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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 six 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.

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 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 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 (100s 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, 1997), 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 (Figure 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 for *C. finmarchicus* repopulating Georges Bank in 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 may also 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 *Calanus finmarchicus*, as described above, and in turn are supplied with *C. finmarchicus* from deep water (Figures 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 re-stock 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 (Figures 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 North East 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 is 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 two months of the approximately six 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.*, this volume).

The abundance of individuals emerging from dormancy and transported onto the shelf sets the initial conditions for production on the continental shelves in the active season, typically associated with the spring bloom of phytoplankton (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 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 north east and north west 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 time-scales 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?

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 which 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 the Scotian Shelf from the Bedford Institute of Oceanography and National Ocean Data Center databases (Pringle, this volume). The 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 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 *Calanus finmarchicus* in slope waters of the western North Atlantic are greater than the maximum bottom depth of the Gulf of Maine (Wiebe *et al.*, this volume; E.J.H. Head, unpubl. data). In slope water south of Georges Bank, dormant *C. finmarchicus* occupy a depth range from about 300 m to 1000 m but are most abundant around 500 m (Miller *et al.*, 1991). 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.*, this volume, 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.*, this volume). 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.*, this volume).

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 time scales of hours, perhaps by ion exchange (R. W. Campbell, unpubl. data). 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 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 was 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, this volume). Winds were divided into alongshore and cross-shore components.

The alongshore component corresponds to the Maine coast, 55º 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 in Pringle (this volume). 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, this volume). 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 (Figure 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 1 until January 1. To evaluate the sources and fates of copepods, retention in sub-regions of the Gulf of Maine and upstream regions (Figure 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.

Results

Passive particle pathways in the deep Gulf of Maine

Passive particles in transport simulations seeded 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 simulated 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 (Figure 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 (Figure 3a). Particles that originated in and around the deep Jordan Basin area and left the Gulf of Maine within six 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 four months before passive particles seeded at 150 m in the Jordan basin region began to leave the Gulf of Maine (Figure 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 of Georges Bank and across the Northeast Peak or through the Great South Channel (Figure 3b), with about twice as many leaving via the Northeast Peal. 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 (Figure 3c). Particles from Georges Basin also moved both into the Jordan Basin / northeast Gulf of Maine and into Wilkinson Basin during six 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 six months for passive particles started at 150 m on July 1) than retention of particles seeded in the Wilkinson (59%) or Georges Basin (47%) regions (Figure 3d, e, and f). This is probably because particles in Jordan Basin must travel the furthest before leaving the Gulf. The percentage of particles retained in and around Jordan Basin itself was low (20%), and many of the particles seeded in the Jordan basin region moved to the Wilkinson Basin region (Figure 3a) over the six month simulation. Particle retention over six 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 (Figure 3f). Retention in the Wilkinson Basin region was relatively high compared to the other basin regions, 54% over six months (Figure 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 six 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 (Figure 3g and h). Particles from the deep western Scotian Shelf moved primarily into the Jordan and Georges Basin region during the first two 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 three months (Figure 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, particles either moved into the Jordan Basin region or were transported out of the Gulf of Maine through the western Northeast Channel.

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

Retention of simulated copepods in the deep Gulf of Maine over six 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 (Figure 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 absolute difference 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 region is restricted to several distinct regions, retention is related to the initial particle distribution, which changes for different initial depths in the simulations (Figure 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 250m, 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 increased (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 greater from May 1 to January 1 than for September 1 to January 1 (Table 2). Transport of depth-seeking particles at these depths from Georges Basin to Jordan Basin, where retention of depth-seeking particles is very high, was greater for particles started in May than for particle simulations started in July and September.

The transport pathways of passive particles seeded at 100 and 200 m in upstream slope water and Georges, Jordan, and Wilkinson Basins, and at 100 m on the western Scotian Shelf, were qualitatively similar to paths of particles seeded at 150 m. Transport out of the initial region slowed with increasing initial depth (Figure 5a – d), and the relative export of particles out of the Gulf of Maine via the Great South Channel, compared to export via the Northeast Peak and Northeast Channel, decreased with initial particle depth. Depth-correction behavior had relatively little influence on the fates of particles seeded at 100m, primarily reducing retention slightly in the Gulf of Maine as a whole (Figure 5a - d). At greater initial depths, depth-correction behavior reduced transport out of Jordan, Wilkinson, and Georges Basins in transport simulations (Figure 5 a – c, 150 and 200 m). Curtailment of transport pathways as a result of depth-correction behavior was greatest for particles seeded in the Jordan Basin region (Figure 5 a). Depth-correction behavior reduced transport out of Jordan Basin more than density-correction behavior (Figure 6). Enhancement of retention in the initial region due to depth-correction behavior was greatest in 200 m simulations in Jordan and Wilkinson basins (Figure 5 a - 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 Basin, although particles continued to be transported into Georges Basin, which has a deeper sill depth (Figure 5 d). Depth-correction behavior increased retention on the western Scotian Shelf and decreased transport into the Gulf of Maine (Figure 5 d).

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 were significantly related to six-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 six-month mean of alongshore winds. Particle retention was not related to the six-month standard deviation of alongshore winds. Neither was it related to either six-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 (Figure 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 retention (Greenberg *et al.*, 1997; Pringle, this volume). The mean, absolute increase in retention resulting from alongshore winds ranged from 4%, for depth-seeking particles, to 8%, for density-seeking particles (Figure 7). Although six-month mean cross-shore winds were not correlated with retention, cross-shore wind forcing reduced retention (Figure 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 absolute 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 enhanced or reduced retention (Figure 7). For passive particles, increasing (decreasing) inflow by one standard deviation of the six-month mean resulted in a 9% decrease (10% decrease) in retention (Figure 7). The magnitude of changes in retention resulting from inflow variability in depth- and density-seeking particles were similar (Figure 7).

Discussion

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 behaviors, 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.*, 2000; Durbin *et al.*, 1997; Wiebe *et al.*, this volume) and because dormant copepods occupy a broad depth range in the Gulf of Maine, with total retention an integration 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 is 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. Particles were transported from both the Georges and Jordan Basin regions to Wilkinson Basin, and Jordan and Georges Basins were recipients of particles from upstream sources in the Northeast Channel, slope water, and Scotian Shelf. These transport patterns suggest that in the latter part of the dormant period, in late-fall – winter, the deep western Gulf of Maine is stocked primarily with copepods that entered dormancy in both 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. Advection from the Scotian Shelf has a greater influence on

Jordan Basin, in the northeast Gulf of Maine, and advection from the slope water is greater in Georges Basin. These transport patterns suggest that in the latter part of the dormant period, in late-fall – winter, the deep western Gulf of Maine is stocked primarily with copepods that entered dormancy in both 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.

Some elements of the retention patterns and transport pathways simulated here are corroborated by temporal and spatial changes in the prosome lengths of dormant *C. finmarchicus* (Saumweber, 2005; Wiebe *et al.*, this volume). Copepod prosome length at a given developmental stage is a function of temperature and food conditions (reviewed in Mauchline, 1998), and therefore size often can be used as an indicator of the conditions under which copepods grew and developed. This can provide clues about the surface source of dormant copepods. Surface-living *C. finmarchicus* fifth copepodid stages in the Gulf of Maine decrease in length from spring to fall, probably due primarily to increasing surface temperature (Durbin *et al.*, 2000; Saumweber, 2005). In the deep Gulf of Maine, large copepod size indicates individuals that entered dormancy in the spring, when surface temperatures are cold.

