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 analysed specifically 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, scallop survey data, and a population dynamics model. Closed area I located in the Great Southern Channel (GSC) had a persistently high rate of larval retention (86% on average). For closed area II located on eastern GB, a considerable quantity of larvae was dispersed out of the domain. For the Nantucket Lightship Closed Area located on Nantucket Shoals, larvae consistently drifted away from the region during the 11 years simulated. Our simulation revealed three high-retention regions that 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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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). Sea scallop abundance within these closed areas has increased by as much as 25-fold compared with 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) were 3.96 before the closure, from 1980 to 1994, and 4.22 after the closure, from 1996 to 2003 (Hart and Rago, 2006). The question we are asking here is: to where do the scallop larvae spawned in the closed areas go?

Larval retention and dispersal are of particular concern on GB owing 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 alongshelf current can transport larvae away from the region (Figure 1). Sherman *et al*. (1984) reviewed the fish spawning strategies on the US northeastern shelf and concluded that the anticyclonic around-bank recirculation helped 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), as well as 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 inter-annual basis. In 1987, for example, an unusually strong alongshelf current transported a large number of fish larvae out of the GB region (Polacheck *et al*., 1992), and in April 1982, persistent strong northeasterly wind caused a significant quantity of larvae to be dispersed off 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 three-dimensional flowfields driven by M_2 tide, mean windstress, 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 although larvae drifting in surface waters were subject to loss from the bank, those located at mid-depth (~30 m) were more likely to

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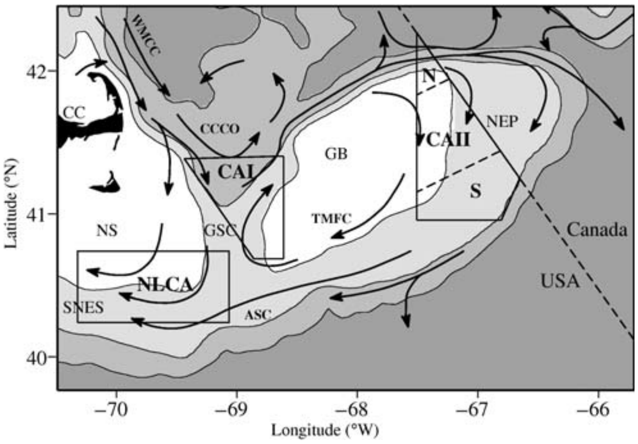

Figure 1. Summertime general subtidal circulation pattern over GB (reproduced from Beardsley *et al.*, 1997) and fishery closed areas. ASC, alongshelf current; CAI, closed area I; CAII, closed area II (N and S indicate the northern and southern scallop aggregation location); CC, Cape Cod; CCCO, coastal-current cross-over; GB, Georges Bank; NLCA, Nantucket Lightship Closed Area; NEP, Northeast Peak (Canadian portion of GB); SNES, Southern New England shelf; NS, Nantucket Shoals; TMFC, tidal-mixing-front recirculation; WMCC, Western Maine Coastal Current; GSC, Great Southern Channel. Continuous lines are the 60-, 100-, and 200-m isobaths.

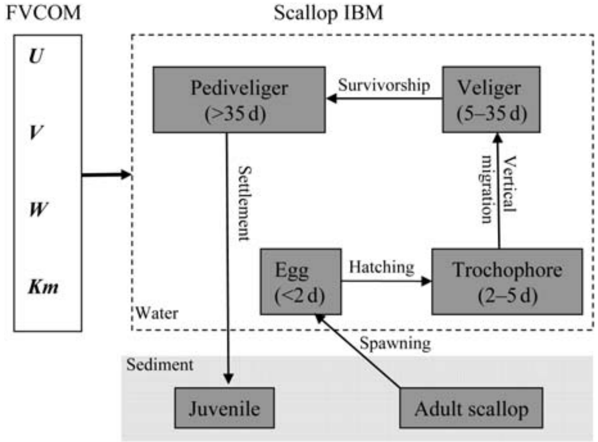

Figure 2. Experiment design. Drift and dispersal of sea scallop larvae predicted by a scallop IBM were tracked in the flow and turbulence fields predicted by FVCOM. The IBM was age-based, and the age limit of each pelagic phase was from Stewart and Arnold (1994). Vertical migration was implemented for trochophore (0.3 mm s^{-1} upwards), veliger (0.1 mm s^{-1} upwards), and pediveliger (1.7 mm s^{-1} downwards), whereas eggs were essentially subject to passive current drift and turbulence dispersal in the bottom layers.

