THE IMPACTS OF SPATIAL AND TEMPORAL VARIABILITY OF LARVAL TRANSPORT ON THE DISTRIBUTION AND POPULATION DYNAMICS OF THE SEA SCALLOP (*PLACOPECTEN MAGELLANICUS*)

by

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ABSTRACT OF THE DISSERTATION

The Impacts of Spatial and Temporal Variability of Larval Transport on the Distribution and Population Dynamics of the Sea Scallop (*Placopecten magellanicus*)

by CHARLES GRANT LAW III

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John Wilkin

This project focuses on the population dynamics of sea scallops in the Middle Atlantic Bight and Georges Bank/Southern New England regions. Most sea scallop biomass now occurs within the confines of large federally mandated closed areas and the fishery has moved toward a rotational harvesting strategy. With this dissertation we develop a biophysical model that enables the role of physical variability in this system, and how it interacts with life history processes to shape local and global population dynamics for sea scallops. The modeling effort will link hind-cast circulation simulations, an individual-based model for larval drift and an adult, size-structured, spatial population model. The results of these modeling efforts are compiled and interpreted in such a way as to be useful to managers of the sea scallop fishery. The final goal is to provide information about the impacts of environmental factors on sea scallop population dynamics so that the fishery can be managed proactively instead of reactively. Understanding the connections between sea scallop sub-populations, and how they vary from year to year, should be
valuable in assessing the impacts of various real-world management strategies. The thesis is organized in four chapters: the first is an introduction, the second develops the dispersal kernels, the third integrates them into a metapopulation model, and the fourth describes the entire project in a style appropriate for a technical magazine.
Acknowledgements

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INTRODUCTION TO THE THESIS

OVERVIEW

This project focuses on the population dynamics of sea scallops in the Middle Atlantic Bight and Georges Bank/Southern New England regions. Most sea scallop biomass now occurs within the confines of large federally mandated closed areas and the fishery has moved toward a rotational harvesting strategy. We have developed a biophysical model that will help delineate the role of physical variability in this system and how it interacts with life history processes to shape local and global population dynamics for sea scallops. The modeling effort links hind-cast circulation simulations, an individual-based model for larval drift and an adult, size-structured, spatial population model. The results of these modeling efforts are then compiled and interpreted in such a way as to be useful to managers of the sea scallop fishery. Finally, we attempt to understand the mechanisms behind environmentally driven variability of sea scallop populations, and to develop methodologies that will apply this knowledge to management efforts. Understanding the mechanisms of variability allows managers to optimally distribute fishing mortality in time and space in such a way as to ensure a robust, resilient and sustainable scallop fishery. Most importantly, the development of these tools marks an important transition from the traditional, primarily reactive, management methods towards a more proactive, and ultimately effective, management paradigm. In addition to the better management outcomes an understanding of mechanisms provides, this knowledge also helps us anticipate the impacts of climate change, allowing the fishery to plan and adapt to future changes.
OBJECTIVES

The underlying objective of this work is the exploration, through modeling, of sea scallop population dynamics in a spatially-explicit context with realistic larval-transport and population size structures, within specific environmental regimes. To accomplish this goal, we have done the following:

1. Characterized variability in ecologically-important environmental factors within the system.
2. Developed a spatially-explicit, size-structured, scallop population model.
3. Developed a series of simulations representing spawning events in the system to characterize drift and connectivity under various plausible environmental scenarios.
4. Coupled the size-structured adult life history model to the early pelagic stage drift modeling activity ‘closing the life-cycle loop’ between spawning and recruitment.
5. Applied tools from network theory to facilitate direct analyses of the connectivity data generated by the simulations.
6. Identified correlations between environmental factors (i.e. NAO) and transport patterns, which can be used to anticipate population-level effects in the context of the environment.
7. Identified systemic changes in circulation, water mass characteristics, productivity, etc., which may help explain recent increases in the Middle Atlantic Bight sea-scallop populations.
MOTIVATION

Sea scallops are notable for being one of the great management success stories, having rebounded dramatically in response to groundfish closures on Georges Bank. Although population increases would seem to be a natural consequence of reduced fishing pressures, the groundfish these closures were implemented to protect did not benefit as much as sea scallops. It would appear that a simple reduction in fishing pressure is not enough in all cases to facilitate population rebounds. Was the success of sea scallops simply due to the closures? How would the sea scallop populations respond if the closed areas were instead sited 500 kilometers to the southwest of Georges Bank? The sea-scallop success must be understood if we want to successfully continue these practices, or extend them to other species. The relatively high environmental data density overlying the geographic range of sea scallops, coupled with the annual sea scallop survey data generated by NMFS provides the basic data needed to understand what happened. This work also provides some insight into the dynamics of other shelf species subject to the same environmental factors.

IMPACT

This research is highly relevant to contemporary fisheries programs that more and more are using the imposition of spatially structured fishing activity as a tool to manage resource populations (NEFSC 2007). Highly charged issues such as marine protected areas, no-fishing areas, marine reserves, and rotating closures all utilize management systems that spatially alter the application and intensity of fishing pressure. In some cases, such as Mid-Atlantic sea scallops (NEFSC 2007), this strategy imposes an artificial
spatial structure on a metapopulation and alters the effective connectivity between distant subpopulations. The effects of these changes are difficult to predict, and could interact with natural environmental variability in unexpected ways. The efficiency of spatial management strategies has not been adequately studied with respect to these variations.

The use of circulation models to track the potential paths of propagules is not a new idea, and has been utilized by several researchers (Quinlan et al., 1999; Lewis et al., 2001; Pederson et al., 2001; Armsworth 2002; Batchelder et al., 2002; Siegel et al., 2003; Bode et al., 2006). This effort differentiates itself from these prior efforts by characterizing transport between nodes in a continuous grid covering the entire shelf from Cape Hatteras north to Nova Scotia. Additionally, a set of tools borrowed from network theory (Roberts 1976) are compiled to help interpret the simulation results. Practical measures of strong and weak connectivities, self-seeding potentials, variabilities and other characteristics of connectivity can be used by managers to proactively manage populations for robust populations and high yields.

BACKGROUND

Recent work has begun to challenge the commonly held paradigm of well-mixed stocks or populations within management units. Close examinations of genetic patterns (Ruzzante 1998) and trace-element “fingerprints” (Thorrold, Campana et al. 1997; Thorrold, Jones et al. 1997; Thorrold, Jones et al. 1998; Thorrold and Shuttleworth 2000; Thorrold, Jones et al. 2006) within what appear to be homogenous populations suggest the presence of structure at both local and regional scales. In some cases, this intra-population structure correlates well with physical characteristics of the environment
(Ainley, Sydeman et al. 1993), a possibility suggested by Sinclair (Sinclair and Iles 1985; Sinclair 1988), and observed in other species of scallops (Bogazzi, Baldoni et al. 2005). Despite the enormous implications of these findings with regard to management, current practices treat populations as undifferentiated units.

It is easy to postulate many intra-population differences that could have profound effects on the efficacy of management strategies. Subpopulations with lower growth rates, smaller numbers or higher vulnerabilities to fishing practices could be more likely to fail than more robust sub-populations (Stephenson 1999). The loss in genetic diversity caused by such failures could negatively impact overall population resilience in the face of longer-term stresses, such as changes in climate or fishing practices (Agashe 2009). The failure of the fishing moratorium to replenish cod populations in the Northwestern Atlantic could be attributable to several processes (Frank et al., 2011), all of which may be complicated by the these changes in population structure (Ruzzante, Taggart et al. 1999), which limit “seeding” from the healthier off-shore populations.

