Dispersal and settlement of sea scallop larvae spawned in the fishery closed areas on Georges Bank

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Three fishery closed areas in the Georges Bank (GB) region were implemented in 1994 to protect depleted groundfish stocks for population replenishment. However, the drift and ultimate destination of larvae spawned in the closed areas have not been specifically analyzed within the framework of ocean currents. To assess the efficiency of the closed areas as population replenishment sources, we conducted a simulation-based analysis on the dispersal and settlement of sea scallop larvae spawned in the closed areas from 1995 to 2005 using circulation fields computed by the Finite-Volume Coastal Ocean Model (FVCOM), scallop survey data and a population dynamics model. Closed Area I (CAI) located in the Great South Channel (GSC) had a persistently high larval retention rate (86% on average). For Closed Area II (CAII) located on eastern GB, a considerable amount of the larvae were dispersed out of the domain. For the Nantucket Lightship Closed Area (NLCA) located on Nantucket Shoals (NS), larvae consistently drifted away from the region during the 11 simulated years. Our simulation revealed three high-retention regions which are the most suitable for closed-area selection and rotational fishery management in terms of larval supply to the GB-GSC region.

Keywords: Fishery closed area, Georges Bank, Lagrangian simulation, Larval dispersal, Sea scallop.
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**Running title:** Dispersal of scallop larvae from fishery closed areas
Introduction

Since 1994, three mobile-gear fishery closed areas have been implemented on Georges Bank (GB), in the Great Southern Channel (GSC) and on Nantucket Shoals (NS), respectively (Figure 1). These closed areas were aimed at protecting a number of groundfish species, including cod, haddock, pollock, flounders, hakes and the sea scallop Placopecten magellanicus (Murawski et al., 2000). The sea scallop abundance within these closed areas has increased by as much as 25-fold as compared to the pre-closure period (Stokesbury, 2002; Stokesbury et al., 2004; Hart and Rago, 2006). However, the increase in the scallop population did not significantly alter the recruitment on GB. The log-transformed mean recruitment indices (mean log e per tow) was 3.96 prior to the closure from 1980-1994 and 4.22 after the closure from 1996-2003 (Hart & Rago, 2006).

The question we are asking here is: where do the scallop larvae spawned in the closed areas go?

Larval retention and dispersal are of particular concern on GB due to its complex hydrodynamics and current systems (Beardsley et al., 1997). The tidal-mixing-front recirculation is believed to play a key role in larval retention and population maintenance, whereas the along-shelf current can transport larvae away from the region (Figure 1). Sherman et al. (1984) reviewed the fish spawning strategies on the US northeastern shelf ecosystems and concluded that the anticyclonic around-bank recirculation helps to retain fish larvae on GB. However, these current systems are subject to both local forcing such as wind (Noble and Butman, 1985; Houghton et al., 1988) and remote forcing such as cold water intrusion from the Nova Scotian Shelf (Greene and Pershing, 2003) and warm core ring detachment from the Gulf Stream (Beardsley et al., 1985). Variations in the
current system can lead to changes in larval dispersion and retention on an interannual basis. In 1987, for example, unusual strong along-shelf current transported a large number of fish larvae out of the GB region (Polacheck et al., 1992) and in April 1982, persistent strong northeast wind caused a significant amount of larvae dispersed off of GB (Lough et al., 1994).

The development of ocean circulation models provided a useful tool for evaluating the influence of physical forcing on larval dispersal and fishery recruitment. Using late winter/early spring 3D flow fields driven by $M_2$ tide, mean wind stress and inflow from the Nova Scotian Shelf, Werner et al. (1993) carried out an analysis on the dispersal of fish larvae spawned on the Northeast Peak (NEP) of GB. They found that while larvae drifting in surface waters were subject to loss from the bank, those located at mid depth (~30 m) were more likely to be retained in the region. Lough et al. (2006) conducted a modeling analysis on the dispersal and retention of cod and haddock larvae on Georges Bank based on field observations of spawning and composite weekly mean flow fields. They assumed two major spawning grounds where particles representing fish larvae were released during winter and spring seasons. They found that for the particles released on the NEP, the retention on GB ranged from <20% in winter to ca. 50% in mid-April. For particle released on the western GB, the retention remained around 20% from January through April, but increased to ca 50% in May. After 4-8 weeks of drift, most of the particles released from western GB drifted to the southern flank of GB and those from the NEP drifted to the northern flank of GB. As the sea scallop is concerned, Tremblay et al. (1994) undertook a similar analysis to examine the retention of scallop larvae on GB. Particles were released from the NEP, the GSC and the southern flank of GB to mimic
scallop spawning in these three areas. The particles were tracked for 30 to 60 days and they found a retention rate ranging from 10 to 73%, depending on the physical model configuration, pawning ground, drifting depth and duration. A key conclusion of these experiments is that the dispersal of fish larvae on GB is strongly dependent on a large number of physical and biological factors such as the large-scale along-shelf current, local wind forcing and the timing and location of spawning.

