particles continued to be transported into Georges Basin, which has a deeper sill depth (Fig. 5D).

### 3.3. *Effects of variability in wind and upstream transport on retention*

In simulations run with NCEP alongshore winds for years 1990–2000, passive and density-seeking particle retention results were significantly related to

Table 2
Particle retention in the Gulf of Maine in simulations forced by monthly mean hydrography

| Dormant period | Initial depth and behavior | | | | | |
|---|---|---|---|---|---|---|
| | 100 m | | 150 m | | 200 m | |
| | Passive | Fixed depth | Passive | Fixed depth | Passive | Fixed depth |
| May 1–January 1 | 46.3 | 36.0 | 56.3 | 82.9 | 59.0 | 91.1 |
| July 1–January 1 | 53.0 | 44.6 | 63.8 | 82.7 | 65.2 | 87.7 |
| September 1–January 1 | 62.5 | 56.2 | 74.4 | 81.2 | 74.0 | 87.4 |

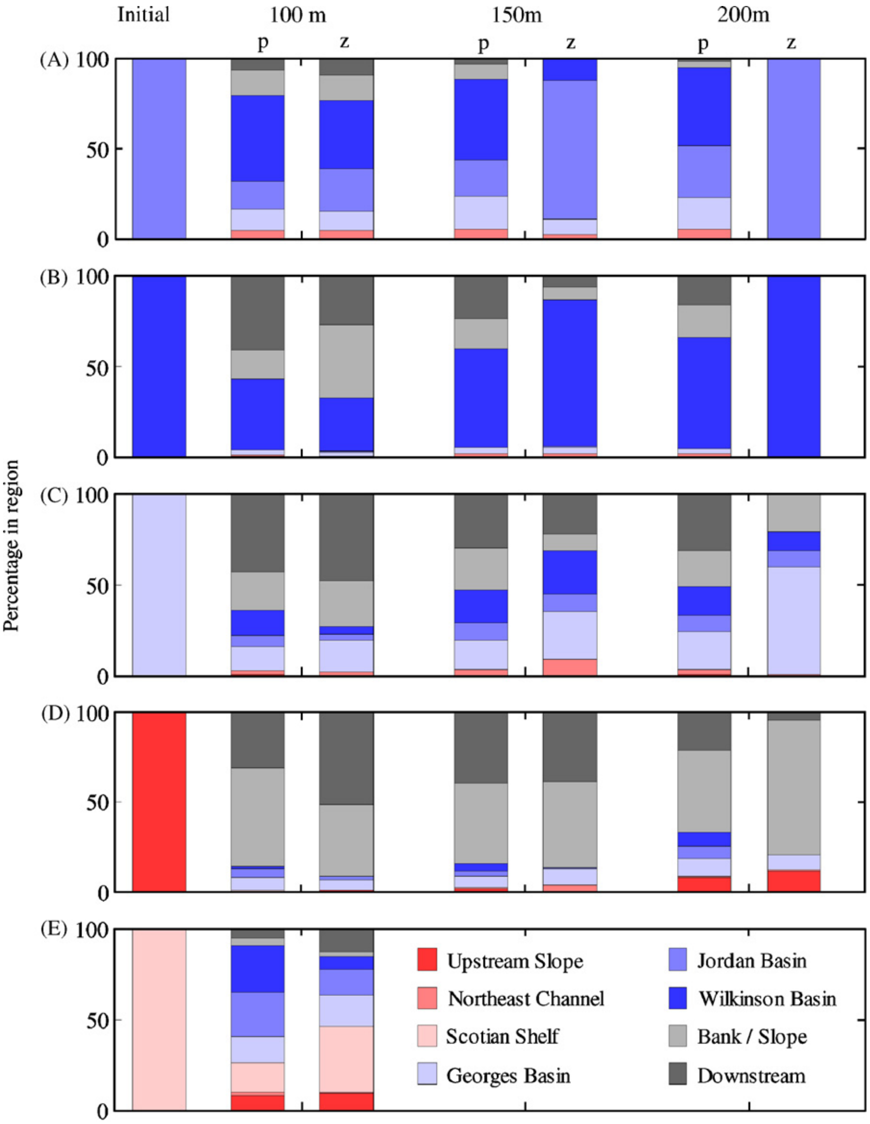

Fig. 5. Effect of initial depth and behavior on particle fate in the deep Gulf of Maine. In each panel, initial particle distribution is indicated by the bar at left, (A) Jordan Basin, (B) Wilkinson Basin, (C) Georges Basin, (D) upstream slope water, (E) western Scotian Shelf. Pairs of bars compare passive (*p*) and depth-seeking (*z*) particle distributions after 6 months of transport from initial depths of 100, 150, and 200 m. Transport simulations were forced by monthly mean hydrography and ran from July 1 to January 1.