be retained in the region. Lough *et al.* (2006) conducted a modelling analysis on the dispersal and retention of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae on GB based on field observations of spawning and composite weekly mean flowfields. They assumed two major spawning grounds where particles representing fish larvae were released during winter and spring and found that for particles released on the NEP, the retention on GB ranged from <20% in winter to ~50% in mid-April. For particles 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 the western GB drifted to the southern flank of GB, and those from the NEP drifted to the northern flank of GB. For sea scallop, 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 the three areas. The particles were tracked for 30–60 d, and the retention rate ranged from 10 to 73%, depending on the physical model configuration, spawning 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 alongshelf current, local windforcing, and the timing and location of spawning.

The previous modelling studies provided helpful insights into understanding fish larva dispersal and retention on GB, but the fishery closed areas have rarely been targeted specifically. To this end, we conducted a series of Lagrangian simulations to analyse the dispersal and retention of scallop larvae spawned in the closed areas over a decadal time-scale from 1995 to 2005. The turbulence and flowfields 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 was 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 consisted 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 flowfield and turbulence diffusivity calculated by FVCOM were used to track the Lagrangian movement of larvae predicted by the IBM in which behavioural vertical migration was implemented for each life stage.

Physical model and simulation

FVCOM is a prognostic coastal ocean circulation model originally developed by Chen *et al.* (2003) and continually improved through team effort (Chen *et al.*, 2006; Cowles, 2008). The model can resolve complex irregular coastlines and steep seabed topography through the use of 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, salinity) over the period 1995–2005. The model was driven by windforcing 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 in subtidal currents

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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 is described in detail in Tian *et al.* (2009). Briefly, the model consists of four pelagic phases (egg, trochophore, veliger, pediveliger; Figure 2). Individual development in the model is based on age: eggs <2 d, trochophores 2–5 d, veligers 5–35 d, and pediveligers >35 d (Stewart and Arnold, 1994). Behavioural vertical migration is specified for each life stage. Eggs are spawned 1 m above the seabed and drift passively without vertical migration. Trochophores migrate upwards to surface waters at a speed of $0.3\ \mathrm{mm\ s^{-1}}$ (Tremblay *et al.*, 1994). Veligers are essentially subject to current drift in the surface layers, but with a minimum upward migration ($0.1\ \mathrm{mm\ s^{-1}}$) applied to prevent larvae from being dispersed to the deep layers through random walk. Pediveligers migrate downwards to the seabed ($1.7\ \mathrm{mm\ s^{-1}}$) to settle. 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). Those data were used to specify the spawning stock (Figure 3), although the survey did not include the Canadian portion of GB. To have a complete estimate of the spawning stocks on GB, we used the scallop abundance data reported by Thouzeau *et al.* (1991) on the Canadian side. This dataset only includes scallops aged 3 and older in abundance estimates, whereas the 2003 survey data of Stokesbury *et al.* (2004) included the scallop population from 1 year old up. Young scallops from age 2 may begin to reproduce, but their fecundity and egg viability are much lower than those of adults (McGarvey *et al.*, 1992). To have a consistent age range for both the US and Canadian portions of GB, we determined the abundance of scallops older than 3 years from the video-survey data using the von Bertalanffy growth function (Thouzeau *et al.*, 1991). Although the two datasets were 15 years apart, we used the same spawning stock for all simulated years so that the interannual variations in model-computed larval dispersal and settlement were driven only by physical forcing.

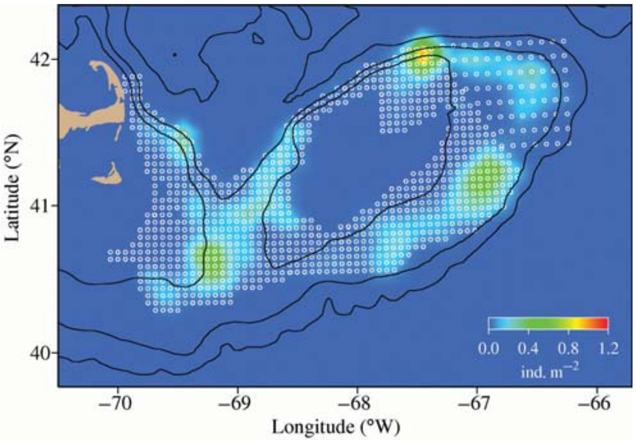

Figure 3. Spawning stocks determined by interpolating scallop abundance data onto the model grids. Scallop data (white circles) are from Stokesbury *et al.* (2004) and Thouzeau *et al.* (1991). Solid lines are the 60-, 100-, and 200-m isobaths.