Mean prosome lengths of dormant *C. finmarchicus* vary spatially, with depth and Gulf sub-region, and seasonally. Mean lengths of deep-living, dormant *C. finmarchicus* are greater than mean lengths of surface-living *C. finmarchicus* in the late spring – fall (Saumweber, 2005). The consistent difference between surface- and deep-living copepods in the spring to fall period implies that copepods that entered dormancy at an earlier time are retained in deep water. Further, mean prosome lengths of dormant copepods increase with depth in the deep Wilkinson and Jordan Basins in the fall and winter (Wiebe *et al.*, this volume), corroborating the trend of increasing retention with depth identified in transport simulations. Saumweber (2005) observed a decrease in the mean prosome lengths of dormant *C. finmarchicus* from spring to fall in Jordan and Georges Basins. This decline suggests addition of smaller copepods and possible loss of the larger individuals that entered dormancy early. Small copepods may either enter the deep Jordan and Georges Basins from local surface waters or from deep upstream sources on the Scotian Shelf or in slope water (Fig. 2), where mean lengths were lower than the mean lengths in the Gulf of Maine (Saumweber, 2005). Transport simulations indicate both advection of deep-dwelling copepods from upstream regions into Jordan and Georges Basins and loss of deep-dwelling copepods from the Georges and Jordan regions. In contrast to Georges and Jordan Basins, the mean length of dormant copepods in Wilkinson Basin decreased between May and August and then increased in November to a mean length only observed in August in Jordan basin (Saumweber, 2005); consistent with simulated transport from Jordan to Wilkinson Basin.

It must be noted, however, that vertical, intrabasin, and interannual variability in prosome lengths of dormant copepods can be a similar magnitude as interbasin variation in the fall and winter, and prosome lengths of dormant copepods observed by Wiebe *et al.* (this volume) were greater in Wilkinson Basin than in Jordan Basin in only two of three Octobers (1997 – 1999). The interbasin patterns observed by Saumweber (2005), sampled at single basin stations and depth bins greater that 150 m, may be biased by this variability. However, because deep particles appear to move along well-defined transport ‘highways,’ intrabasin variability in prosome length may prove informative, when combined with transport simulations and hydrographic information, in identifying the sources of deep copepods. Further sampling will be required to resolve horizontal and vertical patterns of variability in copepod length in deep basins of the Gulf of Maine.

The spatial shifts in dormant copepod distributions, identified in transport simulations, suggest that dormant copepods in the Wilkinson (western), Jordan (northeast), and Georges Basin (southeast) regions of the Gulf of Maine have distinct, though not mutually exclusive, sources at the beginning of winter, when they begin to emerge from dormancy and seed surface waters. We did not attempt a quantitative analysis of the deep water sources of dormant copepods, because flux depends on copepod concentrations in the source regions in addition to volume transport, and seasonal and interannual variability of dormant copepod concentrations in the deep Gulf of Maine and upstream source regions have not yet been well characterized. Qualitatively, the Wilkinson region will be dominated by copepods that entered dormancy in the western and eastern Gulf of Maine at the end of the fall. Jordan and Georges Basins will contain mixture of copepods from the eastern Gulf of Maine and upstream sources.

The distinct sources of dormant copepods in different regions of the Gulf of Maine may contribute to differences in abundance that have been observed among Gulf of Maine regions. The abundance of *C. finmarchicus* is higher 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 *C. finmarchicus* below 150 m by Saumweber (this volume); however, the abundance patterns of deep-dwelling *C. finmarchicus* observed by Wiebe *et al.* (this volume) did not consistently follow this pattern. The inflow of deep water from upstream sources may contribute to the 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 south of the Scotian Shelf (E. J. H. Head, unpubl. data), and concentrations of *C. finmarchicus* are very 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.

Dormant copepods on the western Scotian Shelf are retained and aggregated in basins 250 – 270 m deep in the late summer through fall (Herman *et al.*, 1991; Sameoto and Herman, 1990). Sameoto & Herman (1990) observed that, except for basin aggregations below 200 m, concentrations of *C. finmarchicus* below 50 m were relatively low, < 50 m^{-3}, in summer and fall. However, higher concentrations (means of order 100s m^{-3}) have been observed in water above Roseway Basin in the summer (Baumgartner and Mate, 2003; Baumgartner, unpubl. data). These differences appear to reflect interannual variability in dormant *C. finmarchicus* concentrations on the inner Scotian Shelf, which likely contributes to interannual variability in flux of deep-water *C. finmarchicus* into the Gulf of Maine. Additional variability in flux may be driven by episodic events, such as Scotian Shelf basin flushing and episodic bursts of high flow through the Northeast Channel (Herman *et al.*, 1991; Ramp *et al.*, 1985). Water in the deep basins of the Scotian

Shelf can be replaced with slope water several times during the winter (Herman *et al.*, 1991). Herman *et al.* (1991) suggested that because this process was slow, dormant copepods could resettle in the basins and would not be lost from the basins. However, dormant *C. finmarchicus* were anomalously abundant in deep basins during the years of the Herman *et al.* (1991) and Sameoto and Herman (1990) studies (Head *et al.*, 1999), and basin flushing dynamics in these years may not have been typical. Interannual differences in vertical distribution, perhaps influenced by basin flushing processes (Osgood and Checkley, 1997) or slow seasonal shifts in copepod vertical distribution (Johnson and Checkley, 2004) may influence dormant copepod retention/loss in basins and transport into the Gulf of Maine. Further sampling will be required to resolve these processes, but based on data currently available, the flux of dormant *C. finmarchicus* from slope water appears to be low, and flux from the western Scotian Shelf is probably variable, advecting water containing dormant copepod concentrations similar to or lower than the Gulf of Maine. Processes that decrease retention in the deep Gulf of Maine will tend to increase the influence of Scotian Shelf variability more in the eastern Gulf of Maine than the western Gulf of Maine.