6-month mean alongshore winds ($F_{0.05(1),1,9} = 86.72$ and 33.65, $p < 0.0001$ and 0.0003, and $r^2 = 0.91$ and 0.79, respectively; initial depth = 150 m). Depth-seeking particle retention was not significantly related to the 6-month mean of alongshore winds. Particle retention was not related to the 6-month standard deviation of alongshore winds. Neither was it related to either 6-month mean or standard deviation of cross-shore winds (initial depth = 150 m for all), perhaps because these winds are relatively inefficient at driving circulation in the Gulf (Greenberg et al., 1997). Mean alongshore wind was positive (i.e. southwesterly) in general, and retention was significantly enhanced in simulations forced by alongshore wind, compared to simulations forced by mean climatological hydrography (Fig. 7; $t_{0.05(1),10} = 7.21$, 8.82, and 6.26 for passive, density- and depth-seeking particles, respectively, $p < 0.0005$ for all). This is likely to have occurred because the mean alongshore winds tend to force a circulation in opposition to the mean flow, thus retarding the flow and enhancing

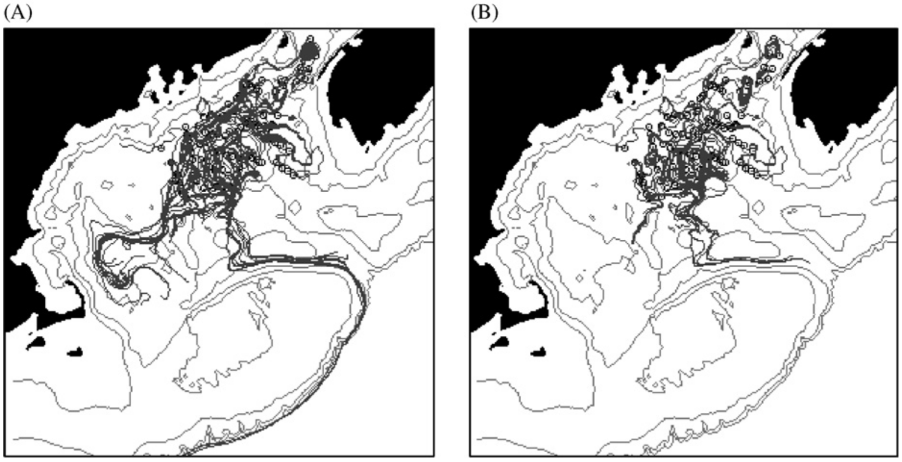

Fig. 6. Pathways of (A) density-seeking and (B) fixed-depth particles seeded at 150 m in Jordan Basin. Transport simulations were forced by monthly mean hydrography and ran from July 1 to January 1. Black circles are particle initial positions. Pathways of 100 particles are shown.

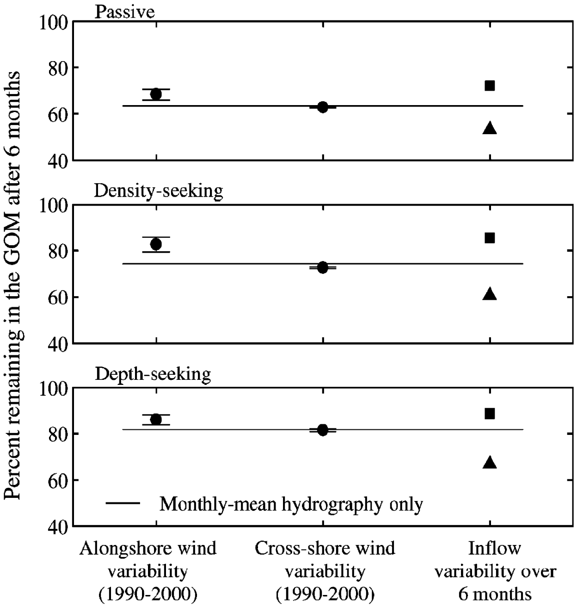

Fig. 7. Effect of alongshore wind, cross-shelf wind, and Scotian Shelf inflow variability on retention of passive, density and depth-seeking particles in the Gulf of Maine. Particles were released at 150 m on July 1, and transport was simulated until January 1. Solid lines represent retention of copepods in simulations of flow forced by monthly-mean hydographic fields alone.