The previous modeling studies provided helpful insight in understanding fish larvae dispersal and retention on GB, but the fishery closed areas have rarely been specifically targeted. To this end, we conducted a series of Lagrangian simulations to analyze the dispersal and retention of scallop larvae spawned in the closed areas over a decadal time scale from 1995 to 2005. The turbulence and flow fields were computed using the state-of-the-art Finite-Volume Coastal Ocean Model (FVCOM), vertical migration and settlement of larvae were predicted using an individual-based population dynamics model (Tian et al., 2009), and high-resolution scallop video survey data (Stokesbury et al., 2004) were used to specify the spawning stocks. Our objective is to determine the larval dispersal and retention of each closed area as well as the retention rate of the whole region in a spatially-resolved manner. Our analyses demonstrated persistent larval retention hotspots which should be considered in the design of Marine Protected Areas and implementation of area-rotation scallop fisheries management.

**Methods**

Our experiment consists of coupling an individual-based population dynamics model (IBM) of sea scallop with the hydrodynamic model FVCOM to track the drift and
dispersal of larvae during their pelagic phase (Figure 2). Essentially, the three-dimensional flow field and turbulence diffusivity calculated by FVCOM were used to track the Lagrangian movement of larvae predicted by the IBM in which behavioral vertical migration was implemented for each life stages.

Physical model and simulation

FVCOM is a prognostic coastal ocean circulation model originally developed by Chen et al. (2003) and continually improved through a team effort (Chen et al., 2006; Cowles, 2008). This model is capable of resolving complex irregular coastlines and steep bottom topography by using unstructured triangular grids in the horizontal and a terrain-following coordinate transformation in the vertical. A hindcast experiment was conducted to establish the physical fields (velocity, turbulence, temperature and salinity) over the period from 1995 to 2005. The model was driven by wind forcing and heat fluxes computed by the MM5 meteorological model, observed river discharge from the primary rivers of the Gulf of Maine, tidal forcing constructed from the five principal constituents of $M_2$, $S_2$, $N_2$, $K_1$ and $O_1$, and an upstream open boundary influx on the Nova Scotian Shelf (see Cowles et al., 2008 for a more detailed description of the model setup). The model adequately predicted the temporal and spatial variations of subtidal currents and water stratification on the New England shelf (Cowles et al., 2008). The IBM was driven by the hourly archived current and turbulence fields predicted by FVCOM and the vertical random walk scheme of Visser (1997) was included to simulate the influence of turbulent mixing on larval distributions (Figure 2).
Scallop IBM

The sea scallop IBM was described in detail in Tian et al. (2009). Briefly, the model consists of 4 pelagic phases (egg, trochophore, veliger and pediveliger) (Figure 2). Individual development in the model is based on age: eggs < 2 days, trochophores 2-5 days, veligers 5-35 days and pediveligers > 35 days (Stewart and Arnold, 1994). Behavioral vertical migration is specified for each life stage. Eggs are spawned at 1 m above the bottom and passively drifting without vertical migration. Trochophores migrate upward to surface waters with a speed of 0.3 mm s\(^{-1}\) (Tremblay et al., 1994). Veligers are essentially subject to current drifting in the surface layers, but with a minimum upward migration (0.1 mm s\(^{-1}\)) applied to prevent larvae from being dispersed to the deep layers through random walk. Pediveligers migrate downward to the bottom (1.7 mm s\(^{-1}\)) for settlement. Simulated results showed that the vertical random walk dominated over vertical migration at the veliger stage such that the larvae remained distributed within the surface mixed layer (Tian et al., 2009).