Differences in sources of dormant *C. finmarchicus* among Gulf of Maine regions will influence initial conditions for population growth in surface water not only in the Gulf but also on Georges Bank, which is seeded in large part by copepods emerging from dormancy in the Gulf of Maine. Copepods in the surface mixed layer can reach Georges Bank from any part of the Gulf of Maine, but the different regions have different time scales and seasonal flow patterns for reaching the Bank (Gentleman, 1999; Hannah *et al.*, 1998; Lynch *et al.*, 1998; Miller *et al.*, 1998). Copepods can be transported from the southern Gulf of Maine onto the Northeast Peak of Georges Bank both from deep water, via the northern flank jet (Gentleman, 1999, and see Figure 3), and in the surface mixed layer (Hannah *et al.*, 1998) throughout the late fall through spring. Transport from the western, central, and eastern regions of the southern Gulf of Maine to the Crest of the Bank and Northeast Peak vary seasonally with changes in wind stress and Georges Bank stratification, and flow onto the Bank is maximal, particularly from the central and eastern regions of the southern Gulf of Maine, in early winter (Gentleman, 1999; Hannah *et al.*, 1998). After emergence from dormancy and return to surface waters, copepods in Georges Basin can be transported onto the Northeast Peak in less than one month; transit times from the Jordan Basin to the Northeast Peak are 1-3 months (Gentleman, 1999; Lynch *et al.*, 1998), and copepods in surface waters above Wilkinson Basin proper can be transported to the Crest in about two months (Gentleman, 1999; Lynch *et al.*, 1998; Miller *et al.*, 1998). The distinct sources for and timescales of *C. finmarchicus* transport onto Georges Bank may contribute to the relatively low interannual variability of this species on Georges Bank, compared to other dominant species (Durbin and Casas, this volume). In addition, spatial variation in the sources of dormant *C. finmarchicus* to the deep Gulf of Maine may contribute to driving differences in interannual variability patterns between *C. finmarchicus* and other dominant copepod species in the surface Gulf of Maine (Pershing *et al.*, in press). Understanding seasonal changes in the dominant sources of *C. finmarchicus* to Georges Bank, and the processes that influence these sources, may be critical to identifying sources of interannual variability of this species on the Bank.

Behavior

Initial depth selection changed retention of dormant copepods by 20 to 60%, and depth-correction behavior changed retention by 10 – 40% (both absolute difference) over the range of conditions simulated. These effects are related to increasingly restricted flow into and out of the Gulf of Maine with depth. The major deepwater passages into and out of the deep Gulf of Maine are the 70 m deep Great South Channel and the 232 m deep Northeast Channel (Smith *et al.*, 2001). Organisms that can maintain their depth below the Northeast Channel sill depth will be 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 keeps particles in deeper water where the probability of transport out to the Gulf of Maine is lower. 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 behavior is a major source 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 depth distribution and properties of water occupied by copepods of the same species or population can vary regionally (Heath *et al.*, 2004), thus it is unclear what factors or cues might control depth-correction behavior. Meta-analysis of field observations (e.g. Heath *et al.*, 2004) or experimental manipulation of dormant copepods will be required to understand these processes. The two depth-adjustment behaviors simulated in the present study resulted in similar levels of retention. Passive behavior and depth-correction are likely to 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.

Broad depth distributions of dormant *C. finmarchicus* in Gulf of Maine basins in summer, fall, and winter (Durbin *et al.*, 1997; Wiebe *et al.*, this volume, M. F. Baumgartner, unpubl. data, M. C. Benfield, unpubl. data) imply a broad range of initial dormancy depths. The factors that control initial dormancy depth selection are not known, and target dormancy depths or conditions may not be available to copepods entering dormancy even above shelf basins, which are shallow compared to slope waters. The greater depths and lower temperatures occupied by dormant *C. finmarchicus* in slope waters off Georges Bank and the Scotian Shelf, compared to the Gulf of Maine (Wiebe *et al.*, this volume, E. J. H. Head, unpubl. data), suggest that Gulf of Maine copepods may ‘settle’ for non-target depths or conditions when they migrate to deep water at the start of dormancy. If copepods entering dormancy throughout the surface Gulf of Maine migrate to the maximum acceptable depth at their particular location, then this would lead to a broad, though initially near-bottom, initial depth range for the deep population. The deep

Gulf of Maine is subject to periodic shifts in deep water temperature, which are 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 the temperature range occupied by dormant copepods changes more during deep-water temperature shifts than their depth range (Wiebe *et al.*, this volume). 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.

Four months' difference in the timing of entry into dormancy, and the associated increase in dormancy duration, changed retention in simulations by up to 20% (absolute difference). The effect of dormancy timing on retention was similar for passive particles across all initial depths and for depth-seeking particles at 100 m initial depth. In contrast, retention was enhanced slightly by early dormancy in depth-seeking particles deeper than 100 m, due to seasonal shifts in transport pathways that moved deep particles into the northeast Gulf of Maine in May and June. Given the uncertainty associated with depth-adjustment behavior, the potential change in retention resulting from dormancy timing ranges from very low, if depth-correction occurs, to a maximum of about 15 – 20%. Onset of dormancy is believed to be controlled by an environmental cue, or multiple cues, such as temperature, photoperiod, or food availability, but the precise cues are currently unknown (Dahms, 1995; Hind *et al.*, 2000; Hirche, 1996; Miller *et al.*, 1991; Speirs *et al.*, in press). The timing of dormancy may change from year to year in response to variability in environmental cues, but since onset of dormancy is spread over a broad range of times, interannual variability in retention resulting from such shifts is probably minor. In addition to advective loss from the Gulf of Maine, predation and metabolically-driven mortality both contribute to loss of dormant copepods. These sources of loss must increase if dormancy duration increases due to early entry into dormancy, and they may result in greater loss of early-dormant copepods than advection (Saumweber, 2005).

Environmental forcing

Cross-shore winds significantly reduced retention of dormant *Calanus finmarchicus* in the Gulf of Maine compared to simulations with no wind. However, the mean reduction in retention was always very small, less than 2% (Figure 7). The standard deviation of retention in the years simulated, indicative of interannual variability in retention, was also low, less than 1% for all three depth-adjustment behaviors. Thus, cross-shore wind forcing will have a negligible effect on interannual variability in retention. Alongshore winds enhanced retention by 4 – 8% ± 2 – 3% under the same simulation conditions (Figure 7). The standard deviation of alongshore wind forced retention, while higher than that of cross-shore winds, is still low, indicating that alongshore winds also have a minor effect on interannual variability in retention. Variability in Scotian Shelf inflow has the greatest influence on interannual variability in retention. Increasing inflow by one standard deviation of its six-month mean reduces retention by 10 – 15%, compared to simulations with mean Scotian Shelf inflow, and decreasing inflow by one standard deviation enhances retention by 7 – 11% (Figure 7). While the methods used to estimate the effects of wind and inflow on retention are not directly comparable, it is clear that variability in Scotian Shelf inflow has a greater effect on retention.

Gulf of Maine *Calanus finmarchicus* exhibited decadal-scale shifts in abundance during the latter half of the twentieth 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). Interannual variability of *C. finmarchicus* abundance was correlated with the North Atlantic Oscillation (NAO), the dominant mode of wintertime climate variability in the North Atlantic, during the 1960s through 1980s (Conversi *et al.*, 2001; Greene and Pershing, 2000), although this relationship is not significant when 1990s data are included (Greene *et al.*, 2003). Shifts in the phase of the NAO are associated with changes in Labrador Current transport and with the position of the warm Atlantic Temperate Slope Water (ATSW) and cold Labrador Subarctic Slope Water (LSSW) along the continental slope in the western North Atlantic. Shifts in the position of slope water masses along the continental slope lead to changes in the temperature of deep water in Scotian Shelf basins and in the Gulf of Maine (Greene *et al.*, 2003; MERCINA, 2001; Pickart *et al.*, 1999).