retention (Greenberg et al., 1997; Pringle, 2006). The mean enhancement in retention resulting from alongshore winds ranged from 4%, for depth-seeking particles, to 8%, for density-seeking particles (Fig. 7). Although 6-month mean cross-shore winds were not correlated with retention, cross-shore wind forcing reduced retention (Fig. 7; $t_{0.05(1),10} = -7.46$, $-19.02$, and $-2.38$ and $p < 0.0005$, $< 0.0005$, and $< 0.025$ for passive, density- and depth-seeking particles, respectively). The mean reduction in retention in simulations with cross-shore winds was slight, ranging from 1% for depth-seeking particles to 2% for density-seeking particles. Inflow variability at the Scotian Shelf upstream boundary either could enhance or reduce retention (Fig. 7). For passive particles, increasing (decreasing) inflow by one standard deviation of the 6-month mean resulted in a 9% decrease (10% increase) in retention (Fig. 7). The magnitude of changes in retention resulting from inflow variability in depth- and density-seeking particles were similar (Fig. 7).

## 4. Discussion

### 4.1. Retention patterns and transport pathways

Retention of dormant copepods in the Gulf of Maine was high under all conditions simulated, even for the least retentive behavior, that is for passive particles at shallow initial depths. Estimates of retention for particles starting at the shallowest initial depth simulated, 75 m, represent a conservative lower limit of retention, both because this depth is often shallower than the shallow end of dormant copepods' depth range (Durbin et al., 1997, 2000; Wiebe et al., unpublished results) and because dormant copepods occupy a broad depth range in the Gulf of Maine, with total retention an integral of retention across all depths where copepods are resident. Although simulations suggest that a high proportion of dormant copepods are retained in the Gulf of Maine as a whole, transport within the Gulf of Maine was significant during the summer–fall, and loss from individual basin regions can be high. The Wilkinson Basin region was the most retentive sub-region, and also a recipient of particles from Jordan and Georges basins, which were themselves recipients of particles from upstream sources in the Northeast Channel, slope water, and Scotian Shelf. These transport patterns suggest that in the late part of the dormant period, late-fall-winter, the deep western Gulf of Maine is stocked primarily with copepods that entered dormancy in both the western and eastern Gulf of Maine, while dormant copepods in the deep eastern Gulf of Maine are a mixture of individuals that entered dormancy in the eastern Gulf of Maine and individuals transported from upstream waters of the western Scotian Shelf and Slope.

These distinct, but not mutually exclusive, sources of dormant copepods in different Gulf of Maine regions may contribute to observed regional differences in abundance. *C. finmarchicus* is more abundant in the western Gulf of Maine than in the northern and eastern Gulf of Maine in late fall and early winter (Fish, 1936; Meise and O'Reilly, 1996, depths 0–200 m). A similar pattern was observed in deep-dwelling *C. finmarchicus* collected below 150 m by Saumweber (2005), but abundance patterns of deep-dwelling *C. finmarchicus* observed by Wiebe et al. (unpublished results) did not consistently follow this pattern. Although currently available spatial data on copepod concentrations are not adequate for quantitative flux analysis of dormant copepod among regions, the limited data available suggest that inflow of deep water from upstream sources, in addition to advective loss to the western Gulf, could contribute to lower abundance of dormant *C. finmarchicus* in the eastern Gulf of Maine in the fall and winter. Dormant copepods in slope water are found at depths greater than the Northeast Channel sill depth (232 m) both south of Georges Bank (Miller et al., 1991) and southeast of the Scotian Shelf (E.J.H. Head, unpubl. data), and concentrations of *C. finmarchicus* are low in the deep Northeast Channel in fall and early winter (Saumweber, 2005; E.J.H. Head, unpubl. data). The circulation of slope water into and back out of the Georges Basin region observed in transport simulations would flush this region with water low in *C. finmarchicus* above the Northeast Channel sill depth, while dormant *C. finmarchicus* deep in Georges Basin would be retained. The generally deeper mean depths of dormant copepods in Georges Basin than in Wilkinson and Jordan basins (Wiebe et al., unpublished results) are consistent with this interpretation. Greater uncertainty is associated with copepod concentrations on the deep western Scotian Shelf and thus flux from this region into the eastern Gulf of Maine. Dormant copepods can be retained and aggregated in Scotian Shelf basins in the late summer through fall (Herman et al., 1991; Sameoto and Herman, 1990). Sameoto and Herman (1990) found relatively low concentrations ($<50\,\mathrm{m}^{-3}$) in the water column above the basins in summer and fall, but higher concentrations ($100\,\mathrm{m}^{-3}$) have been observed in water above another Scotian Shelf basin, Roseway Basin, in the summer (Baumgartner and Mate, 2003; Baumgartner, unpubl. data). These differences may represent interannual differences in dormant *C. finmarchicus* concentrations or vertical distributions on the inner Scotian Shelf, variability in flux driven by episodic events, such as Scotian Shelf basin flushing (Herman et al., 1991; Osgood and Checkley, 1997a, b), or slow seasonal shifts in copepod vertical distribution (Johnson and Checkley, 2004). Further sampling will be required to resolve these processes, but based on data currently available, the flux of dormant *C. finmarchicus* from the western Scotian Shelf into the Gulf of Maine appears to be variable, and dormant copepod concentrations from this source are probably similar to or lower than concentrations in the eastern Gulf of Maine. Processes that reduce retention in the deep Gulf of Maine would increase the influence of Scotian Shelf flux variability more in the eastern Gulf of Maine than in the western Gulf of Maine.