Scallop data and spawning

A comprehensive video survey was conducted to investigate sea scallop abundance and distribution in the GB region in 2003 (Stokesbury et al., 2004). Their data were used to specify the spawning stock (Figure 3). This survey did not include the Canadian portion of GB. To have a complete estimation of the spawning stocks on GB, we used the scallop abundance data reported by Thouzeau et al. (1991) on the Canadian side. This data set only includes scallops age 3 and older in abundance estimates whereas the 2003 survey data of Stokesbury et al. (2004) include the scallop population from 1 year and older.
Young scallops from age 2 may begin to reproduce, but their fecundity and the egg viability are much lower than that of adults (McGarvey et al., 1992). In order to have a consistent age range for both the US and Canadian portions of GB, we determined the abundance of scallops older than age 3 from the video survey data using the von Bertalanffy growth function (Thouzeau et al., 1991). Although the two data sets were 15 years apart, we used the same spawning stock for all the simulated years so that the interannual variations in model-computed larval dispersal and settlement were driven only by physical forcing.

An average of 50 million eggs per female adult scallop during one spawning season (Langton et al., 1987) was used in the model. On GB, fall spawning generally occurs in late September or early October (Shumway et al., 1988; McGarvey et al., 1992; DiBacco et al., 1995) and lasts from less than 1 week to more than 1 month (Posgay and Norman 1958; Posgay, 1976; Mullen & Moring 1986; DiBacco et al. 1995). To mimic the spawning activity, we assumed that the scallop spawning had a normal distribution in time with peak spawning on the 20th of September and a standard deviation of one week. As such, the spawning lasts about 1 month (the cumulative probability of 4 standard deviations amount to 95%). As the above spawning parameters were based on field observation, we called this the “Standard run”. However, the timing and duration of spawning can vary from year to year. In order to assess the potential impacts of the variations in spawning on the dispersal and settlement of scallop larvae, we conducted two additional sensitivity-analysis runs by (1) delaying the spawning by 1 month (peaking spawning on the 20th of October) and (2) reducing the spawning period to ~1 week by using the standard deviation of 2 days.
Simulation setup

The simulation was restricted in the GB-GSC-NS domain between 30°40' and 42°20' N in latitude and between 65°40' and 70°20' W in longitude (Figure 1). The model was integrated over a three-month period from Sep. 1 to Nov. 30 each year using a time step of 120 seconds in the Standard run and in the 1-week spawning run. For delayed-spawning run, the model was integrated from Oct. 1 to Dec. 30 each year.

To avoid unrealistic computational requirements deriving from tracking each spawned egg, we employed the technique of Lagrangian ensemble particles with each particle representing $10^{11}$-$10^{13}$ individuals at the time of release. The employment of Lagrangian ensemble particles, also known as “super-individuals”, is commonly used in plankton and fish larvae simulation when the number of individual organisms is far beyond the computational capacity (Scheffer et al., 1995; Bartsch and Coombs, 2004; Woods, 2005).

The depth range between the 18-m to the 110-m isobaths in the GB-GSC-NS domain is considered suitable habitat for scallop survival (Hart and Chute, 2004). Larvae settling in this depth range throughout the domain were considered “successful” (i.e. retained in the region). Due to important mortality losses during the pelagic phase (23% daily was used in the model; McGarvey et al., 1992), comparison between the numbers of successfully settled larvae and those spawned in a given closed area is impractical. Consequently, mortality losses were not accounted for in the retention rate calculation.

The retention rate of a particular closed area was calculated as the number of larvae retained in the whole GB-GSC-NS domain divided by the total spawned from that closed area. In regions where no adult scallops were observed, the retention rate was set to 0.
(otherwise division by zero of total spawning would generate an infinitely great retention rate).

Results

Sensitivity analysis

The sensitivity-analysis runs were not significantly different from the Standard run (Table 1). The Standard run predicted a global retention rate of 49% on average over the 11 simulated years, and the two sensitivity-analysis runs resulted in similar global retention rates, 47% by delaying the spawning 1 month and 51% by reducing the spawning duration from 1 month to 1 week. If 0.05 is chosen as the significant level, two-tailed t-test also failed to reject the null hypothesis of similarity for CAI and CAII including the northern scallop aggregation. The p-value was below the significant level for only two cases: the 1-week spawning run for the southern scallop aggregation of CAII and the delayed spawning for NLCA. For the first case, the difference occurred in 1996 when the retention rate increased from 40 to 52%, in 2000 with retention rate increased from 49 to 62% and in 2005 when 9% of the larvae spawned by the southern scallop aggregation were retained in the simulation domain in the 1-week spawning run whereas all were dispersed out in the Standard run (results not listed in Table 1). However, the effect of the aforementioned deviation in retention rate is limited, given that the difference in retention for the whole CAII remained insignificant between the two runs (Table 1). In the case for NLCA, the difference occurred in 1998 when 16% of the larvae released from NLCA were retained in the delayed-spawning run whereas only 3% in the Standard run, and in 2003 with a retention rate of 18% versus 5%. Because of the low
retention rate in general of this closed area, the different retention predicted by the two
runs did not significantly affect the overall retention. The results of the sensitivity
analysis indicate that the model assumptions tested do not significantly influence the
calculated retention rate.