Periods of low deep-water temperature tend to be associated with low *C. finmarchicus* abundance in the Gulf of Maine (Greene and Pershing, 2000; Greene *et al.*, 2003; MERCINA, 2001). This pattern is counterintuitive for two reasons. First, high deep water temperatures increase the metabolic rates of dormant copepods and probably result in an increase in mortality due to insufficient energy for emergence or due to early emergence (Ingvarsdóttir *et al.*, 1999; Saumweber, 2005; Saumweber and Durbin, this volume). Second, dormant *C. finmarchicus* are more abundant in (cold) LSSW than in

ATSW south of Nova Scota (E. J. H. Head, unpubl. data), but they are less abundant in deep water of the Gulf of Maine during cold years than in warm years (Wiebe *et al.*, this volume). Cold periods in deep water are, however, associated with anomalously high flow to the southwest on the inner Halifax line (Loder *et al.*, 2001; Petrie and Drinkwater, 1993). The decrease in dormant copepod retention in the Gulf of Maine associated with high Scotian Shelf inflow may contribute to lower *C. finmarchicus* abundance in deep water during cold years: dormant copepods may be flushed out of the Gulf of Maine when the water is cold, because currents are stronger when deep water is cold. This hypothesis assumes that dormant *C. finmarchicus* are more abundant in the deep Gulf of Maine than in deep upstream waters, since changes in retention are associated with changes in inflow of water from upstream. For slope water entering the Northeast Channel, this assumption is likely to be true. It also appears to be true at times for water entering the Gulf of Maine from the Scotian Shelf, but the processes that control deep-water abundance of *C. finmarchicus* in this area are not yet well understood. Other factors likely also contribute to abundance shifts between warm and cold years, as deep-dwelling *C. finmarchicus* are about one tenth as abundant in the deep Gulf of Maine in fall and winter of cold years (Wiebe *et al.*, this volume), a larger change than expected from reduction in retention alone.

The present study estimated the effects of two relatively well characterized sources of environmental variability, Scotian Shelf inflow and changes in the winds, on retention of dormant *C. finmarchicus* in the Gulf of Maine; however, Pringle (this volume) found that on timescales of 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 source of variability is driven by changes in the horizontal distribution of density at depths from 50 to 200 meters within 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, this volume). Unfortunately, the available density data are too sparse to allow the numerical model to be run for individual years, and thus the estimate of the impact of this source of variability on the retention of dormant copepods must be, necessarily, indirect.

Pringle (this volume) found that the standard deviation of the transport in the central Gulf of Maine 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 the amount of retention can be greatly increased when the anomaly is of the same magnitude, but of opposite sign, as the mean, or can be roughly halved, when the mean and anomaly are of the same sign and magnitude, doubling the transport. 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, this analysis 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 which can resolve the yearly changes in the density field, and relate them to changes in larger scale changes in the water entering the Gulf and the strength of wintertime storms and cooling.

Summary and conclusions

The availability of *Calanus finmarchicus* to emerge from dormancy and seed surface waters of the Gulf of Maine and Georges Bank in late winter and spring is set both by inputs of copepods entering dormancy and losses of deep-dwelling individuals through advection and mortality during the summer and fall. The simulations presented in this study indicate that retention of dormant *C. finmarchicus* is relatively high under most conditions, even for copepods entering dormancy in late spring. Mortality or early emergence from dormancy due to energy limitation is likely the dominant loss term for copepods that entered dormancy in spring to early summer: respiration rates suggest that dormant copepods may have only enough stored energy to survive four to five months during warm years in the deep Gulf of Maine (Saumweber, 2005; Saumweber and Durbin, this volume). Predation mortality rates can very high in local areas where dormant copepods are aggregated (Baumgartner and Mate, 2003), but mean predation mortality rates and their spatial and temporal variability are as yet unknown. Because predator communities may differ in slope water masses, predation could also be an important source of interannual variability in dormant *C. finmarchicus* abundance.

Dormancy behavior is a major source of uncertainty in estimating retention. Although discovery of the underlying factors controlling dormancy migration and depth-correction behavior is not likely imminent, empirical description of vertical distribution patterns over seasonal timescales should be sufficient to constrain the effects of behavior on retention. Description of vertical distribution in late spring and early summer would provide clues about the factors that control initial depth, and simulation experiments initialized with realistic early vertical distributions may be able to infer depth-correction behavior from seasonal changes in vertical distributions.

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. Because of these differences, variability in the two regions may reflect differences in processes acting on the Gulf of Maine and the western Scotian Shelf. Physical processes and variability on the Scotian Shelf are likely of critical importance to *C. finmarchicus* in the Gulf of Maine, because of all the factors examined in transport simulations, variability in Scotian Shelf inflow appears to have the greatest influence on interannual variability in retention of dormant *C. finmarchicus* in the deep Gulf of Maine. However, recent work by Pringle (this volume) suggests that processes influencing the horizontal density gradients in intermediate and deep water of the Gulf of Maine are also likely to have a major impact on retention. The reduction in retention in response to increased Scotian Shelf inflow provides a mechanism linking observed changes in *C. finmarchicus* abundance with changes in deep water temperature in the Gulf of Maine and Scotian Shelf. Variability in both transport on the inner Western Scotian Shelf and in copepod vertical distribution and abundance in this region and in the Northeast Channel have not been well characterized; however, these regions appear to play an important role in driving *C. finmarchicus* abundance variability in the Gulf of Maine.

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Table 1. Lagrangian particle simulations presented.

Forcing	Initial depth (m)	Depth-adjustment	Time period
mean hydrography	75, 100, 150, 200, 250	passive, depth-seeking, density-seeking	1-Jul to 1-Jan
mean hydrography	100, 150, 200	passive, depth-seeking	1-May to 1-Jan
mean hydrography	100, 150, 200	passive, depth-seeking	1-Sep to 1-Jan
mean hydrography + alongshore wind (1990 – 2000)	150	passive, depth-seeking, density-seeking	1-Jul to 1-Jan
mean hydrography + crossshore wind (1990 – 2000)	150	passive, depth-seeking, density-seeking	1-Jul to 1-Jan
mean hydrography + Scotian Shelf inflow (1990 – 2000)	150	passive, depth-seeking, density-seeking	1-Jul to 1-Jan

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

	Initial depth and behavior					
	100 m		**150 m**		**200 m**	
Dormant period	passive	fixed-depth	passive	fixed-depth	passive	fixed-depth
1 May to 1 Jan	46.3	36.0	56.3	82.9	59.0	91.1
1 Jul to 1 Jan	53.0	44.6	63.8	82.7	65.2	87.7
1 Sep to 1 Jan	62.5	56.2	74.4	81.2	74.0	87.4