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, autumn spawning is generally in late September or early October (Schumway *et al.*, 1988; McGarvey *et al.*, 1992; DiBacco *et al.*, 1995), and lasts from less than a week to more than a month (Posgay and Norman, 1958; Posgay, 1976; Mullen and Morning, 1986; DiBacco *et al.*, 1995). To mimic the spawning activity, we assumed that scallop spawning had a normal distribution in time, with peak spawning on 20 September, and a standard deviation of 1 week. As such, the spawning lasts about a month (the cumulative probability of four standard deviations amounts 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. 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 (i) delaying the spawning by 1 month (peaking spawning on 20 October) and (ii) reducing the spawning period to ~1 week by using a standard deviation of 2 d.

Simulation setup

The simulation was restricted in the GB–GSC–NS domain between 30°40 and 42°20′N and between 65°40 and 70°20′W (Figure 1). The model was integrated over a 3-month period from 1 September to 30 November each year using a time-step of 120 s in the Standard run and in the 1-week spawning run. For the delayed-spawning run, the model was integrated from 1 October to 30 December each year.

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

The depth range between the 18- and 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). Because of the 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 each closed area. In regions where no adult scallops were observed, the retention rate was set to 0 (because division by zero of total spawning would generate an infinitely great retention rate).

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Table 1. Retention rate (± s.d.) before mortality of each closed area: 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-analysis run is undifferentiated from the Standard run; 1 month, the timing of spawning was delayed by 1 month; 1 week, the spawning duration was reduced to 1 week.

Run	Variable	CAI	CAII	CAII-N	CAII-S	NLCA	Global
Standard	Retention	87 (±8)	54 (±22)	79 (±21)	36 (±32)	3 (±5)	49 (±15)
1 month	Retention	82 (±9)	54 (±17)	87 (±10)	29 (±24)	6 (±7)	47 (±11)
	t-test *p*	0.11	0.86	0.25	0.41	0.01	0.58
1 week	Retention	88 (±6)	58 (±20)	84 (±26)	40 (±32)	3 (±4)	51 (±13)
	t-test *p*	0.35	0.10	0.34	0.03	0.09	0.27
Average	Retention	86 (±8)	55 (±20)	83 (±38)	35 (±29)	4 (±5)	49 (±13)

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 years simulated, and the two sensitivity-analysis runs resulted in similar global retention rates, 47% by delaying the spawning by 1 month and 51% by reducing the spawning duration from 1 month to 1 week. If 0.05 is chosen as the significant level, a two-tailed *t*-test also failed to reject the null hypothesis of similarity for closed area I (CAI) located in the GSC, and for closed area II (CAII), located on GB, 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 the Nantucket Lightship Closed Area (NLCA) located on the NS. For the first case, the difference was in 1996, when the retention rate increased from 40 to 52%, in 2000, when the 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 was in 1998, when 16% of the larvae released from NLCA were retained in the delayed-spawning run, whereas only 3% were retained in the Standard run, and in 2003, with retention rates of 18 vs. 5%, respectively. Because of the low retention rate in general of this closed area, the different retention predicted by the two runs did not significantly influence the overall retention. The results of the sensitivity analysis indicate that the model assumptions tested do not significantly influence the retention rate calculated.

Closed area contribution to total spawning and settlement

In all, 100×10^{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% (Figure 4). Given that historical data collected during the late 1980s were used for the Canadian portion of GB, the simulated spawning cannot be compared directly with that in the US waters. By subtracting the larvae released in 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 although ~66% of scallops were in the closed areas, the 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 total spawning may be greater than that predicted by the model.

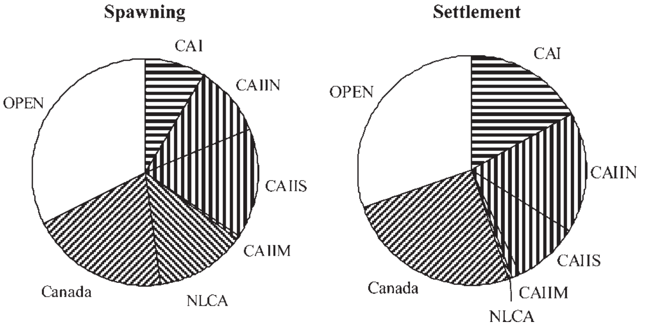

Figure 4. Contribution of each region to the total spawning and settlement in the simulation domain. CAI, closed area I; CAIIN, CAIIS, and CAIIM, northern and southern scallop aggregations and middle portion of closed area II; NLCA, Nantucket Lightship Closed Area; Canada, Canadian portion of GB; OPEN, US open areas.