In total, $100 \times 10^{15}$ eggs were released in the simulation domain. In this total spawning, the
three closed areas contributed 48%, with the Canadian GB contributing 20% and the US
open areas 32% (Fig. 4). Given that historic data collected during the late 1980s were
used for the Canadian portion of GB, the simulated spawning can not be directly
compared with that in the US waters. By subtracting the larvae released in the Canadian
waters from the total spawning, the three closed areas accounted for 60% of the total
spawning in the US regions, with CAII contributing the largest share (33%), followed by
NLCA (16%) and CAI (11%). Stokesbury et al. (2004) reported that scallops in the
closed areas were larger on average than those in the open region. They estimated that
while ca. 66% of scallops were found in the closed areas, these larger scallops accounted
for 80% of scallop resources in terms of harvestable biomass (adductor meat) over the
entire US portion of GB and the GSC. As large adult scallops have higher fecundity than
small ones, the actual contribution of the closed areas to the total spawning may be higher
than that predicted by the model.

The contribution of each closed area to the total number of successfully settled larvae
differed from that to the total spawning. The total number of successfully settled larvae
was ca. $10.9 \times 10^{12}$ individuals, of which 25% were spawned in the Canadian portion of
GB and 75% from the US region. The NLCA contributed less than 1% of the total successful settlement but accounted for 13% of the total spawning. On the other hand, CAI’s contribution to the total settlement (17%) was much higher than to the total spawning (8.5%), whereas the CAII’s contribution to spawning and settlement were nearly equal (27%). However, the relative contribution of the northern and southern scallop aggregations of CAII to the total settlement differed from that to the total spawning. The northern aggregation contributed 17% to the total settlement and 10% to the total spawning. On the other hand, the contribution of the southern aggregation to settlement (9%) was much lower than to spawning (16%).

Retention rate and settlement ground of the closed areas

Changes in the relative importance of each closed areas in the total spawning and settlement resulted from their differential retention rates (Table 1). CAI had a consistently high retention rate with a global average of 86% over the 11 simulated years and a coefficient of variation (CV) of 0.09. This high retention rate enabled the relative contribution of CAI to the total settlement twice the spawning contribution. The relative importance of CAII in the total spawning and settlement was primarily determined by its northern and southern scallop aggregations which accounted for 97% of its total scallop population. Scallop larvae spawned by the northern aggregation also showed persistently high retention rates, with a global average of 83% and a CV of 0.46. However, larvae spawned by the southern scallop aggregation had low retention rate (35% in average) and high CV (0.83). As a result, CAII as a whole had an intermediate retention rate (55% on average over time and among different sensitivity-analysis runs) and interannual
variability (CV=0.36). NLCA had the lowest retention rate among all the closed areas, only 4% on average and a CV of 1.25. Due to its extreme low retention rate, the relative contribution of this closed area to the total number of settled larvae was considerably reduced (< 1%) as compared to that to the total spawning (13%).