Figure 1

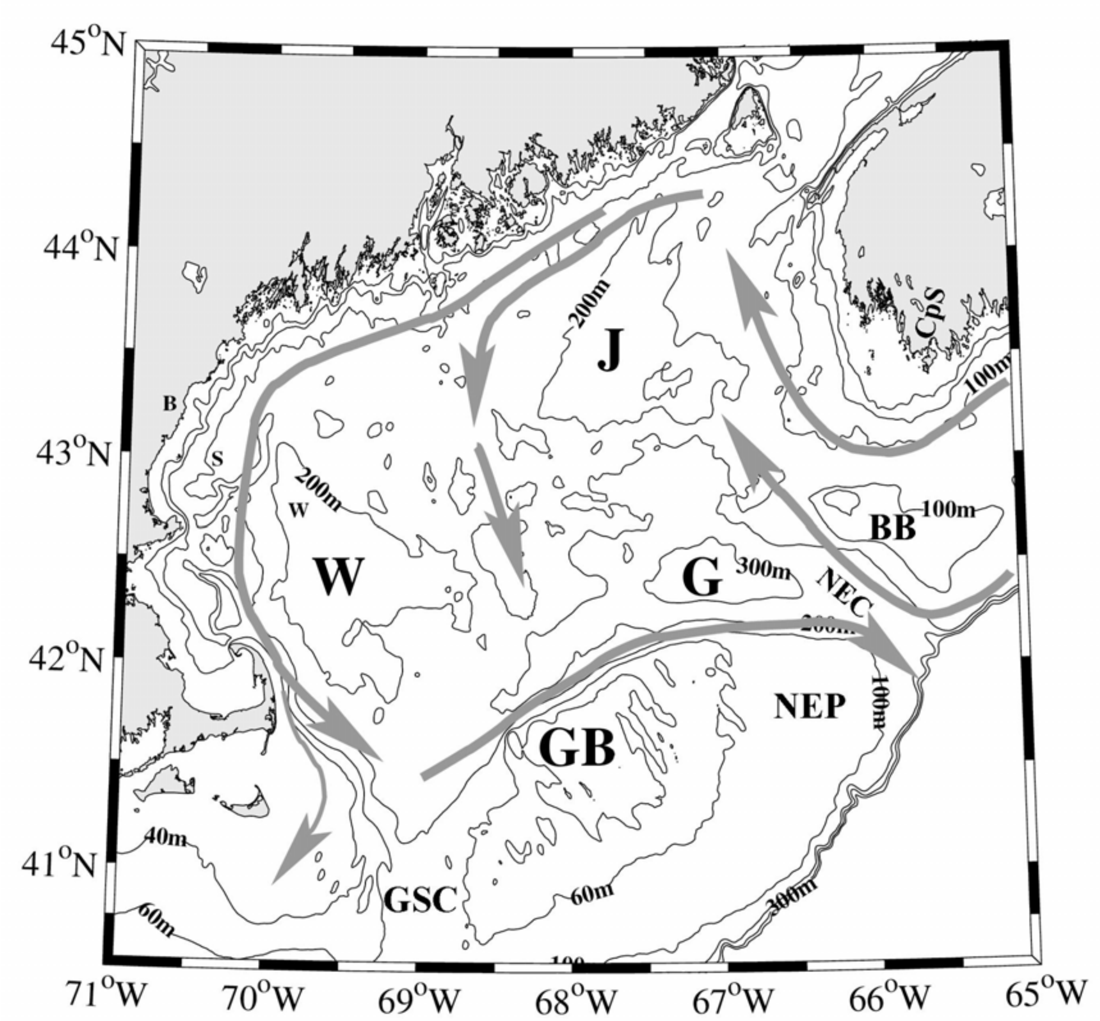


Figure 1. Circulation in the deep Gulf of Maine. BB – Browns Bank, CpS – Cape Sable G – Georges Basin, GB – Georges Bank, GSC – Great South Channel, J – Jordan Basin, NEC – Northeast Channel, NEP – Northeast Peak, W – Wilkinson Basin.

Figure 2

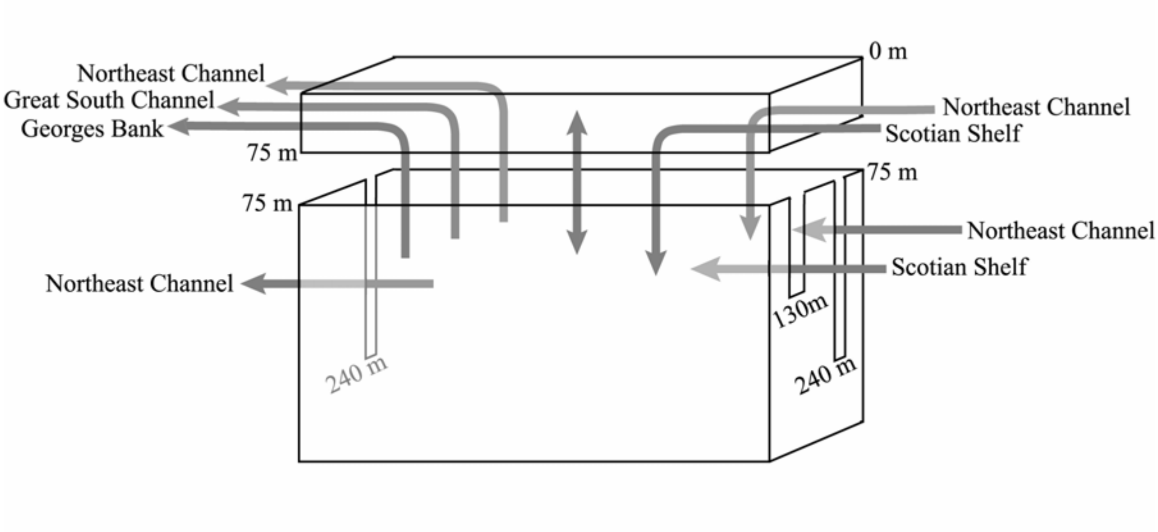
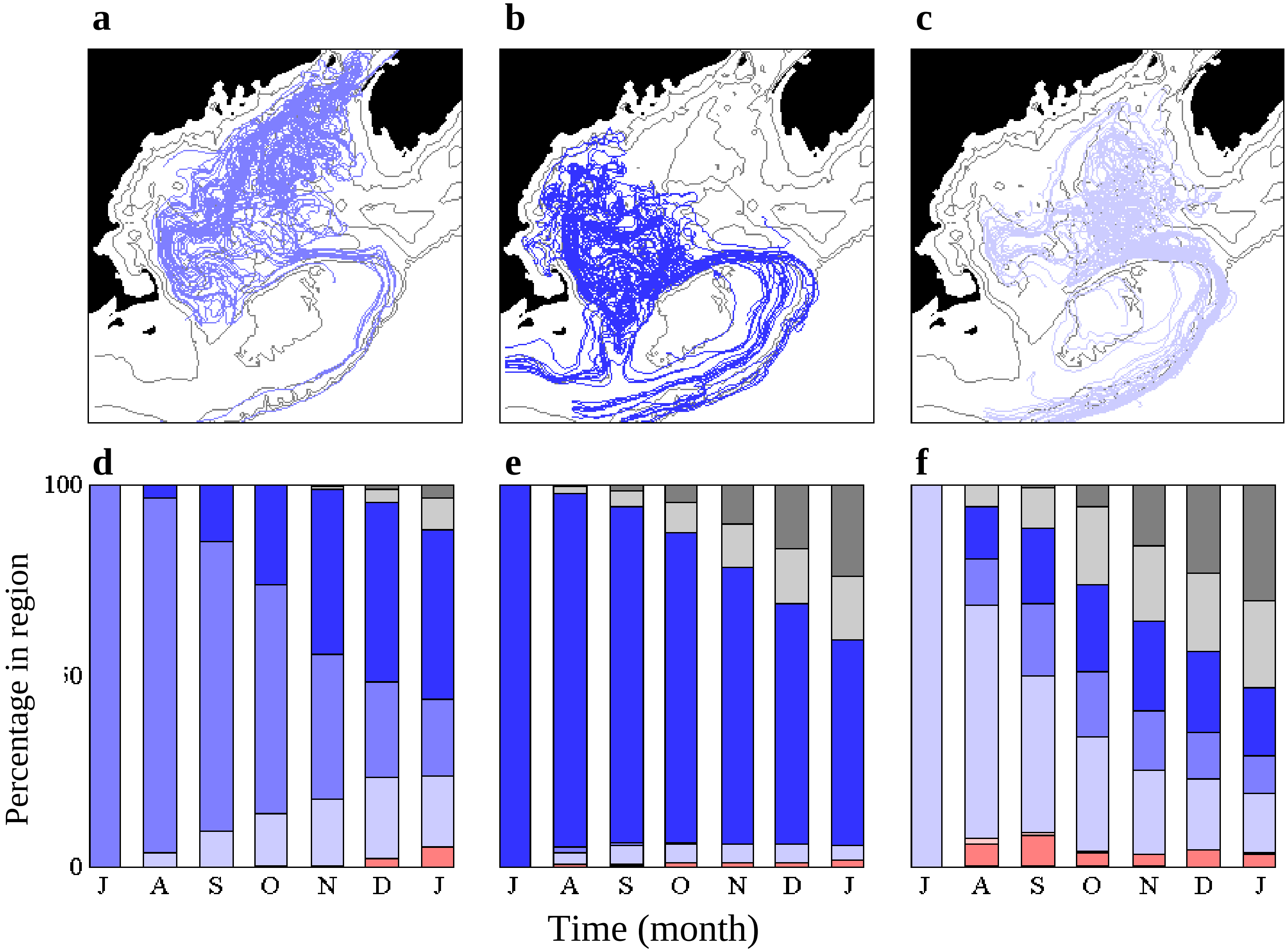