The contribution of each closed area to the total number of successfully settled larvae differed from that contributing to total spawning. The total number of successfully settled larvae was ca. 10.9×10^{12}, of which 25% were spawned in the Canadian portion of GB and 75% in the US portion. The NLCA contributed <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 its own contribution to total spawning (8.5%), whereas the CAII's contributions 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 the contribution 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 it was to spawning (16%).

Retention rate and settlement ground of the closed areas

Changes in the relative importance of each closed area in the total spawning and settlement resulted from their differential retention

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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 rate of retention permitted the relative contribution of CAI to the total settlement to be 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 rates of retention, with a global average of 83% and a *CV* of 0.46. However, larvae spawned by the southern scallop aggregation had a low rate of retention (35% on average) and a 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 closed areas, only 4% on average and a *CV* of 1.25. Owing to its extremely low rate of retention, the relative contribution of that closed area to the total number of settled larvae was considerably lower (<1%) than its contribution to the total spawning (13%).

The settlement ground of scallop larvae differed among the closed areas. For this work, we use 4 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 rate of retention was low. The larvae spawned in CAI settled mainly on GB, particularly on the southern flank (Figure 5), and the settlement sites were consistent from year to year. Except 1995, when a portion of the larvae settled in the shelf-break region between the 100–200-m isobaths, most larvae settled near the 60-m isobath close to the tidal-mixing front. Spillover of larvae (i.e. export from the closed area) attributable to dispersion by currents dominated over settlement within the closed area. On average, just 9% of the larvae spawned in CAI were retained in CAI over the 11 years simulated. Greater interannual variation was observed for CAII than for CAI. For the northern scallop aggregation, most larvae settled in the GSC in 1995, but in 2003 they settled on the southwestern flank (Figure 6). For the 2 years of low global retention, most larvae spawned by the CAII northern scallop aggregation settled on the shelf off southern New England. For the southern scallop aggregation in CAII (Figure 7), most 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 settling within the same closed area. For NLCA, most of the larvae drifted systematically out of the simulation domain, with an overall average retention of just 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 (Figure 8). In 1995, high rates of larval retention resulted for a vast region around GB, including the GSC, the northern flank, the NEP, and the southern flank of GB, particularly the region between the 60- and the 100-m isobaths. CAI and CAII were both within the high-retention region, but NLCA retained few larvae. In 1998, when overall larval retention was low, high retention was also simulated for the GSC and the northern flank, where CAI and the northern scallop aggregation of CAII were located, and again the NLCA delivered low rates of retention. On the southern flank, however, the high-retention region was considerably smaller. Only a limited area close to the 60-m isobath showed relatively high retention, whereas most of the larvae

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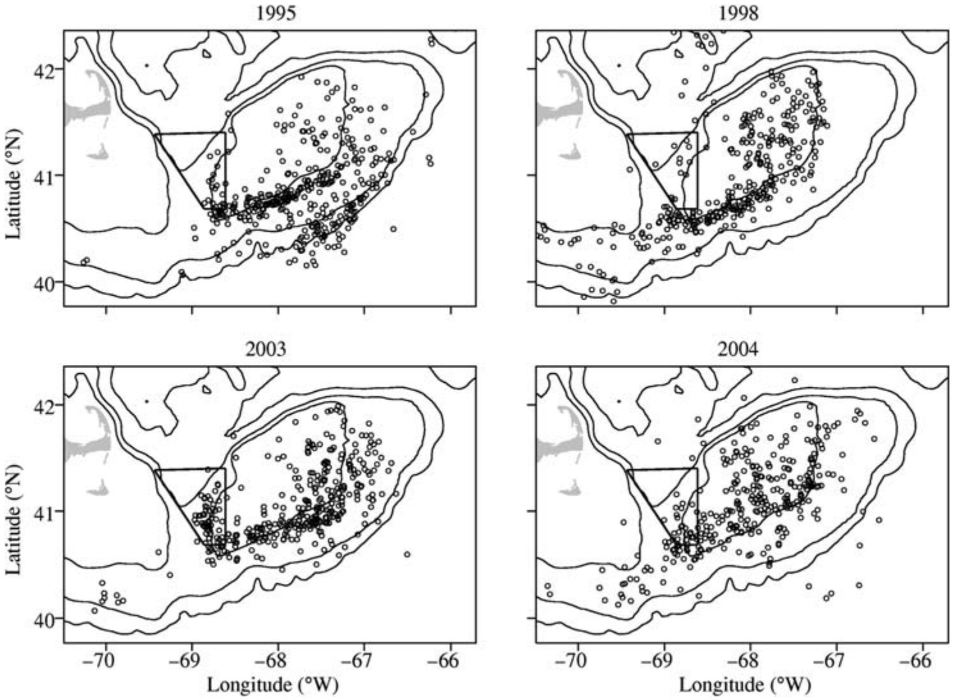