The settlement ground of scallop larvae differed among the closed areas. In this section we use four years to illustrate the settlement ground of the larvae spawned in the closed areas and interannual variations: 1995 and 2003 when abundant larvae settled within the simulated domains and 1998 and 2004 when the overall retention rate was low. The larvae spawned in CAI mainly settled on GB, particularly on the southern flank (Figure 5). The settlement sites were consistent from year to year. With the exception of 1995 when a portion of the larvae settled in the shelf-break region near the 100-200 m isobaths, most of the larvae settled near the 60 m isobath close to the tidal-mixing front. Larvae spillover (export from the closed area) due to current dispersion dominated over settlement within the closed area. On average only 9% of the larvae spawned in CAI were retained in CAI over the 11 simulated years. Greater interannual variation was observed for CAII than for CAI. For the northern scallop aggregation, most of the larvae settled in the GSC in 1995, but in 2003 they settled on the southwestern flank (Figure 6). For the two years of low global retention, the majority of the larvae spawned by the CAII northern scallop aggregation settled on the Southern New England shelf. For the southern scallop aggregation in CAII (Figure 7), the majority of the larvae settled in the GSC and on the northern flank of GB in 1995, but on the southern end of the GSC in 2003. In 1998 and 2004, few larvae spawned by the southern scallop aggregation were retained within the simulation domain. Spillover also dominated over settlement in situ for CAII, with <
2% of larvae settled within the same closed area. For NLCA, most of the larvae systematically drifted out of the simulation domain with an overall average of retention of only 4% (Table 1).

**Distribution of retention rate**

The overall distribution of retention rates was exemplified by 1995, a good settlement year class and by 1998, a poor settlement year class, and the averaged distribution over the 11 simulated years (Fig. 8). In 1995, high larval retention rate resulted for a vast region around GB including the GSC, the northern flank, the Northeast Peak and the southern flank of GB, particularly the region between the 60 and 100 m isobaths. CAI and CAII were both within the high-retention region, but NLCA retained few larvae. In 1998 when the overall larval retention was low, high retention was also simulated for the GSC and the northern flank where CAI and northern scallop aggregation of CAII were located, and again the NLCA had low retention. On the southern flank, however, the high-retention region was considerably reduced. Only a limited area close the 60-m isobath showed relatively high retention whereas most of the larvae spawned on the southern flank including the southern scallop aggregation of CAII drifted out of the GB-GSC-NS region. The long-term average over the 11 simulated years revealed three persistently high-retention regions. The northern part of the GSC and the northwestern part of GB had constantly higher retention rates over all 11 years. CAI is located in this region and thus has a high retention rate with limited interannual variation. The northeastern part of GB also had a relatively high retention rate, including the northern scallop aggregation of CAII. Persistently high larval retention rates was also simulated
for the open areas west to CAII on the southern flank (Figure 8). Note that NLCA is located in a region where larval retention was consistently low during the 11 years whereas the southern part of CAII is in an intermittent region where the larval retention rate showed large interannual variations.

Discussion

Scallop larval dispersion and retention are primarily determined by the current system and the location of the adult spawning populations. Three major currents constitute the basic current framework in the region: the tidal-mixing-front recirculation along the 60-m isobath on GB, the along-shelf current at the shelf-break region around the 100-200-m isobaths and the Western Main Coastal Current (WMCC), which bifurcates near Cape Cod, with one branch crossing the northern end of the GSC and joining the GB recirculation (Figures 1 and 9). These current systems are subject to both remote forcing such as the Nova Scotian Shelf inflow and warm-core ring activity from the Gulf Stream and local forcing such as wind, stratification and river discharge.

The tidal mixing-front recirculation tends to retain scallop larvae on GB whereas the along-shelf current on the southern flank of GB tends to transport larvae out of the domain. Closed Area I is located in the eastern and northeastern sides of the GSC, on the paths of the tidal-mixing-front recirculation and the cross-over of the coastal current. These two currents transport scallop larvae from CAI onto GB, resulting in high retention rates. There are two places where scallop larvae can drift out of the domain: the northwestern corner of GB where larvae can be dispersed into the deep gulf and along the slope region of NS where larvae can be transported out of the domain toward the SNES.
In 2002, for example, a considerable amount of larvae spawned in CAI were dispersed into the deep gulf waters from the northwestern corner of GB (not shown in figures). That year was characterized by a weak coastal current and the absence of the cross-over on the northern end of the GSC (Figure 9). Larval dispersion into the deep gulf also occurred in 1997 and 1999 when the coastal current was weak. Consequently, the coastal current and the cross-over to GB play a key role in preventing larvae from being transported into the deep regions of the Gulf of Maine.

Losses of larvae from the NS slope is limited for CAI primarily because most of the larvae spawned in CAI were first transported eastward along the coastal-current cross-over and the tidal mixing-front recirculation. These larvae were settled before reaching the NS slope during the around-bank drift. Moreover, a considerable amount of the larvae spawned in CAI dispersed around or inside the tidal-mixing front which prevented them from being “washed out” to the shelf-break region where they can be transported out of the domain by the along-shelf current.