Figure 2. Conceptual model of dormant copepod transport into and out of the deep Gulf of Maine.

Figure 3 (1 of 2)



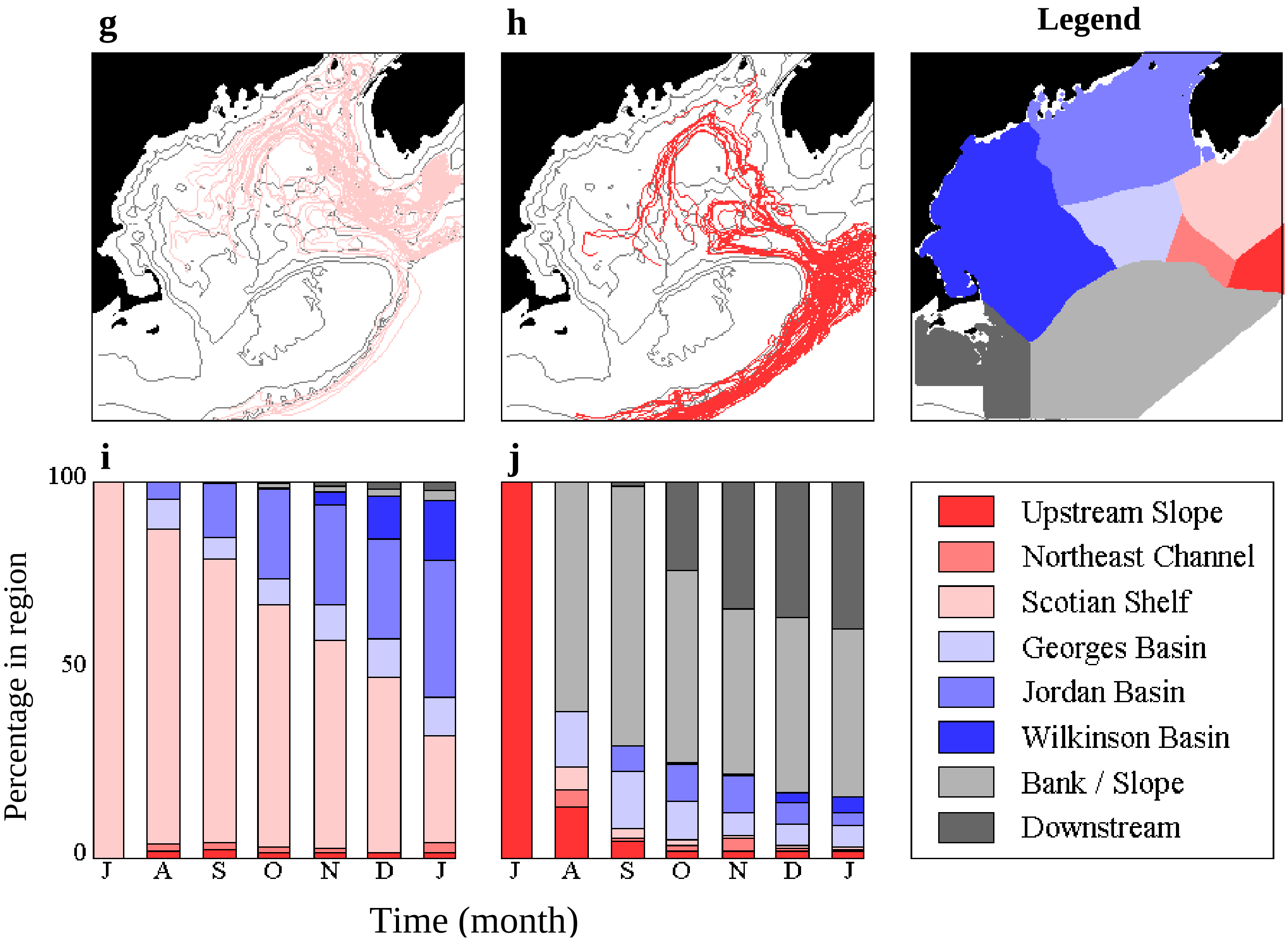


Figure 3. Particle pathways and fates in and around the Gulf of Maine. Passive particles were seeded at 150 m in transport simulations forced by monthly mean hydrography and running from 1 July to 1 January. Paths of 100 particles from each region are shown. Particle fates were plotted for the first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