The presence of structured sub-populations of cod in the coastal shelf environment is somewhat surprising given the fact that currents will tend to disperse eggs and larvae (Hastings and Botsford 2006). Local circulation processes are extremely varied throughout the eastern shelf, potentially retaining (Sinclair 1988), dispersing or aggregating pelagic stages depending on the nature of flow regimes. These processes may vary spatially, as shown by Ruzzante et al (1999), who found that large aggregations of mixed cod larvae broke up into consistent cohorts when observed at smaller spatial scales. For species with highly mobile adult stages, retention can be achieved through migration (Sinclair and Iles 1985; Sinclair 1988; Quinlan, Blanton et al. 1999; Ruzzante,
Taggart et al. 1999), effectively counteracting the dispersing effect of physics. By maintaining consistent sub-populations, a species gains the benefits of higher genetic diversity, potentially increasing their resilience to selective pressures.

Species with less motile juvenile or adult life histories, such as sea scallops, are harder to understand under this view of population structure. The pelagic larvae of sea scallops, like those of cod and menhaden, are incapable of counteracting the advective and dispersive ocean circulation processes observed in their habitat range. Unlike these finfish, however, adult and juvenile sea scallops are unable to migrate significant distances, limiting their ability to “close the loop” against the prevailing currents. This suggests the possibility that sea scallop population dynamics function in a way wholly different than those of finfish. It then follows that they may respond differently than finfish to management policies, and in fact, may benefit from a different strategy entirely.

Sea scallops inhabit the eastern shelf from the Gulf of St. Lawrence south to Cape Hatteras – a range that is similar to that of cod. Unlike cod, however, the spatial distribution of sea scallops is almost entirely a function of larval transport. For sea scallops, this means that their population dynamics are heavily influenced by both local circulation patterns, and the spatial distribution of adult biomass. Decades of sea scallop surveys give us a good idea of the spatial distributions of adults, but before we can understand the dynamics of the entire population as a whole, it is critical that we understand the trajectories taken by the pelagic stages released throughout the range.

The sea scallop, representing the United States’ second largest fishery (NEFSC 2007), has been well studied from a number of different perspectives. Lab and field measurements of larval behavior and distributions are well documented, and there exists
a substantial literature on sea scallop vital rates from aquaculture specialists. Additionally, detailed spatial measurements of population numbers, demographics and gonad/somatic indices (GSI), have been made by the National Marine Fisheries Services (NMFS).

In addition to being well described in the literature, sea scallops also feature an interesting history as a living harvested resource under federal management. The mandated closures on Georges Bank and in Southern New England for groundfish protection have had a profound effect on scallop biomass. Sea scallop spawning-stock biomass is currently at its highest level in at least 40 years and is concentrated in specific areas (NEFSC 2007). Because adult sea scallops possess limited ability to migrate, these changes are primarily a result of higher rates of recruitment and modification of local size structure. Sea scallop recruitment on Georges Bank and Nantucket shoals since the closures (1996-2000 year classes) has averaged over twice that which had been seen previously (1980-1995 year classes). Interestingly, recruitment in some areas did not improve much (e.g., southeast part of Georges Bank and the closed area off Virginia), while recruitment in other areas increased spectacularly (e.g., Nantucket Lightship Closed Area and southern portion of Closed Area II).

Reproduction in these densely populated areas may produce patches of larvae that settle in definable areas, thereby creating a spatial pattern of recruitment different from that seen before establishment of the closures. This mapping has lead to a great deal of speculation regarding connectivity between local areas and the role of early stage transport on population dynamics. Increased recruitment in the Mid-Atlantic is presumably linked to the closures on Georges Bank and Nantucket shoals via transport
processes. The assumption being that larvae generated by populations in the closed areas are seeding the Mid-Atlantic.

However, this system is complicated and appears to be exhibiting dynamics that are not necessarily explained by increased biomass in 'upstream' source areas. For instance, recruitment in the Mid-Atlantic appears to be increasing over a time period that predates the Georges Bank/Nantucket Shoals (Fig. 1) closures. An explanation for this is currently not available, but it suggests that the Mid-Atlantic Bight scallop population dynamics are not a simple linear function of Georges Bank/Nantucket Shoals scallop abundances.

Early stage transport plays a role in the Mid-Atlantic as well. In 1998, two areas of the Mid-Atlantic were closed to scallop fishing for three years. As in the Georges Bank closures, biomass in these areas increased considerably during the closures. The strong 1996 year-class that settled in the larger of these areas (the Hudson Canyon South Closed Area, off of New Jersey) was protected, and started to produce large numbers of gametes in 2000. Observations of the 2000 and 2001 year-classes from the 2002 NMFS scallop survey suggested the possibility that the high concentration of older scallops in the Hudson Canyon South area were seeding the “downstream” areas to the south and west. These large year-classes were protected through the establishment of the Elephant Trunk Closed Area in 2004. NMFS began allowing limited scallop harvesting in the Hudson Canyon Closed Area. These harvests were regulated, but by the summer of 2005, sea scallop densities had unexpectedly fallen to background levels. The Elephant Trunk Closed Area was opened for limited scallop harvesting from 2007 through 2011, providing significant opportunities for the scallop fishery. These outcomes imply a role
for both local population dynamics and transport processes in the global dynamics of sea scallops.

Physical oceanographers recognize consistent circulation patterns and gyres in the Gulf of Maine, Georges Bank, and the Mid-Atlantic Bight that have been used to infer connectivity in sea scallops (Aretxabaleta et al. 2008). Georges Bank lies underneath a clockwise gyre driven largely by tidal forces (Mountain 2003). This gyre suggests that self-seeding may be relatively common among Georges Bank populations. Circulation in the Mid-Atlantic Bight is more unidirectional, with net southward flow over the shelf (Mountain 2003). These potential transport pathways invite consideration of a source/sink population dynamics model, with downstream populations replenished by “leakage” from those positioned upstream. Both Georges Bank and the Mid-Atlantic Bight possess frontal systems known to vary in intensity and location (Fratantoni and Pickart 2003), and, because they have surface manifestations, may be significantly affected by local winds over short time scales (Lewis, Chen et al. 2001). Because frontal systems are also known to concentrate particles, early stage transport may be tied to these features (Lough and Manning 2001; McCulloch and Shanks 2003). Additionally, vertical migration behavior in sea scallop larvae could have profound impacts on not only distances traveled (Metaxas 2001), but depending on the timing of the vertical migrations relative to tidal oscillations, also the direction (Manuel and O'Dor 1997; Manuel, Pearce et al. 1997). Because this overall system is undoubtedly sensitive to environmental processes, the alternation between high and low North-Atlantic Oscillation (NAO) indices and their associated environmental regimes may result in identifiable regimes for sea scallop population dynamics. Identifying these patterns could give an idea of how sea
scallop populations function over longer time scales, and enable prediction of the potential impacts of global warming and climate change on scallop recruitment and population dynamics.

Direct observation of transport distances is impractical for estimating connectivity in sea scallops, and Lagrangian experiments using passive drogues cannot capture the dynamics of small particles that vertically migrate. The most appropriate tools for estimating connectivity of sea scallop populations are bio-physically coupled models, initialized with temporally and spatially appropriate data. To this end, we have:

1. Acquired, compiled and interpolated appropriate environmental data
2. Developed a circulation model that accepts these environmental data as forcings
3. Developed an individual-based model of sea scallop larval behavior that interacts with the circulation model
4. Converted the resultant trajectories into dispersal kernels – probability-of-settlement maps associated with each release point
5. Used network theory tools to evaluate the dispersal kernels in the context of management
6. Constructed a metapopulation model for sea scallops on the shelf using these dispersal kernels to define the connectivity between local populations.