Figure 5. Final settlement of scallop larvae spawned in area CAI simulated by the Standard run. Solid lines are the 60-, 100-, and 200-m isobaths.

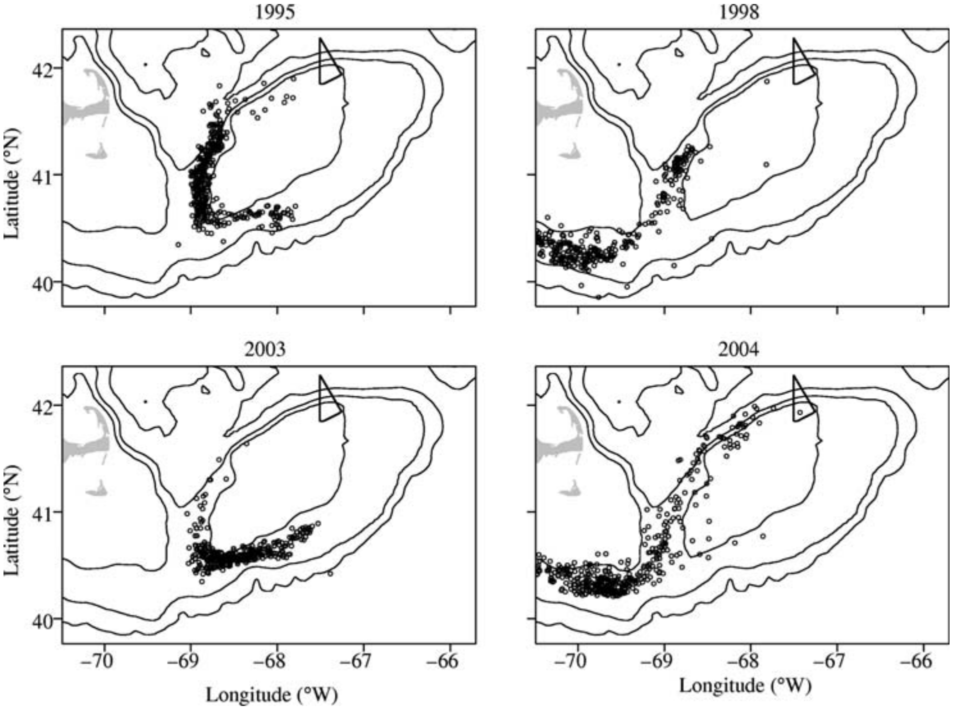

Figure 6. Final settlement of scallop larvae spawned by the northern scallop aggregation of area CAII simulated by the Standard run. Solid lines are the 60-, 100-, and 200-m isobaths.