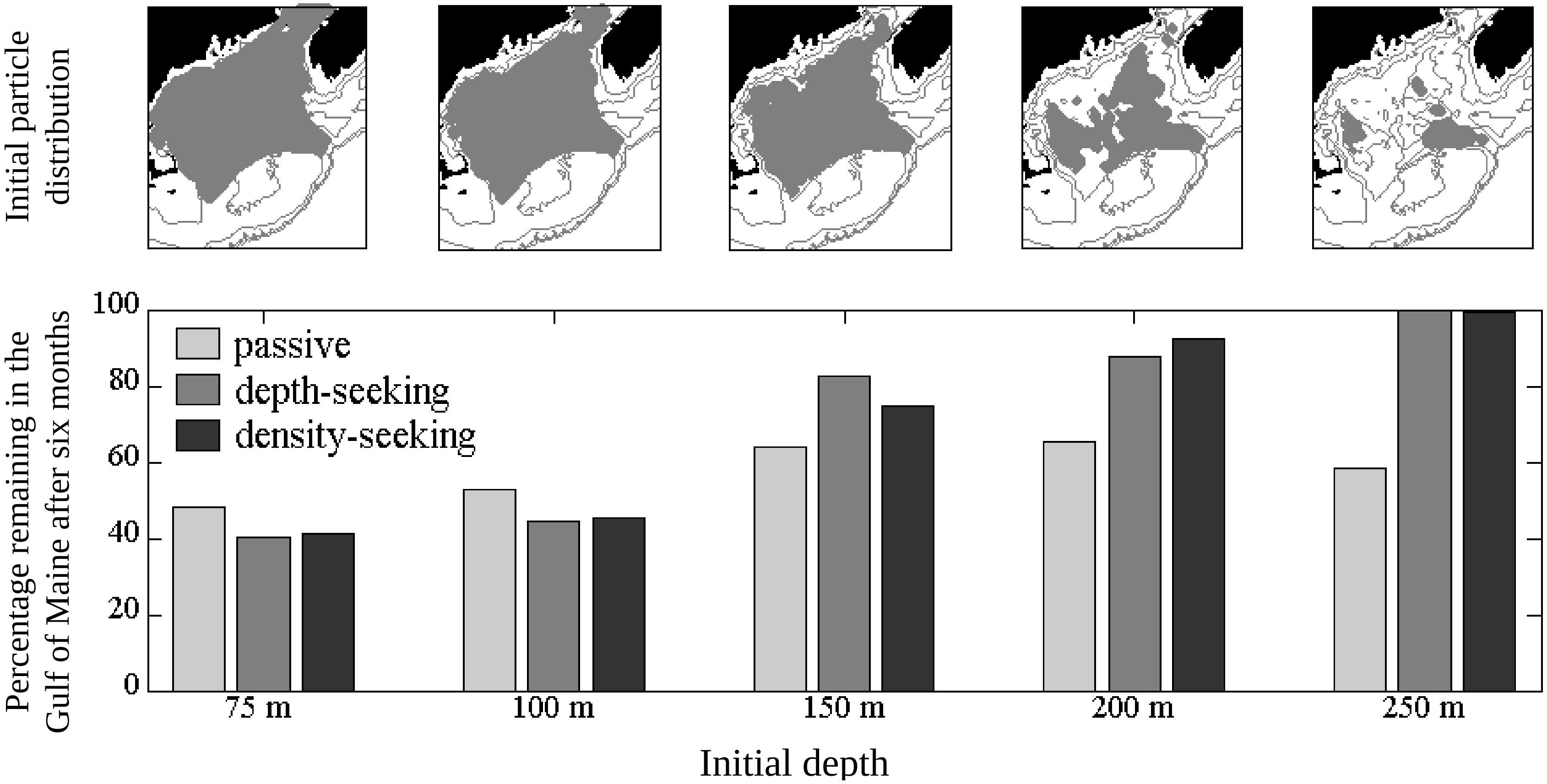


Figure 4. Retention of deep particles in the Gulf of Maine after six months, July 1 to January 1. Initial horizontal positions of particles are in upper row panels, above corresponding initial depth.

Figure 5

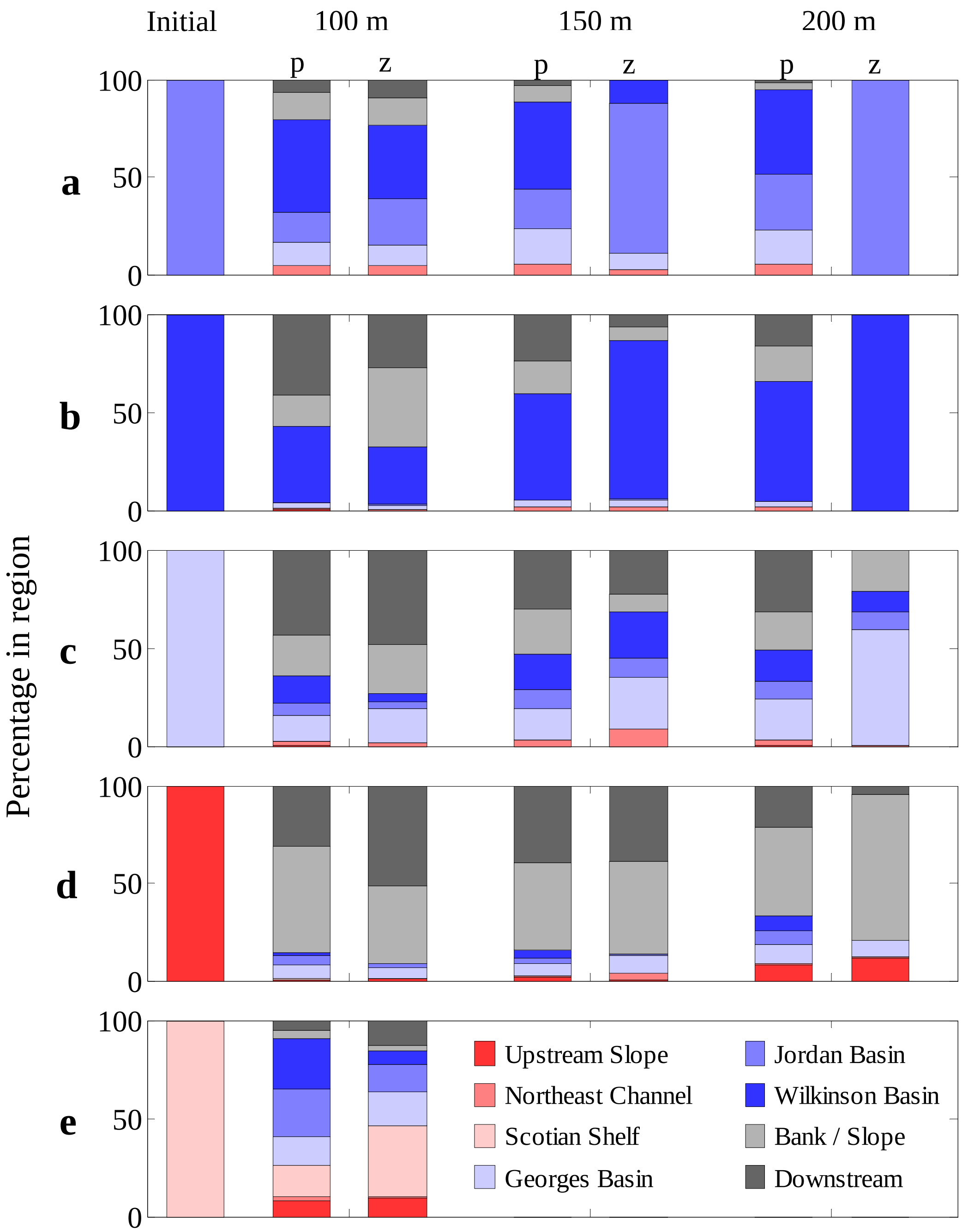


Figure 5. Effect of initial depth and behavior on particle fate in the deep Gulf of Maine. In each panel, initial particle distribution is indicated by the bar at left, (a) Jordan Basin, (b) Wilkinson Basin, (c) Georges Basin, (d) upstream slope water, (e) western Scotian Shelf. Pairs of bars compare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