Some elements of the retention patterns simulated here are corroborated by spatial variation in the prosome lengths of dormant *C. finmarchicus* (Saumweber, 2005; Wiebe et al., unpublished results). Copepod prosome length at a given developmental stage is a function of the temperature and food conditions to which the copepod has been exposed (reviewed in Mauchline, 1998), and therefore size often can be used as an indicator of the conditions under which copepods grew and developed. Mean lengths of surface-living *C. finmarchicus* fifth copepodid stages in the Gulf of Maine decrease from spring to fall, probably due primarily to increasing surface temperature (Durbin et al., 2000; Saumweber, 2005). Mean lengths of deep-living, dormant *C. finmarchicus* were greater than mean lengths of surface-living *C. finmarchicus* in the late spring–fall (Saumweber, 2005), implying deep-water retention of copepods that entered dormancy in the past. Mean prosome lengths of dormant copepods also increase with depth in the deep Wilkinson and Jordan basins in the fall and winter (Wiebe et al., unpublished results), consistent with the trend of increasing retention with depth identified in transport simulations.

### 4.2. *Behavior*

Both initial depth selection and depth-correction behavior strongly influenced retention of particles in the Gulf of Maine. The effect of behavior on retention was related to increasingly restricted flow into and out of the Gulf of Maine with depth. Organisms that can maintain their depth below the 232-m-deep Northeast Channel sill depth are retained in the Gulf of Maine, as is evident in depth-correcting particle simulations started at 250 m. The influence of depth-correction behavior increases with depth, because passive particle vertical distributions broaden over time during the simulation period, and passive particles that move to shallower depths have a higher probability of transport out of the Gulf of Maine. Depth-correction behavior has relatively little influence on retention at the upper end of the depth range of dormant *C. finmarchicus*, 75 and 100 m, where flow out of the Gulf of Maine is less restricted.

Depth-correction and initial-depth selection behavior are both major sources of uncertainty in estimating retention in the Gulf of Maine. As described above, the ability of dormant copepods to adjust their depth by swimming or by altering their chemical composition is an unresolved question. Depth-adjustment ability may vary regionally (Hirche, 1983; Miller et al., 1991) or seasonally, perhaps changing with the phase of dormancy (sensu Hirche, 1996; e.g., Johnson and Checkley, 2004). The two depth-adjustment behaviors simulated here resulted in similar levels of retention. Passive behavior and depth-correction likely represent two extremes of possible depth-adjustment behavior during dormancy. Therefore, until depth-adjustment behavior during dormancy is better understood, these two behaviors can provide a reasonable estimate of the range of possible retention outcomes. Depth-adjustment behavior seems unlikely to vary from year to year, and thus it is unlikely to contribute to interannual variability in dormant copepod retention in the Gulf of Maine.