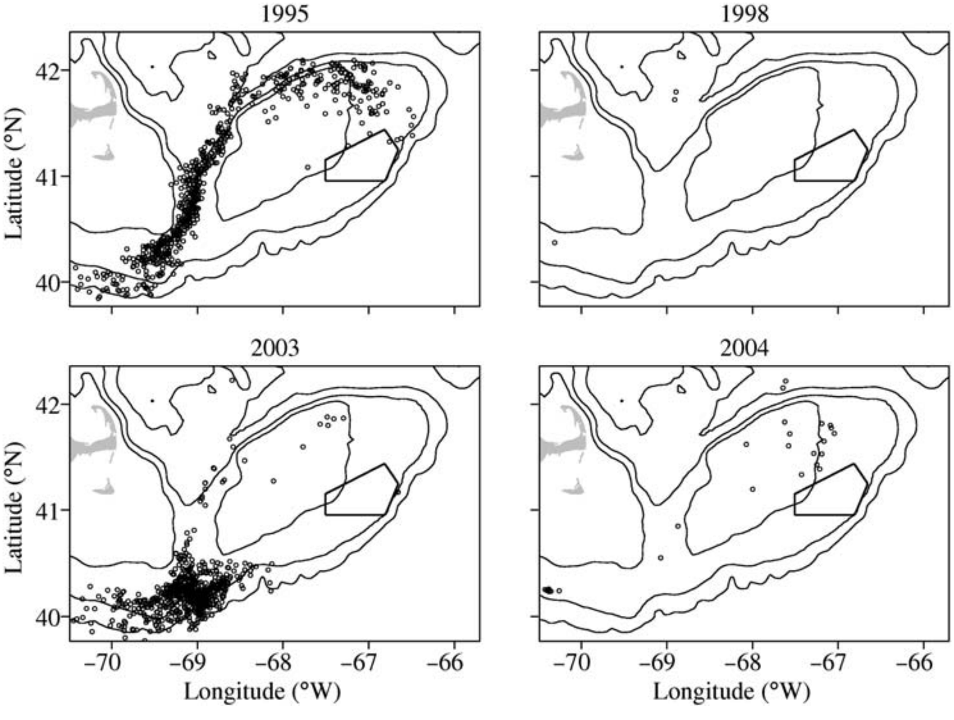

Figure 7. Final settlement of scallop larvae spawned by the southern scallop aggregation of area CAII simulated by the Standard run. Solid lines are the 60-, 100-, and 200-m isobaths.

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 years simulated 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 there, so has a high rate of retention with limited interannual variation. The northeastern part of GB also had a relatively high rate of retention, including

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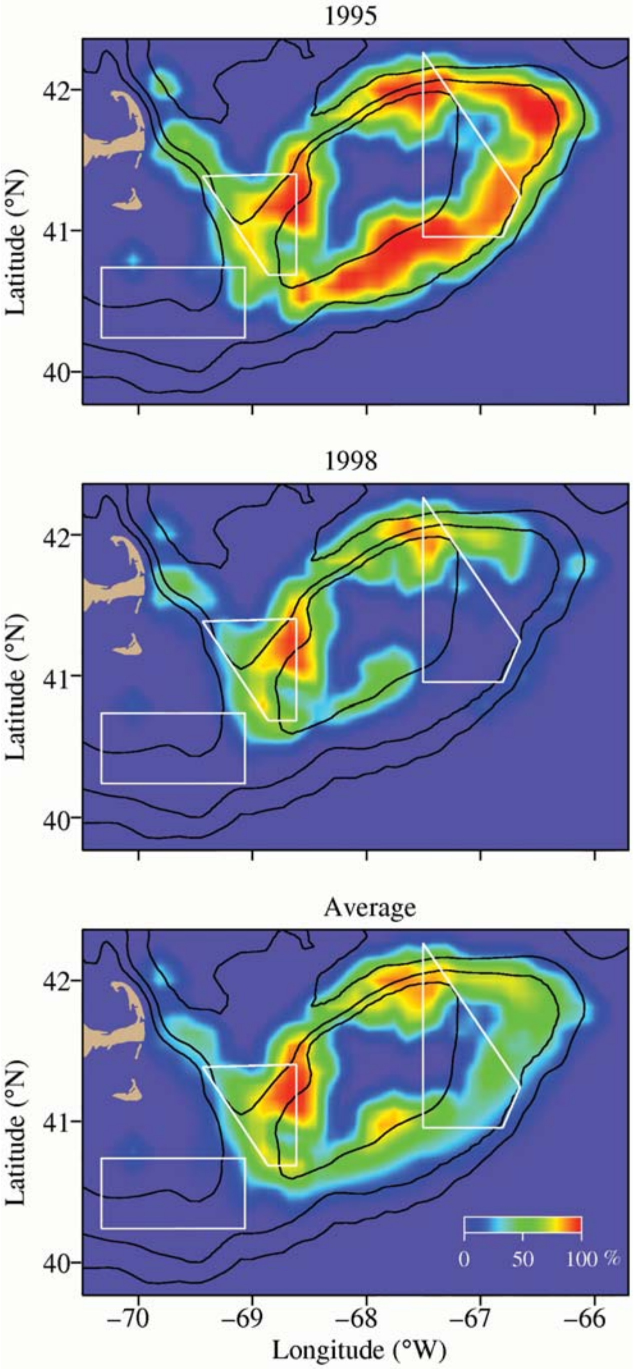

Figure 8. Distribution of scallop larvae retention percentage in 1995 (high retention year), 1998 (low retention year), and average over the 11 years simulated by the Standard run. The positions of the three closed areas are demarcated in white. Continuous lines are the 60-, 100-, and 200-m isobaths.

the northern scallop aggregation of CAII. Persistently high rates of larval retention were 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 rate of larval retention showed large interannual variation.