For CAII, the northern population had high retention rates (Figures 5 and Table 1), as it is close to the tidal-mixing front. The larvae spawned in the northern part of CAII were transported by the tidal-mixing-front recirculation and settled in the GSC and on the northern flank. On the other hand, the CAII southern scallop aggregation is located between the 60-m and 100-m isobaths close to the along-shelf current. Larvae spawned there are more susceptible to be drifted out of the domain with the along-shelf current (Figure 7). The relative strength of the tidal-mixing-front recirculation and the along-shelf current primarily determines the retention rate of the larvae spawned in the southern part of CAII. For example, the strong tidal-mixing-front recirculation in 1995 led to a
good year class and the strong along-shelf current in 1998 led to a poor year class in larval retention and settlement and the weak along-shelf current in 2003 led to a good year class in larval retention (Figures 7 and 9).

Interannual variability in recruitment represents a major challenge in fishery management. Our model showed that even with the same closed areas, larval dispersal and supply to the region can vary on an interannual basis due to changes in the current system, particularly for the CAII southern scallop aggregation. In 1998, for example, in response to a shift in the North Atlantic Oscillation, cold water streamed into the region via the Nova Scotian Shelf which significantly strengthened the along-shelf current on the southern flank of GB (Greene and Pershing, 2003; Tian et al., 2009). Subsequently, most of the larvae spawned in the southern part of CAII were carried away from the region (Fig. 7). As an example of local forcing effect, abundant larvae spawned by the CAII southern aggregation settled in the simulation domain in 2003 whereas only a limited number of larvae were retained in 2004. The primary difference in forcing between these two years was the wind stress (Figure 10). Persistently strong northerly and northeasterly wind prevailed in October 2004 (scallop larvae drifting period) whereas weak southerly wind was observed in the same period in 2003. We believed that the wind forcing in 2004 is the primary factor leading to the massive larvae loss from the southern flank of GB. The winds affect not only the current system, but also the position of larvae within the current system. Northerly and northeasterly wind can disperse larvae on GB toward the shelf-break region where they will be transported away from the region by the along-shelf current.
NLCA is located on the path of the along-shelf current, which explains the systematic losses of larvae from this closed area. Larvae spawned in NLCA can be potentially beneficial to other downstream regions of the along-shelf current. As the GB-GSC-NS region is concerned, our work demonstrates that the contribution of larvae from NLCA is negligible (Figure 4).

Even with these interannual variations, the model predicted several persistent high-retention areas, which might be more beneficial to the whole region as fishery closed areas in terms of larval supply and population replenishment (Figure 8). First, the northeast end of the GSC and the northwest corner of GB have the highest retention rates. CAI is partly within this region. Based on the model predictions, the efficiency of CAI can be improved by displacing it farther northeastward to cover the entire high-retention region. The northern flank of GB represents the second largest high-retention areas. The northern part of CAII is located within this high-retention region, but a large portion of CAII, including the middle and southern parts, are located in a low or intermittent-retention region. A closed area comprising the persistent high-retention region on the northern flank could potentially provide more scallop larvae to the whole region compared with the present CAII boundaries. NLCA is located in typically low retention areas which provides few larvae for the region. An alternative location on the central southern flank could be more beneficial for scallop recruitment. A rotational closure among the three persistently high retention areas represents an optimal combination based the modeled results.

It should be pointed out that our model has a number of limitations. First, only physical dispersion was considered in this model analysis. Other factors can also
influence larval settlement and recruitment, such as variability in fecundity, predation and mortality losses (Garrison et al., 2000). Although a constant mortality was included in the model to approximate larval losses during the pelagic phase, these factors can vary in space and time which were overlooked during this study. Also, a particular spawning stock (2003) was used for all the simulated years. The potential impacts of interannual variation in the adult scallop density were not resolved. Secondly, the closed areas on GB were initially designed to protect all groundfish species (Murawski et al., 2000). The modeling analysis was conducted only on the sea scallop. Larval dispersal of other groundfish species can differ so that a comprehensive analysis is needed for management purpose. Thirdly, the model provided estimation on larval settlement, but recruitment to the fishery population also depends on the survivorship after settlement. Even if the larvae were retained and settled in the region, their survivorship can vary depending on substrate types and benthic physical and biological environment. Finally, in addition to physical and biological consideration, social and economical factors are involved in fishery management. Larval dispersal and retention is only one of the multiple parameters based on which decisions of fishery management and closed area implementation are made.