Although the population model we develop is parameterized for sea scallops, this problem is generalizable to many current problems in spatial management of marine fisheries. Larval behavior is easily modified, and migration dynamics may be
incorporated for animals more motile than scallops. The completed scallop model can be useful in evaluating the ecological value of shelf habitats, or in choosing the sites of marine protected areas. Managers of commercially important species can use this method to simulate population dynamics under a variety of spatially and demographically targeted management strategies, providing them with another tool to help them better steward our marine resources.

For this work, we used a three-dimensional circulation model (Quoddy) forced with spatially/temporally variable winds and density gradients, and M2 tides. The circulation model was coupled with a larval advection and behavior model (4th order Runge-Kutta) which featured time-dependent vertical migrations parameterized using observational data of scallop larvae depth distributions. Surface heat fluxes were not applied in these simulations. A rectilinear grid of 667 'stations', encompassing the observed distribution of sea scallops, was deployed in areas with water depths down to 150m. These equidistant stations formed the nodes for the construction of the transition or 'connectivity' matrix. Particles were released from each station over a two-week period in the fall to simulate spawning. Each particle 'searched' an area around it for stations at which to settle. The search started immediately with the radius of the search area increasing with time throughout the 40-day drift using a turbulent diffusion equation. When a station was located within this radius, a connection between the 'source' station and the identified 'sink' station was tallied. After the run, station scores were normalized such that the source station with the highest tally of 'sinks' had a total score of one (i.e., at least one station experienced no advective particle losses). This list of station connectivities was then transformed into a transition matrix. An analysis of the transition
matrix’s properties was then made using concepts borrowed from the fields of digraph theory.

The analysis yielded the identification of strongly connected areas (stocks), connectivity pathways, number of generations a pulse (recruitment) event should impact the population, explanations for some aspects of recruitment variability, and the identification of critical areas that serve as sources while maintaining high rates of self seeding.

This work provides methods to move coupled biophysical modeling into the management arena. The techniques are straightforward, easily interpretable, and predictive. We conclude that scallop populations function more as a network and that key areas should be protected to preserve larval source production and that the fishery focus trawl efforts at regions marked by high rates of exogenous larval supply.

METHODS

We used the three-dimensional, finite element circulation model Quoddy (Lynch and Werner 1991) which has been applied previously in the Gulf of Maine and Mid-Atlantic Bight regions in SABRE (Quinlan, Blanton et al. 1999; Werner, Blanton et al. 1999) and US GLOBEC. This model, along with archived hydrographic and wind data, was used to construct a number of circulation simulations for the region extending from the Scotian Shelf into the South Atlantic Bight. The simulations provided realistic depictions of the circulation for forcing ‘particle tracking’ simulations to investigate scallop drift and exchange between regions in the study area (Quinlan has unpublished data in this area, see also Quinlan et al. 1999). Lagrangian particles have been given
specific behaviors (from passive to vertically migrating) to investigate the effects of active behavior on drift trajectory (Hare, Quinlan et al. 1999). The initial conditions for the model were established using bimonthly averages of hydrographic data. Wind forcings were applied at as fine a temporal and spatial scale as possible using quality controlled historic databases. The boundary conditions were specified using hydrographic information, $M_2$ tidal oscillations, and sea surface height along the northern boundary to mimic observed inflow into the model domain.

Hydrographic data were compiled from several sources, with the goal of good spatial and temporal coverage throughout the model domain, from 1980 to 2004. The hydrographic data were interpolated to the domain grid using the objective-analysis method, integrating 61 days of data, centered on the first day of each simulation. Analyses of hydrographic inter and intra annual variability were then carried out using the resultant bimonthly averages.

The wind fields used to drive circulation were from NCEP/NCAR Reanalysis 1 solutions (Kalnay et al. 1996). This product provides 6-hourly wind velocities at 10 meters on a T62 Gaussian grid with 144x73 points, situated 2.5 degrees from each other vertically and horizontally. These wind velocities were interpolated to the model domain grid using an inverse-squared-distance method.

To interpret the connectivity results in the context of scallop life history, a size-structured, spatially-explicit population model for sea scallops (Quinlan and Crowder 1999; Caswell 2001) was developed. The model was used to project the adult population forward in time, incorporating the magnitudes of scallop spawning and settlement in various regions. These efforts allowed exploration of the connectivity between existing
closed/open areas, the dynamics of the population under rotational harvest management strategies and an identification of shelf areas exhibiting high/low self-seeding or dispersal potentials. We also identified a network of closed/fishable areas that helped the population remain robust to environmental variability, and examined the interaction between size-structure, circulation and how those features define population resiliency.

We conducted simulations with 4-dimensional variable wind and density fields to explore the role of short term, event scale variability in transport (Hare, Quinlan et al. 1999; Quinlan, Blanton et al. 1999). Particles (which feature active vertical migration) were released broadly in the model domain from all potential habitats. Run-duration and settlement probabilities were determined using the best available empirical data. Probability distributions of drift outcomes (“dispersal kernel”) were developed for all points throughout the model domain. We identified conditions under which, and how often, particular regions on the shelf act as sources, sinks, or self-seeding populations. These variabilities were also compared with Atlantic Multi-decadal Oscillations (AMO), a broad-scale metric of climate variation in the North Atlantic.
TEMPORAL AND SPATIAL VARIABILITY IN POPULATION CONNECTIVITY ON THE NORTHWEST ATLANTIC SHELF

INTRODUCTION

For many benthic species, dispersal occurs during a planktonic larval stage. Over the duration of this pelagic development, larvae may encounter variable environmental conditions, including thermal regimes and transport patterns. Thermal regime has the potential to alter pelagic larval durations (PLD), and coupled with variation in physical transport processes, can result in great diversity of potential settlement locations and exchange among subpopulations, potentially producing widely separated settlement locations. The complex factors driving larval transport make it hard to directly observe or predict the connectivity between populations within a species’ range (Gawarkiewicz et al. 2007). Nevertheless, the importance of population connectivity on local and metapopulation dynamics, community dynamics and structure, genetic diversity, and the efficacy of spatially-imposed fishery closures and marine protected areas (MPA’s) emphasizes the need for metrics of population connectivity (Cowen and Sponaugle 2009; Fogarty and Botsford 2007)

Empirical methods for establishing patterns of connectivity, such as elemental fingerprinting (Becker et al. 2007; Thorrold et al. 2007), genetic variation (Lowe and Allendorf 2010; Saenz-Agudelo et al. 2009; Bentzen et al. 1996; Kinlan and Gaines 2003; Purcell et al. 2006) and larval mark/recapture experiments (Arnold et al. 2005) have been successfully implemented, but they all possess limits that restrict their use to smaller scales or complexly structured habitat complexes. Many ecologically significant
questions about population connectivity – such as metapopulation dynamics, recruitment variation, or long-term self- (Botsford et al. 2009) potentials of populations within MPA’s – require a broader understanding of connectivity patterns and the way they vary in time and space than can currently be provided by empirical methods. In the absence of these data, population connectivity research has largely relied on models to estimate dispersal kernels (Pineda et al. 2007). The complexity of models deriving dispersal kernels – the distribution of settlement distance probabilities from a larval source (Botsford et al. 1994; Kaplan et al. 2006) – varies from simple advection-diffusion models to temporally and spatially-explicit numerical circulation models that provide transport pathways of prescribed particles from known sources (Pineda et al. 2007). In their one-dimensional form, dispersal kernels from simple advection-diffusion equations give a good intuitive sense of the distance a given larva may be transported before settling. In some marine systems, especially where the shelf is relatively narrow, distance from source to settlement alone may be enough to explore population connectivity. For the Northwest Atlantic, however, the presence of wide shelves, multiple banks and complex gyres require more detail than simply distance to describe transport pathways. For this reason, we expanded our dispersal kernels into two dimensions, establishing a spatially arranged set of transport probabilities – the transport “footprint” – from a source population situated on the shelf.