Discussion

Scallop larval dispersion and retention are determined primarily 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 alongshelf current at the shelf break around the 100–200-m isobaths, and the Western Maine 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 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 alongshelf current on the southern flank of GB tends to transport larvae out of the domain. CAI is located along 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 rates of retention. 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 towards the SNES. In 2002, for example, a considerable number of larvae spawned in CAI was dispersed into the deep gulf waters from the northwestern corner of GB (not shown in the 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). There was also larval dispersion into the deep gulf 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 to the deep regions of the Gulf of Maine.

Losses of larvae from the NS slope are limited for CAI, mainly because most of the larvae spawned in CAI were first transported eastwards along the coastal-current cross-over and the tidal-mixing-front recirculation. Those larvae settled before reaching the NS slope during the around-bank drift. Moreover, a considerable number 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 alongshelf current.

For CAII, the northern population had high rates of retention (Figure 5, Table 1) because 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- and the 100-m isobaths, close to the alongshelf current. Larvae spawned there are more likely to drift out of the domain with the alongshelf current (Figure 7). The relative strength of the tidal-mixing-front recirculation and the alongshelf 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 alongshelf current in 1998 led to a poor year class in terms of larval retention and settlement, and the weak alongshelf current in 2003 led to a good year class in terms of larval retention (Figures 7 and 9).

Interannual variability in recruitment represents a major challenge for fishery management. Our model showed that even with

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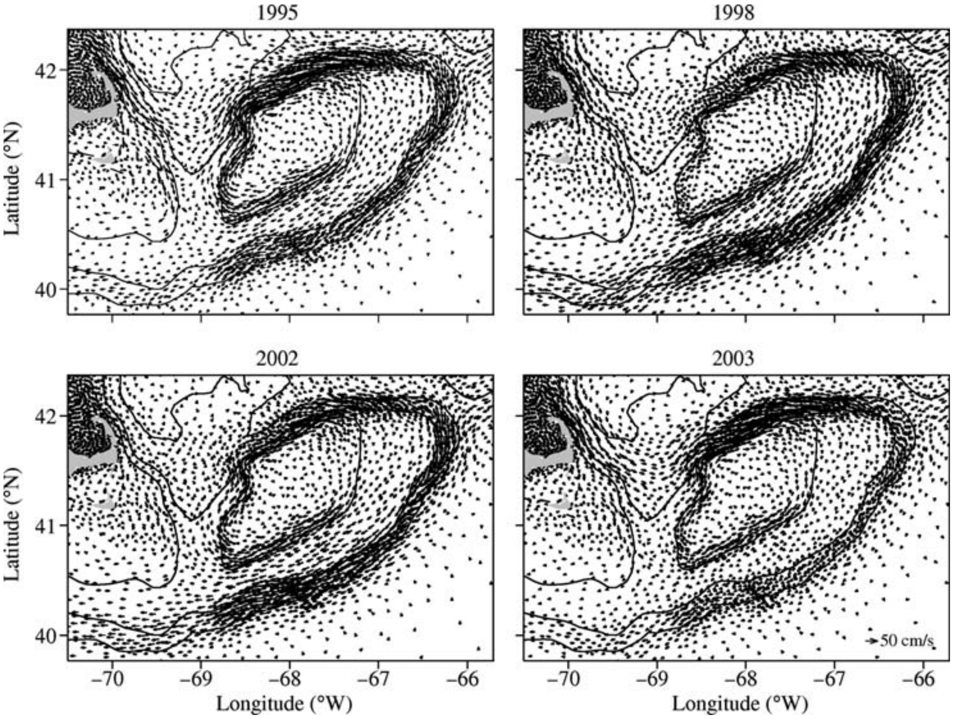

Figure 9. Subtidal residual surface current in October (scallop larvae drift period). Four years were depicted, with 1995 and 2003 as high retention years for larvae, and 1998 and 2002 as low retention years for larvae.