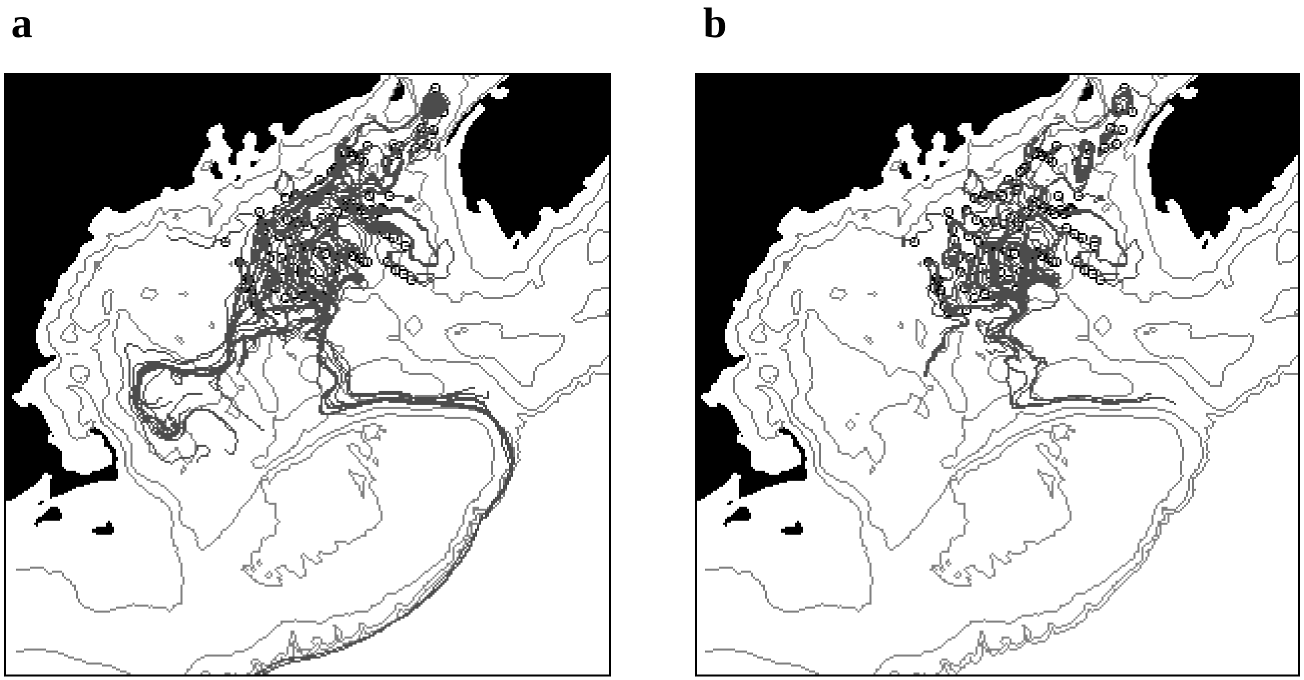


Figure 6. Pathways of (a) density-seeking and (b) fixed-depth particles seeded at 150 m in Jordan Basin. Transport simulations were forced by monthly mean hydrography and ran from 1 July to 1 January. Black circles are particle initial positions. Pathways of one hundred particles are shown.

Figure 7

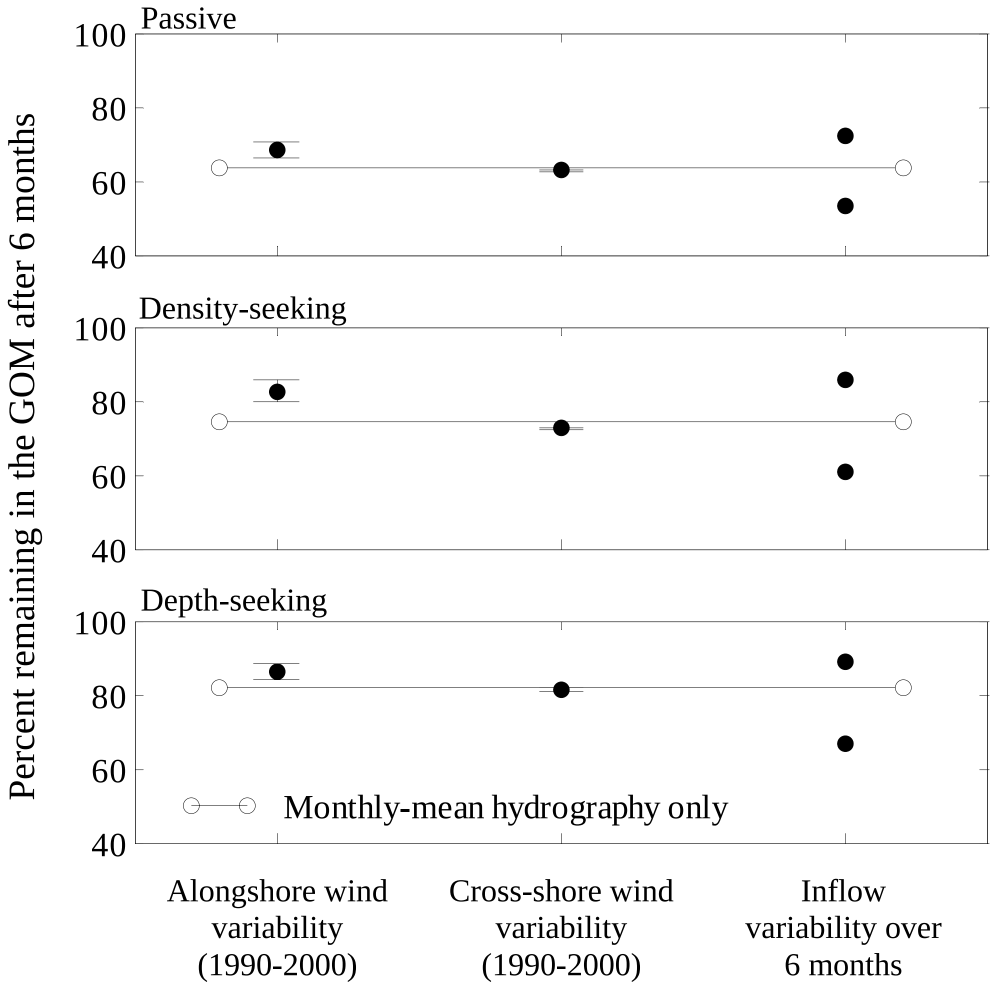


Figure 7. Effect of alongshore wind, cross-shelf wind, and Scotian Shelf inflow variability on retention of passive, density-seeking, and depth-seeking particles in the Gulf of Maine. Particles were released at 150 m on July 1, and transport was simulated until January 1. Solid lines represent retention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