Although much of the focus on population connectivity concerns the magnitude of transport distances, the variability of dispersal kernels can also play an important role in population dynamics (Weersing and Toonen 2009) – particularly with regard to the management of marine fisheries. Interannual or intraseasonal shifts in the position and
shape of the dispersal kernel can dramatically alter connectivity between stationary MPA’s, or the fraction of larvae that “self-seed” into a protected source population (Gaines et al. 2003; Cowen et al. 2006; Kaplan et al. 2006). Although this variability is a critical factor in whether or not an MPA is successful, it is poorly represented by the idealized, spatially uniform larval dispersal used in some theoretical studies of reserve design (Gerber et al. 2003). The Gaussian distributed dispersal kernels created by advection/diffusion models are better (Roughgarden et al. 1988), but are difficult to accurately parameterize (Largier 2003), and insensitive to the spatial patterns in the environment critical to accurate measures of connectivity (Cowen et al. 2000; Largier 2003; Siegel et al. 2003). Mean or climatological ocean flow-field statistics have also been used in the creation of dispersal kernels (Largier 2003; Siegel et al. 2003; Aiken et al. 2007), but by decoupling the particle tracking operations from time-varying physical forcings, these methods fail to consider physical forcing at time scales shorter than seasonal, and the interactions of those higher frequency transport dynamics with biological processes, such as development rate and behavior. These methods also fail to capture the tendency for dispersing marine larvae to be retained along their transport pathways (Arnold et al. 2005), a factor that could influence metapopulation dynamics (Lockwood et al. 2002; Kaplan et al. 2006) by contributing to the kurtosis and skew typical of empirically derived dispersal kernels (Chesson and Lee 2005).

Clearly there is a need for more detailed information on connectivity patterns that cannot currently be obtained empirically and is not adequately addressed by theoretical efforts based on idealized assumptions of linear space, temporally constant advection and uniform alongshore dynamics (Pineda et al. 2007). These facts, coupled with the
increasing sophistication and accuracy of physical circulation models, make population connectivity an excellent process for numerical simulation-based studies (Werner et al. 2007) – a fact realized recently in an evaluation of marine population connectivity and spatial management that concludes “the principle challenge is to go beyond simple model structures to provide more realistic representations of dispersal and connectivity linked to oceanographic conditions and to the behavior and the life history characteristics of managed species” (Fogarty and Botsford 2007). Several biophysically-coupled simulations have been used to evaluate transport pathways using a particle-tracking routine that moves virtual larvae through flow-fields created by circulation models under a variety of assumptions and conditions (Cowen et al. 2000; Cowen et al. 2006; Guizen et al. 2006). For our larval transport simulations, we identified several factors we believed to be important components of transport on the Northwest Atlantic shelf. These included density gradients, winds, tides, seafloor topology, and diel vertical migration behavior of larvae. A literature review failed to find any larval tracking simulation work that incorporated all these factors, but an unpublished study (Lynch et al.) on transport of sea scallop (*Placopecten magellanicus*) larvae did. These earlier simulations by Lynch et al. were primarily concerned with the effects of regional trawl closures on Georges Bank scallop populations (e.g., the efficacy of no-harvest regions on Georges Bank to sustain large individuals and abundant populations of scallops both within and outside the closed regions). Because the physical circulation model (Quoddy) used by Lynch et al. reasonably approximated known physical conditions (e.g., stratification, transports) and was coupled with a biological model for the pelagic larval period of sea scallops, we chose to use that same model for our simulations.
The Quoddy circulation model we used encompassed the shelf and slope regions from Cape Hatteras to Nova Scotia – a region where several commercially important species are or have been historically abundant and commercially exploited. Extensive historical oceanographic sampling in this region provides information critical for the initialization and evaluation of the model simulations. The complexity of the circulation patterns in this region, comprised by the Gulf of Maine, Georges Bank and the Mid-Atlantic Bight, are well described (Townsend et al. 2006), but also quite complex, making it a compelling region for transport simulations. Our goal was to use the circulation model to simulate particle transport pathways along the shelf as accurately as possible using highly resolved wind and hydrographic observations, and to convert the resultant pathways into 2-dimensional dispersal kernels – spatial probability-of-settlement maps – for each location in the domain. We then used the full set of dispersal kernels to relate patterns of connectivity with environmental factors, such as bathymetry, hydrography, and the Atlantic Multi-decadal Oscillation (AMO).

Despite the increasing amount of effort expended by marine ecologists producing and evaluating dispersal kernels, a coherent set of methods for applying them to real world problems has yet to be developed. This is unsurprising considering both the complexity of connections in natural populations and the relative novelty of dispersal kernels to the field of marine ecology. Nevertheless, the “future research directions” section of the most recent review on fisheries management and population connectivity (Fogarty and Botsford 2007) makes no mention of dispersal kernels, let alone the development of the analytical methods necessary to interpret them. Of course, connected networks are quite common, and have spawned analytical methods that are easily
extended into the field of ecology. Digraph theory in particular (Roberts 1976) – a robust set of analytical tools used to describe the behaviors of connected networks – is uniquely applicable to the evaluation of dispersal kernels (Treml et al. 2008). For example, simple linear algebra functions applied to dispersal kernels can track the impacts of pulse-disturbance events as they pass through a metapopulation. Similar methods are able to condense complex networks down to strongly connected subsets, improving their intuitive and analytical tractability, and providing a precise and objective means for population managers to establish the spatial extent of marine management units. The tools of digraph theory, coupled with accurately rendered dispersal kernels, provide an important first step away from reactive fishery management strategies towards a more proactive paradigm – managing fishery efforts spatially to create stock distributions that capitalize on transport patterns in the natural environment.

The overarching goal of this effort is to condense a complex set of environmental observations and modeled circulation patterns into a form that is intuitive and easily interpretable by non-specialists. Rather than create a predictive system of population connectivity, we resolve a set of general rules concerning patterns of connectivity on the Northwest Atlantic Shelf and the ways they change from year to year. Furthermore, we seek to understand the physical mechanisms driving these interannual changes in connectivity, allowing us to link transport processes with climatic regimes.

**METHODS**

The Quoddy numerical circulation model (Lynch and Werner 1991) has a proven record, having been applied to several regions along the U.S. east coast (Lynch et al.
1996; Naimie 1996; Lynch et al. 1997; Quinlan et al. 1999; Werner et al. 1999; Lynch et al. 2001; Bilgili et al. 2005; He et al. 2005). Quoddy is a 3-dimensional finite element model that is fully non-linear and tide resolving. Vertical mixing attributable to sub-grid scale processes is handled using the turbulence closure parameterizations of Mellor and Yamada (Mellor and Yamada 1982). The time step used in our simulations was ca. 87 seconds, and the spin-up time was 5120 model time steps (10 tidal cycles). The boundaries were left open over the shelf at the northern and southern limits of the domain, but all other boundaries were fixed to the sum of an M2 tidal constituent and a flow-induced residual, effectively combining tidal oscillations and boundary. The domain grid (Fig. 2) was developed using bathymetry (Smith and Sandwell 1997) from just south of Cape Hatteras to southwestern Nova Scotia, encompassing the Mid-Atlantic Bight (MAB), Georges Bank (GB) and the Gulf of Maine (GOM). All depths shallower than 10 meters or deeper than 2000 meters were truncated. The finest horizontal resolution was 2-3 km near the coast, whereas in the deep continental slope waters it was ca. 12 km. The grid was discretized vertically using 21 bathymetry-following sigma levels. The distance between sigma levels was proportional to depth, with some increased vertical resolution near the surface and bottom to better resolve Ekman layers. To limit the effects of sigma level rounding errors, the distance between nodes was reduced proportional to depth.