The factors that control depth selection at the initiation of dormancy also are not understood, as the depth distribution and water mass occupied by dormant copepods of the same species or population can vary regionally (Heath et al., 2004) and may be influenced by predator distributions (Dale et al., 1999; Kaartvedt, 1996). This question is further complicated in the Gulf of Maine, because target depths or physical conditions may not be available to copepods entering dormancy in Gulf waters, which are shallow and warm compared to the depths and temperatures at which copepods spend dormancy in slope waters (Wiebe et al., unpublished results; E.J.H. Head, unpubl. data). The deep Gulf of Maine is subject to periodic shifts in deep-water temperature associated with changes in the type of slope water entering the Northeast Channel (Petrie and Drinkwater, 1993). If temperature were used as a cue for initial depth, then these shifts could alter the vertical distribution and thus retention of dormant copepods. However, it appears that dormant copepods in the Gulf of Maine change their the temperature range much more than their depth range during these shifts (Wiebe et al., unpublished results). Thus, while variability in the initial depth of dormant copepods has the potential to strongly influence retention, it probably has a limited effect, due to the broad depth distribution of dormant copepods and low interannual variability in dormant copepods' depth range.

In the Gulf of Maine, *C. finmarchicus* enter dormancy over the course of several months, primarily at the end of the first or second generation following emergence (Meise and O'Reilly, 1996; Miller et al., 1991). Onset of dormancy is believed to be controlled by an environmental cue or multiple cues, such as temperature, photoperiod, or food availability (Dahms, 1995; Hind et al., 2000; Hirche, 1996; Johnson, 2004; Miller et al., 1991; Speirs et al., 2005), and thus timing of entry into dormancy may change from year to year in response to changes in environmental cues. While particle-tracking simulations suggest that retention would change moderately in response to changes in onset timing, persistently high variability in the timing of onset would mitigate these changes in retention. Mortality due to predation and energetic limitation would compound the loss of dormant copepods over longer dormancy periods (Saumweber, 2005), and increased mortality probably has a greater impact on the abundance of dormant *C. finmarchicus* than advection. Maximum dormancy durations of *C. finmarchicus* in the deep Gulf of Maine have been estimated to be 3.5–5.5 months based on copepod energetic reserves and respiration (Saumweber and Durbin, 2006), thus energetic limitation may be a significant source of mortality or early emergence from dormancy. The impact of predation on dormant *C. finmarchicus* in the Gulf of Maine has not yet been estimated, but increased predator abundance has been proposed to reduce *C. finmarchicus* abundance during years when cold slope water entered the deep Gulf (Wiebe et al., unpublished results). Even a relatively low mortality rate of 0.01 $d^{-1}$ (Bagøien et al., 2001) would reduce dormant *C. finmarchicus* abundance by 70% over 4 months and 90% over 8 months. Predation mortality rates can be very high in local areas where dormant *C. finmarchicus* are aggregated (Baumgartner and Mate, 2003), but mean predation mortality rates of dormant *C. finmarchicus* and their spatial and temporal variability are as yet unknown.

### 4.3. Environmental forcing

Both cross-shore and alongshore winds had minor effects on retention of dormant copepods, and they are unlikely to have a major influence on interannual variability in retention. Variability in Scotian Shelf inflow has a greater potential influence on interannual variability in retention. While the methods used to estimate the effects of wind and inflow on retention are not directly comparable, it is clear that remotely forced variability in Scotian Shelf inflow has a greater effect on retention than local winds.

Gulf of Maine *C. finmarchicus* exhibited decadal-scale shifts in abundance during the latter half of the 20th century, with the most persistent periods of low abundance in the 1960s and of high abundance in the 1980s (Conversi et al., 2001; Greene et al., 2003). Periods of low deep-water temperature in the Gulf of Maine, when cold Labrador Subarctic Slope Water (LSSW) rather than warm Atlantic Temperate Slope Water (ATSW) flows through the Northeast Channel into the deep Gulf, tend to be associated with low *C. finmarchicus* abundance (Greene and Pershing, 2000; Greene et al., 2003; MERCINA, 2001; Pickart et al., 1999). The relationship between higher *C. finmarchicus* abundance and warmer deep-water temperature is counterintuitive for two reasons. First, because metabolic rates increase with temperature, higher temperatures probably enhance mortality due to energetic limitation (Ingvarsdóttir et al., 1999; Saumweber, 2005). Second, dormant *C. finmarchicus* are more abundant in cold slope water (LSSW) than in warm slope water (ATSW) south of Nova Scota (E.J.H. Head, unpubl. data; Wiebe et al., unpublished results), thus warm slope water would transport fewer *C. finmarchicus* into the deep Gulf than cold slope water. Cold periods are, however, associated with anomalously high flow to the southwest on the inner Halifax line (Loder et al., 2001; Petrie and Drinkwater, 1993), and so reduced retention in the Gulf associated with high Scotian Shelf inflow may contribute to lower *C. finmarchicus* abundance in deep water during cold years. This hypothesis assumes that dormant *C. finmarchicus* are more abundant in the deep Gulf of Maine than in deep upstream waters, since water transported out of the Gulf is replaced with water from upstream. This assumption appears to be reasonable, but further sampling, especially on the deep western Scotian Shelf, will be necessary to confirm it.