**Conclusion**

In summary, pelagic scallop larvae are first subject to current dispersion before they settle on the bottom and ultimately recruit into the fishery population. The physical three-dimensional fields of current and turbulence established by the FVCOM hindcast experiment and the high-resolution video survey scallop data have enabled us to conduct
a detailed analysis on the dispersion and settlement of scallop larvae spawned in the
fishery closed areas over a decadal time scale. The retention rate of the larvae spawned in
the closed areas are primarily determined by the relative strength of three major currents
in the region: the tidal-mixing-front recirculation on GB, the along-shelf current on the
southern flank of GB and the Western Maine Coastal Current, one branch of which
crosses over the northern end of the GSC and flows towards GB. The tidal-mixing-front
recirculation helps to retain larvae on GB and the coastal current cross-over prevents
larvae from being dispersed into the deep gulf, whereas the along-shelf current transports
larvae away from the region. Closed Area I (CAI) is located on the path of the coastal
current cross-over and the tidal mixing front recirculation so that most of the larvae
spawned in CAI were retained in the region. Larvae spawned in the northern part of
Closed Area II (CAII) were mostly retained in the region whereas a considerable amount
of the larvae spawned in the southern part of CAII were found to drift out of the domain
by the along-shelf current. Given that NLCA is on the path of the westward along-shelf
current, larvae spawned in NLCA were systematically transported to downstream
regions. In general, the northern part of the GSC and the northwestern area of GB have
persistently high larval retention rates, followed by the northern flank of GB and the
central part of the southern flank of GB. Selection of fishery closed areas in these regions
can provide effective population replenishment to the whole system due to the high level
of retention. Our study demonstrates that coupled physical and population dynamics
models represent an efficient tool to analyze the dispersion and settlement of larvae
spawned in fishery closed areas and to evaluate larval retention versus loss through
physical dispersion. Such analyses can also be helpful in the design of Marine Protected
Areas and implementation of area-rotation fisheries management.

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Figure captions

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Figure 7. Final settlement of scallop larvae spawned by the southern scallop aggregation of the closed area CAII simulated by the Standard run. Solid lines are the 60, 100 and 200 m isobaths.

Figure 8. Distribution of scallop larvae retention percentage in 1995 (high retention year), 1998 (low retention year) and average over the 11 simulated years predicted by the
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Figure 9. Subtidal residual surface current in October (scallop larvae drifting period). Four years were depicted, with 1995 and 2003 as high larval retention years and 1998 and 2002 as low larval retention years.

Figure 10. Hourly wind pattern, monthly averages and variance-based wind ellipse in October (larval drifting period) in 2003 (high retention year) and 2004 (low retention year) on top of Georges Bank.
Table 1. Retention rate (± standard deviation) before mortality of each closed areas: CAI: Closed Area I; CAII: Closed Area II; CAII-N: Northern scallop aggregation in CAII; CAII-S: Southern scallop aggregation in CAII; NLCA: Nantucket Lightship Closed Area; Global: The entire simulation domain. t test P: Two-tailed t test probability to wrongly reject the null-hypothesis that a sensitivity run is undifferentiated from the Standard run; 1 month: The timing of spawning was delayed by one month; 1 wk: The spawning duration was reduced to one week.

<table>
<thead>
<tr>
<th>Run</th>
<th>Variable</th>
<th>CAI</th>
<th>CAII</th>
<th>CAII-N</th>
<th>CAII-S</th>
<th>NLCA</th>
<th>Global</th>
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<tr>
<td>Standard</td>
<td>Retention</td>
<td>87(±8)</td>
<td>54(±22)</td>
<td>79(±21)</td>
<td>36(±32)</td>
<td>3(±5)</td>
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<td>54(±17)</td>
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<td>0.25</td>
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<td>1 wk</td>
<td>Retention</td>
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<td>58(±20)</td>
<td>84(±26)</td>
<td>40(±32)</td>
<td>3(±4)</td>
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<td>0.10</td>
<td>0.34</td>
<td>0.03</td>
<td>0.09</td>
<td>0.27</td>
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<tr>
<td>Average</td>
<td>Retention</td>
<td>86(±8)</td>
<td>55(±20)</td>
<td>83(±38)</td>
<td>35(±29)</td>
<td>4(±5)</td>
<td>49(±13)</td>
</tr>
</tbody>
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