Wind data were taken from NCEP/NCAR Reanalysis solutions (Kalnay et al. 1996), providing 6-hourly wind velocities at 10 meters on a T62 Gaussian grid with 144x73 points, situated 2.5 degrees from each other vertically and horizontally. Wind velocities were spatially interpolated to the model domain grid using an inverse-squared-distance technique, and linearly interpolated between each 6-hour interval.
Temperature and salinity observations for the initial conditions were compiled from several sources, including Hydrobase, the National Marine Fisheries Services, and the Department of Fisheries and Ocean of Canada. Hydrographic data assembled for the South Atlantic Bight Recruitment Experiment (SABRE) program (Werner et al. 1999) were also included in the archive. Temperature and salinity bimonthly averages were generated for 1980-2003 using objective analysis (OA) on 61 days of observational data centered on the first day of each simulation – September 1. When the observational data were spatially patchy, the unreliable regions of the resultant OA solutions were approximated using a seasonal climatology built from the entire dataset. The climatological values were applied to the bimonthly averages using a weighting method sensitive to the reliability values produced by the objective analyses. The corrected bimonthly averages were then used to initialize temperature and salinity values for the corresponding Quoddy runs. Temperature and salinity fields were held constant over the course of each run. Boundary sea-surface heights were the sum of a time-varying semi-diurnal M2 tidal constituent and a static, flow-induced residual, generated using equilibrium solutions of Quoddy runs with open boundaries and historically appropriate pressure gradient forcings alone.

To trace transport pathways, virtual larvae, hereafter referred to as particles, were introduced into the circulation model and tracked. The particle release grid was built on a constant tessellation of ~20 km isosceles triangles overlying the seafloor from the coastline to the 150m isobaths, resulting in 667 equidistant points. A new set of particles was released daily, at a uniform depth of 5 meters, over the span of 2 weeks (15 releases). All particles were tracked using a 4th-order Runge-Kutta algorithm, using the same time
step as the model (87 seconds), for the duration of the model run, with particle positions saved to an output file once per tidal-cycle (ca. every 12.5 hours).

Although there is value in avoiding species-specific parameters in a general model of transport (Aiken et al. 2007), several lines of inquiry have demonstrated the importance of larval behavior on transport pathways – vertical diel migration in particular (Manuel and O'Dor 1997; Metaxas 2001). This fact, coupled with the prevalence of diel vertical migration among the plankton (Metaxas 2001), suggests that our results will be more broadly applicable if they include vertical behavior than if they do not, even if the behavior itself is tuned to a particular species. For these simulations, we assign behaviors to the Lagrangian particles based on those observed in larvae of the sea scallop (Tremblay and Sinclair 1990), *Placopecten magellanicus* (Gmelin 1791). Since it is known that Georges Bank sea scallop larvae have a preferred nighttime depth of ca. 5m, and a preferred daytime depth of 30m (Tremblay and Sinclair 1990), we used those depths to define the behavior of the particles. Vertical movement of the particles toward their time-dependent preferred depth was implemented using a maximum vertical swimming speed of 1 mm s\(^{-1}\). The maximum swimming speed was applied only when the particles were more than 2 m away from their preferred depth. For shorter vertical displacements (2 m and less), the swimming speed decreased linearly from 1 mm s\(^{-1}\) (at 2 m distance) to 0 mm s\(^{-1}\) (at 0 m distance). With the adoption of sea scallop larval behavior, it also becomes appropriate to implement the particle-tracking simulations during the fall months, when most sea scallops spawn (Parsons et al. 2002). The maximum length of the simulations was set to 42 days, which is the planktonic larval duration of sea scallops (Posgay 1982).
The conversion of particle pathways into spatial dispersal kernels was implemented using a weighting scheme sensitive to factors such as larval age, turbulent-diffusion processes, and variations in the temporal and spatial release locations. By forcing the circulation model with historically derived winds and density fields, we are able to generate the many dispersal kernels necessary for a detailed look at spatial and temporal variability in population connectivity on the Northwest Atlantic shelf. A series of stations were defined using the grid of particle release points, such that each station could be associated with the initial positions of 7 particles – one corresponding to the station’s location, and 6 others arranged hexagonally around it (Fig. 3). The initial weight for the particle in the center of the release pattern was 1, and 1/6 for those on the periphery. The weights were further modified depending on each particle’s release date within a 15-day spawning cycle. This was accomplished by multiplying the positionally-derived weights by a sine-based temporal-weight function with a minimum of 0.038 at days 1 and 15, and a maximum of 1 at day 8 (Fig. 3). The products of the positionally and temporally-derived weights were finally modified using the age of the particles, increasing weights linearly from zero to their full values in 42 days – roughly corresponding to the PLD of sea scallops. On a lunar cycle, the weight of each particle was added to all stations lying within a time-varying search radius, determined by applying the particle’s age to a turbulent-diffusion equation (K_{turbulence} = 10^7 \text{ m}^2\text{day}^{-1}). The full set of station-to-station weight-sums was then normalized to the maximum possible value to account for particle loss due to advection. The final dispersal kernels each represent the set of transport probabilities between a source and all other potential
sinks in the domain. The sum of the dispersal kernel’s probabilities is \(1-L\), where \(L\) is the probability of loss due to advection.

Each simulation’s set of transport probabilities was arranged in a connectivity matrix \(D\), with an x-axis \(i\) corresponding to particle source, a y-axis \(j\) corresponding to settlement location, and the individual elements of the matrix \(D(i,j)\) being the probabilities of transport \(i \rightarrow j\). The values along the diagonal, \(D(i,i)\) represented the probabilities that a given particle would settle back on its source, a process hereafter referred to as self-seeding – a quality linked to the persistence of sub-populations (Pinsky et al. 2012; White et al. 2010). The adjacency matrix \(A\) is defined as the Boolean transform of the connectivity matrix \(D\) \((A=\text{Bool}[D], A(i,j)=1 \text{ for all } i,j \text{ satisfying the equation } D(i,j)>0)\). Summing the columns of the adjacency matrix provides a metric for the area over which each station’s larvae might disperse – the source-area. Summing the rows provides the area from which each station might receive larvae – the sink-area. The adjacency matrix can also be used to calculate the distance matrix \(d\) containing the minimum number of steps (spawning cycles) necessary to link any 2 connected stations in the network. Each distance \(d(i,j)\), is equal to the minimum value \(k\) such that the \(i,j\) entry of \(\text{Bool}[A^k] = 1\). \(A\) is also used to generate the reachability matrix \(R\). \(R\) is similar to \(A\) except that connections between stations do not have to be immediate. In other words, if a path can be drawn between the two points in the domain \(i\) and \(j\), using valid connections listed in \(A\), then the element \(R(i,j)\) is equal to 1. The reachability matrix \(R\) can be calculated in the following way:

\[
R = \text{Bool}[I + A + A^2 + \ldots + A^{n-1}] = \text{Bool}[(I + A)^{n-1}]
\]

where \(I\) is the identity matrix and \(n\) is the length of \(A\).
Condensations of connectivity matrices were built under the assumption that every station was part of one, and only one, strongly connected subset of the connected network, or *strong component*, the proof for which is demonstrated by Roberts (Roberts 1976). Stations were considered strongly connected if connecting paths existed between them in both directions, i.e., Station 1 could be reached from Station 2 and Station 2 could be reached from Station 1. This was evaluated using an element-wise matrix-multiplication of R and R'. Strong components were connected to others when A demonstrated adjacency between any two of their constituent stations.