The present study estimated the effects of two relatively well characterized sources of environmental variability, winds and Scotian Shelf inflow, on retention of dormant *C. finmarchicus* in the Gulf of Maine; however, Pringle (2006) found that for net transport averaged over several months or longer, inflow and winds are not the dominant sources of transport variability in the Gulf of Maine. At least in the central Gulf of Maine, for example along the pathway from the central Maine coast to Georges Bank, the dominant transport variability is driven by changes in the horizontal distribution of density at depths from 50 to 200 m in the Gulf. These horizontal density gradients are formed by changes in the density entering the Gulf and by vertical mixing driven by wintertime storms and cooling (Pringle, 2006). Unfortunately, the available density data are too sparse to allow the numerical model to be run for individual years, and thus only an indirect estimate of the impact of this source of variability on retention of dormant copepods can be made. Pringle (2006) found that the standard deviation of the central Gulf of Maine transport driven by variability in deep-water density gradients is similar in magnitude to the mean transport during the winter, and about half as large as the mean in the summer. This suggests that retention, which is most strongly affected by the wintertime transport, can be greatly increased when deep-water density gradients are anomalously weak and roughly halved when they are anomalously strong. Unfortunately, this analysis is unable to resolve the magnitude of the variability along the more coastal transport pathways that are important in moving dormant copepods from Wilkinson Basin to Georges Bank, and from Jordan to Wilkinson basin. Nonetheless, it suggests that retention of dormant copepods can be changed substantially by changes in the horizontal density gradient. Quantifying the exact nature of this change must wait until model and observational strategies are developed that can both resolve the yearly changes in the density field and relate them to larger-scale changes in the water entering the Gulf and the strength of wintertime storms and cooling.

## 5. Conclusions

Changes in retention in response to increased Scotian Shelf inflow may provide a mechanism linking observed changes in *C. finmarchicus* abundance with changes in deep-water temperature in the Gulf of Maine and Scotian Shelf. However, seasonal changes in copepod abundance and length imply greater losses of dormant copepods than are predicted from advective losses. The abundance of *C. finmarchicus,* both throughout the water column down to 200 m and in water below 100 m, declines by 70–90% between August and January (Meise and O'Reilly, 1996; Saumweber, 2005, both studies primarily warm deep-water years). During years of cold deep water of the Gulf, dormant *C. finmarchicus* abundance is even lower in fall and winter, about 10% of the abundance in warm years (Wiebe et al., unpublished results), due either to lower initial abundance or to greater loss rates. Mean prosome lengths also decrease in Jordan and Georges basins between June and November (Saumweber, 2005), suggesting addition of smaller copepods and loss of the larger individuals that entered dormancy early. During the summer when dormant copepod abundance is increasing, addition of smaller copepods, either from local surface waters or from deep upstream sources, probably contributes more to declining prosome lengths; but the loss of large individuals likely becomes a greater factor in the fall. (Saumweber, 2005).

The large seasonal declines of dormant copepods from the Gulf of Maine suggest that mortality, either due to energy-limitation or predation, is likely the dominant loss term for dormant *C. finmarchicus* in the Gulf of Maine, rather than advection. However, changes in both Scotian Shelf inflow and transport driven by variability in deep-water density gradients can also contribute to loss of dormant copepods, and may contribute variability that is related to regional-scale circulation and wind-driven winter mixing in the Gulf of Maine. Spatial shifts observed in deep particle simulations indicate that the western Gulf of Maine is dominated by copepods endogenous to the Gulf of Maine, while the eastern Gulf of Maine is influenced more by upstream sources, even in deep water. These differences in sources of dormant *C. finmarchicus* among Gulf of Maine regions may influence initial conditions for population growth in surface water both in the Gulf and on Georges Bank.

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