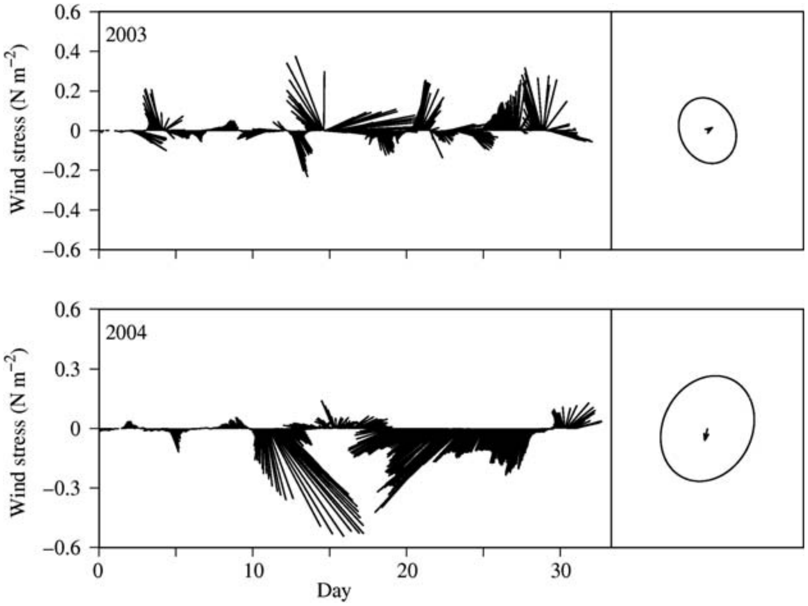

Figure 10. Hourly wind pattern, monthly averages, and variance-based wind ellipse in October (larval drift period) in 2003 (high retention year) and 2004 (low retention year) on the top of GB.

the same closed areas, larval dispersal and supply to the region can vary on an interannual basis through 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 significantly strengthening the alongshelf 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 (Figure 7). As an example of the 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 was retained in 2004. The primary difference in forcing between these 2 years was the windstress (Figure 10). Persistently

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strong northerly and northeasterly winds prevailed in October 2004 (the scallop larvae period of drift), whereas weak southerly wind was observed in the same period in 2003. We believe that the windforcing in 2004 was the primary factor leading to the massive loss of larvae 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 winds can disperse larvae on GB towards the shelf break, where they will be transported away from the region by the alongshelf current.

NLCA is located on the path of the alongshelf 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 alongshelf current. As far 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 sources (Figure 8). First, the northeast end of the GSC and the northwest corner of GB have the highest rates of retention. CAI is partly within this region. Based on the model predictions, the efficiency of CAI can be improved by displacing it northeastwards to cover the entire high-retention region. The northern flank of GB represents the second largest high-retention area. The northern part of CAII is located within this high-retention region, but a large portion of CAII, including the middle and southern parts, is located in a low- or intermittent-retention region. A closed area comprising the persistent high-retention region on the northern flank could provide more scallop larvae to the whole region than the present CAII boundaries. NLCA is located in typically low-retention areas, which provide 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 on the model results.

We stress that our model has a number of limitations. First, only physical dispersion was considered in the model analysis. Other factors can also influence larval settlement and recruitment, such as variability in fecundity, predation, and mortality loss (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, and this was 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. Second, the closed areas on GB were initially designed to protect all groundfish species (Murawski *et al*., 2000), but the modelling analysis was conducted only on sea scallop. Larval dispersal of other groundfish species can differ, so a comprehensive analysis is needed for management purposes. Third, the model provided estimates of larval settlement, but recruitment to the fishery population also depends on survivorship after settlement. Even if the larvae were retained and settled in the region, their survival can vary depending on substratum type and the benthic, physical, and biological environment. Finally, in addition to physical and biological considerations, social and economic factors are involved in fishery management. Larval dispersal and retention is only one of the multiple parameters based on which decisions on 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 seabed and ultimately recruit into the fishable 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 allowed us to conduct a detailed analysis of the dispersion and settlement of scallop larvae spawned in the fishery closed areas over a time-scale of a decade. The retention rate of the larvae spawned in the closed areas is determined primarily by the relative strength of three major currents in the region: the tidal-mixing-front recirculation on GB, the alongshelf 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 alongshelf current transports larvae away from the region. CAI is located on the path of the coastal-current cross-over and the tidal-mixing-front recirculation, so most of the larvae spawned in CAI were retained there. Larvae spawned in the northern part of CAII were mostly retained, whereas a considerable number of the larvae spawned in the southern part of CAII drifted out of the domain with the alongshelf current. Given that NLCA is on the path of the westward alongshelf 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 rates of larval retention, followed in strength of retention by the northern flank of GB, and the central part of the southern flank of GB. Selection of fishery closed areas in those regions would provide effective population replenishment to the whole system through the high level of retention.

Our study has, we believe, demonstrated that coupled physical and population dynamics models represent an efficient tool for analysing the dispersion and settlement of larvae spawned in fishery closed areas and for evaluating larval retention vs. loss through physical dispersion. Such analyses can also be helpful in the design of Marine Protected Areas and to support implementation of area-rotation fishery management.

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