RESULTS

Despite the large number of individual dispersal kernels generated by the particle tracking simulations (more than 16,000), several general patterns are clear, such as the tendency for dispersal kernels to follow isobaths more tightly when originating from offshore positions near shelf-slope fronts, or the limited extent of near-shore dispersal kernels (Fig. 4). Most dispersal kernels are linear, extending downstream from source locations, but two regions display forked dispersal kernels – the north side of the Northeast Channel, and the east side of the Great South Channel. In these areas particles pass both into and across their associated channels. The fraction of the dispersal kernels extending along one fork or the other varies from year to year, suggesting a potential mechanism for recruitment variability in those regions.

The mean dispersal kernels, created by finding the mean value for each element in the transition matrices over the entire time series, are useful tools for evaluating transport
patterns. Mean transport shows that particles carried south from Penobscot Bay in the Gulf of Maine occasionally travel as far south as Georges Bank, creating a connection between the Bay of Fundy system and areas downstream. The MAB sections of dispersal kernels originating from Georges Bank cover the shelf north of the Hudson Shelf Valley, but attenuate along the shelf break south to about Chesapeake Bay – a pattern consistent with the distribution of MAB sea scallops (Fig. 4).

For most regions, the standard deviations of the dispersal kernels look very much like the means, suggesting that the dispersal kernels for individual years tend to shift evenly throughout the region of the mean. Dispersal kernels near the shelf break tend to show the highest variabilities towards their downstream ends, reflecting year-to-year differences in the maximum transport distances – an important component of the sink potential variability demonstrated throughout the MAB in Figure 10. A few dispersal kernels show low variability despite fairly extensive means. This is notably true for dispersal kernels originating from inner and western Brown’s Bank, where the modeled circulation patterns tend to be relatively consistent from year to year. Another interesting exception is found in the New York Bight Apex, just south of Long Island, where a small patch of high standard deviation appears in several dispersal kernels. An examination of the dispersal kernels originating from this region reveals very little transport in 1998 – a year marked by a generally low total connectivity (Fig. 11).

The mean self-seeding potentials (Fig. 5) tend to be higher near shore where current speeds are minimized through friction. Exceptions to this pattern are found on the GOM side of Nova Scotia, and the GOM shore between Gloucester and Muscongus Bay. Self-seeding hot spots are found on the shelf off Penobscot Bay and in the Bay of Fundy.
An isolated spot of higher self-seeding potential also exists on the peak of Georges Bank – likely due to the influence of the gyre. Coefficients of variation for self-seeding show hot spots on Browns Bank, the northeast tip and southern flank of Georges Bank, and the portion of the MAB north of the Hudson Shelf Valley. (Fig. 6).

The means for source-area (Fig. 7) show the highest values at the southern tip of Browns Bank, and on a strip running along the seaward side of Georges Bank, regions marked by relatively high modeled currents. The Georges Bank hotspot lightens below Nantucket Shoals, then again at the Hudson Shelf Valley, and again at the Delaware Shelf Valley, where bathymetric features reduce or redirect modeled currents.

The standard deviations of source-area (Fig. 8) are visibly different than the means. The highest variabilities are found on Browns Bank and the southern flank of Georges Bank, especially on the eastern side of the Great South Channel – the two regions producing forked dispersal kernels. The high variabilities in these regions reflect year-to-year shifts in the proportion of particles traveling along the two forks. Although the values are not as high, elevated levels of source-area variability are also found inshore from Long Island to the Delaware River. This patch is interesting for its sharp demarcation on the seaward edge. The physical model used to generate the dispersal kernels did not include Hudson River outflows, but the bimonthly averages used to initialize the simulations often showed strong near-shore density gradients in this region that are a likely driving this transport variability.

The highest values of mean sink-area (Fig. 9) are found along the MAB shelf, especially towards the south. The region from the Hudson Shelf Valley to the southern edge of Georges Bank is only slightly less strong. Elevated levels of mean sink-area are
also found on the west side of Nova Scotia, the southeast side of Georges Bank, and the
GOM side of the Great South Channel.

The highest sink-area variability (Fig. 10) is found along a thin strip moving
through the MAB just offshore, from Long Island to Cape Hatteras. There is also a
similar, parallel line of high variability at the shelf break. The two stripes of variability
are the result of cross-shelf shifts in the band of high sink-area values. The GOM side of
the Great South Channel also shows high variabilities, generated by changes in the
northward extent of a sink-area high finger ing up the Great South Channel. There is also
a small area on the north side of Georges Bank with elevated levels of variation. These
variabilities are due both to highs and lows in sink-area, localized on that one small spot.

The full set of connectivity matrices can be distilled into a total connectivity
timeline by counting the number of elements in each year’s connectivity matrix that are
greater than zero. The timeline (Fig. 11) shows high total connectivities in the falls of
lowest connectivity is in the fall of 1990, but another low region occurs between the falls
of 1996 and 1999. These highs and lows correlate inversely with shelfwater volume,
estimated by finding the volume of seawater in each year’s OA solution possessing a
salinity lower than 34 PSU.

To better resolve the structure of connectivity in the mean dispersal kernels, it was
necessary to filter transition probabilities falling below a particular threshold. Giving up
half of the total connectivity eliminated 90% of the connections and was achieved by
applying a probability-of-transport threshold of 0.03. A condensation of the mean
dispersal kernel, after removing all elements less than 0.03, produces 469 subsets – 452
of which are single vertices, and 17 that are made up of four or more vertices (Fig. 12). Connections between subsets were said to exist if a direct path could be drawn between any element of one and any element of the other. The directionality of the connection is shown using an arrow.

The strongly connected subsets of the 1980 through 2003 condensations run along a spectrum of complexity, from numerous, small and well-connected, to larger and more isolated. The complex pattern is well represented by the 1999 condensation (Fig. 13), a year marked by relatively high shelfwater volumes and low total transport. The simpler pattern (Fig. 14) is illustrated by the 1996 condensation. Unlike 1999, this year saw lower shelfwater volumes and higher total transports. Source-area, sink-area, and self-seeding anomalies were again unremarkable, but the particle pathways did show strong northward inshore currents, strong southward shifts in wind stress, and a shelf-slope front positioned well up the shelf, which swept large numbers of particles southwards.

The full set of condensations reveals two main systems: one including the regions from Massachusetts to Virginia (including Georges Bank), and another made up of Browns Bank and the Bay of Fundy. Jeffreys Bank, just off the coast of New Hampshire, is not clearly part of either group, alternating connections between the two from year to year. In almost all cases, however, the direction of transport in the Gulf of Maine is unidirectional towards Jeffreys Bank. The years in which Jeffreys Bank is clearly connected with the southern group are invariably high shelfwater volume years, such as in 1999. Each of the two main regions varies from year to year in the number of strong components and the directionality of connections, but with the exception of Jeffreys Bank, they remain independent of each other.
DISCUSSION

Most of Browns bank consistently connects with the Bay of Fundy in our simulations, but the deeper regions on the eastern edge of the bank vary in their connections between the Bay of Fundy, the seaward side of Georges Bank and self-seeding. Variability of this sort has been linked to changes in the tightness of the Browns Bank Gyre and to warm core rings (WCR) impinging on the shelf (Campana et al. 1989; Hannah et al. 2000; Brickman et al. 2001). The effects of WCR’s are visible but inconsistent in our climatologies, but interannual variabilities in fall gyre-strengths show up clearly in the particle trajectories. The 1981 simulation in particular combines high self-seeding potentials and tight gyres over Browns and Lahave Bank, driven by an isolated pool of warm, low-salinity water. Transport across the Northwest Channel, (implied by the dispersal kernels linking outer Brown’s Bank with Georges Bank) has been observed in association with Scotian Shelf crossover (SSC) events. Smith, et al (2003) argue that SSC’s are driven partially by winds, but primarily due to mesoscale density features from offshore (such as WCR’s). Although Smith et al rule out any connection between Interannual variability of freshwater inputs from the Gulf of Saint Lawrence and SSC events, our simulations do show an association between low shelfwater volumes (Mountain 2003), modeled SSC events, and strong particle transport across the Northeast Channel. This association between low shelfwater volumes and transport potential is found throughout the domain and appears to be driven by a shoreward, cross-shelf movement of the modeled shelf-slope front, similar to those described by Frantoni and Pickart (2003). These conditions have the potential to
transport particles extremely long distances – the 1994 simulation in particular, produced dispersal kernels extending from the outer part of Brown’s Bank, across the Northwest Channel, and as far south as the Delaware Shelf Valley.

The Bay of Fundy possesses three distinct regions with regard to transport – the region inside the bay (north of Grand Manon Island and Freeport, Nova Scotia) which consistently self-seeds, the eastern side of the outer bay, which in our simulations is primarily a sink for particles released between here and Browns Bank (Brickman et al. 2001), and the western side of the outer bay, which is primarily self-seeding but also acts as a source to the area near Penobscot Bay. Particle transport animations in this region show a slow net movement of particles across Browns Bank from the north, across the mouth of the Bay of Fundy and on to Penobscot Bay, while the particles in the Bay itself mostly remain. These patterns are generally consistent with known transport pathways, such as the retention of sea scallop larvae in the Bay of Fundy observed by Tremblay & Sinclair (Tremblay and Sinclair 1986), and the transport of Haddock spawned on Brown’s Bank described by Campana et al (Campana et al. 1989). The anti-cyclonic Bay of Fundy Gyre (Aretxabaleta et al. 2009) appears consistently in the simulations, but varying in its intensity from year to year. The position of the gyre at the mouth of the bay corresponds well with a small but consistent patch of high source-area values.

Both the transport animations and the mean flowfield show a decrease in along-shelf flow rates at Jeffreys Bank which tends to concentrate particles in this area, producing sink-area values that are locally high and consistent. Source-areas are very low, and variable. The low values are attributable to the fact that the mean current here flows towards the center of the Gulf of Maine, which is too deep for settlement. During
periods of low shelfwater volume however, this flow is accelerated, forming a noticeable front in the simulations that transports particles all the way to the northwest flank of Georges Bank – hence the variability. The fall hydrographic bimonthly averages (Fig. 15) typically show a pool of relatively warm, fresh water collecting in the western portion of the Gulf of Maine, effectively isolated from tidal mixing processes over Georges Bank. During years of high shelfwater volumes, this residual pool is large and creates shallow fronts far to the east. During low shelfwater years, the residual pools are small with steep density gradients situated closer to the western margin of the Gulf of Maine, driving higher rates of transport from Jeffreys Bank to Georges Bank.

Modeled transport in the region from Cape Cod to Jeffreys Bank is remarkable for its complete reversal of direction in response to shelfwater volumes. When shelfwater volumes are low, most of the dispersal kernels in this region extend towards Jeffreys Bank, but never beyond. During high volume years transport moves southward, both into Cape Cod Bay and towards the Great South Channel. Interestingly, the low-shelfwater dispersal kernels for the more southerly sections of this area sometimes extend towards Nantucket Shoals, and sometimes around to the northern flank of Georges Bank. The hydrography driving these differences appears to be a variable pool of lower density water sitting off Nantucket Sound. When the pool is somewhat isolated from Nantucket Sound, the dispersal kernels extend southwards and when the pool adheres to the sound, the dispersal kernels move out onto Georges Bank. The particle paths do not show clear coherent flows in these areas. Instead, the particles appear to loosely meander around the northern extent of the Great South Channel, reacting primarily to wind stresses. Generally
speaking, this region is exceptionally low in source and sink-area values. Self-seeding potentials are variable, being relatively strong in low shelfwater volume years.

The Georges Bank dispersal kernels clearly reflect the presence of a clockwise-rotating gyre (Lynch and Naimie 1993) with significant particle loss from the southwestern section. The Georges Bank Gyre is the dominant driver of transport in this region, with clear connections to recruitment rates (Posgay 1950). The highest rates of self-seeding occur over the shallow section just west of the bank’s geographic center. Variabilities are elevated in this region, but the set of dispersal kernels still remain near their sources. The source-areas in this region are never especially high, but sink-areas often are. Simulations generating high sink-areas in this region also display northward transport through the east side of the Great South Channel. Particle transport animations demonstrate the presence of strong fronts along the outer western edge of Georges Bank during these years. The hydrographic bimonthly averages developed to initialize these simulations show a shift in the distribution of the low-density water from the western edges of the Gulf of Maine towards Georges Bank. These shifts are associated with high shelfwater volumes throughout the region. In all years, the greatest Georges Bank transport potentials are realized on the bank’s seaward edges, where the shelf-slope front forms. Variability along the entire seaward edge is primarily in the distance covered by the dispersal kernels, although there are a few years in which the dispersal kernels diverge up through the Great South Channel. An interesting transport pathway leading from Georges Bank north to German Bank is displayed in the 1985 simulation. In that year, an extension of the Scotian Shelf shelfwater positioned itself directly over the mouth of the Northeast Channel, producing a sharp density-driven front on it’s western
edge. Self-seeding potentials are virtually non-existent along the seaward edge of Georges Bank, and source-areas are consistently minimal.

Dispersal kernels from Nantucket Shoals to the Hudson Shelf Valley (HSV) are fairly consistent in their patterns – generally following isobaths southward. The distances spanned by the dispersal kernels increase as the source locations approach the shelf break. There is also an inverse relationship between shelfwater volumes and transport distances. The climatologies indicate that this relationship is driven by cross-shelf changes in the position of the shelf-slope front (Fratantoni and Pickart 2003), as inferred from salinity intrusions in the MAB (Lentz et al. 2003). Dispersal kernels tend to follow isobaths until hitting the HSV, where particles often make a sharp turn towards shore and slow down. During high shelfwater volume years, these particles can move northward along Long Island, producing near-shore dispersal kernels whose northernmost portions extend up towards and into Long Island Sound, but never past Martha’s Vineyard. Self-seeding values are highest inshore and match closely the positions of highest variability.

South of the HSV dispersal kernels again follow isobaths southwards, although the particle pathways originating from the south side of the HSV tend to move offshore towards the shelfbreak. This results in a tendency for dispersal kernels just south of the HSV to hug the shelf edge. During low-transport periods, inshore dispersal kernels below the HSV display northward extensions to the valley axis. Dispersal kernel variability in the shelf region between Chesapeake Bay and Cape Hatteras is primarily in cross-shelf extent. The southern extent of the MAB is a major source of particle loss, recognizable by a close inverse relationship between self-seeding rates and source areas – a pattern that is consistent with drifter observations (Lozier and Gawarkiewicz 2001; Gawarkiewicz
and Linder 2006; Kumar et al. 2006). Although transport from the MAB to the SAB is not unknown (Pietrafesa et al. 1994), it appeared in our simulations only in 2000 and 2003 – and then only to a very small degree.

Although there are many important processes driving variability in transport throughout our domain, shelfwater volume appears to be a primary driver. This relationship can be illustrated by evaluating the correlation between the total shelfwater volumes from Nova Scotia to Cape Hatteras, and the total number of connections within our simulations (Fig. 11) The correlation analyses demonstrate a weak but significant inverse correlation between total shelfwater volume and total connectivity ($r = -0.4764$, $p << 0.001$). The mechanism relating transport to shelfwater volume appears to be shifts in the positions of density-driven fronts associated with the eastern edge of the shelfwater mass. Variability in the volume of shelfwater is also correlated with the Atlantic Multi-Decadal Oscillation (AMO). When AMO correlations are evaluated using spatial maps of shelfwater volume (generated from bimonthly hydrographic averages), localized regions of high correlation ($>0.5$) appear to move from the Georges Bank/Nantucket Shoals region in January-February, South to Cape Hatteras by September-October (Fig. 16). These spatial correlations appear to track the main volume of shelfwater from its site of formation on Georges Bank to Cape Hatteras, where the last of its volume is entrained in the Gulf Stream (Mountain 2003). The rate of southward motion of this localized region of high AMO correlation is approximately $0.03 \text{ m s}^{-1}$, a value that is within the range estimated by Mountain (2003) for shelfwater flows ($0.03 – 0.07 \text{ m s}^{-1}$). The correlation between AMO, shelfwater volumes and connectivity suggest a way to link climate-level
processes to biological processes, representing an important tool for policy planning and resource management efforts.

Given the ambitious scale of our circulation model, the results of the particle tracking exercise are encouraging. It seems clear that the integration of biophysically modeled dispersal kernels and population models can be a powerful and robust tool for resource managers, but further work is necessary. With the development of better circulation models and more refined domain grids, the potential for high-quality dispersal kernels will certainly improve. Along with these dispersal kernels, we must continue to develop the tools necessary for their evaluation, so that the powerful information they contain can be put to use by the resource management community. In this way we will be moving closer to the ideal of proactive, ecosystem-based management strategies.
APPLYING DISPERsal KERNELs TO THE POPULATION MANAGEMENT PARADIGM

INTRODUCTION

Recent work has begun to challenge the commonly held paradigm of well-mixed stocks or populations within management units. Close examinations of genetic patterns (Ruzzante 1998) and trace-element “fingerprints” (Thorrold, Campana et al. 1997; Thorrold, Jones et al. 1997; Thorrold, Jones et al. 1998; Thorrold and Shuttleworth 2000; Thorrold, Jones et al. 2006) within what appear to be contiguous, homogenous populations reveal spatial structure. In some cases, this intra-population structure correlates well with physical characteristics of the environment, a possibility suggested by Sinclair (Sinclair and Iles 1985; Sinclair 1988). Despite the enormous implications of these findings with regard to management, current practices often treat populations as undifferentiated units.

Variation in the ecologically significant characteristics of subpopulations could have profound effects on the efficacy of management strategies. Subpopulations with lower growth rates, smaller numbers or higher vulnerabilities to fishing practices could be more likely to fail than more robust sub-populations (Stephenson 1999). The loss in genetic diversity caused by such failures could negatively impact overall population resilience in the face of longer-term stresses, such as changes in climate or fishing practices. The failure of the fishing moratorium to restore Northwestern Atlantic cod populations could be attributed to this sort of population structure (Ruzzante, Taggart et al. 1999), which would limit “seeding” from the healthier off-shore populations.
The presence of structured subpopulations in coastal shelf environments is somewhat surprising given the fact that currents will tend to homogenize populations by dispersing eggs and larvae (Hastings and Botsford 2006). Local circulation processes are extremely varied throughout the Northwest Atlantic shelf, potentially retaining (Sinclair 1988), dispersing or aggregating pelagic stages, depending on local flow regimes. The significance of these small-scale physical processes is emphasized by the results of Ruzzante et al (1999), who found that large aggregations of mixed cod larvae broke up into consistent cohorts when observed at smaller spatial scales. Larval retention due to these fine-scale physical processes could account for the persistence of distinct subpopulations, effectively counteracting the dispersing effect of physics. For species with highly mobile adult stages, retention can be achieved through migration (Sinclair and Iles 1985; Sinclair 1988; Quinlan, Blanton et al. 1999; Ruzzante, Taggart et al. 1999).

Species with less motile juvenile or adult life histories, such as the sea scallop *Placopecten magellanicus* (Gmelin), are harder to understand under this view of population structure. The pelagic larvae of sea scallops, like most finfish, are incapable of counteracting the advective and dispersive ocean circulation processes observed in their habitat range. Unlike finfish, however, adult and juvenile sea scallops are unable to migrate significant distances (Stokesbury and Himmelman 1996), limiting their ability to return to their source populations, closing the loop against strong, unidirectional currents. This suggests the possibility that sea scallop population dynamics may function differently than finfish. Consequently, they may respond differently than finfish to management policies, and in fact, may benefit from a different strategy entirely. Sea
scallops inhabit the eastern North American shelf from the Gulf of St. Lawrence south to Cape Hatteras – a range that is similar to that of western-Atlantic cod. Unlike cod, however, scallops disperse almost exclusively through larval transport. For sea scallops, this means that their population dynamics are strongly influenced by both local circulation patterns, and the spatial distribution of adult biomass. With the recent advances in biophysically coupled models, we are now at the stage where the population level effects of these processes may be evaluated.

In this paper we develop a spatially and demographically discrete population model for sea scallops, and use it to simulate several management strategies and compare their efficacies. The model itself is actually a network of connected models, each possessing a unique location on the Northwest Atlantic shelf. A fundamental premise of our model is that subpopulations will not all function identically, being influenced by local environmental conditions. To achieve this, life parameter functions are defined that take subpopulation density, temperature, depth and size as inputs. Larval transport between subpopulations is defined using a set of dispersal kernels (spatial probability of settlement maps) generated by a biophysically-coupled Lagrangian circulation model (Law & Quinlan in prep). The physical data collected for use in the model span the years from 1980 to 2003 – a period that includes roughly two NAO cycles. The 667 subpopulations are distributed uniformly along the northwestern Atlantic shelf from Cape Hatteras to Nova Scotia, between 10 and 150 meters.

METHODS

The model is a network of connected stage-based (Lefkowitz) matrix models (Caswell 2001), each taking the form of $n^{t+1} = A^t n^t$, where $n$ is a vector containing the
numbers of scallops in each demographic subset, $t$ is time, and $A$ is a population projection matrix, incorporating growth, mortality, and per capita production of recruits at each location and time step (Fig. 17). Connections between the subsets are achieved by distributing each subset’s larvae to the other subsets via dispersal kernels.

There are 10 demographic stages in the vector $n$, ranging from small juveniles to large adult scallops: 0-20, 20-40, 40-60, 60-80, 80-100, 100-120, 120-140, 140-160, 160-180, >180 mm shell height (Sh). To facilitate comparisons between model results and sea scallop survey data, the time step used in the model is one year.

The transition matrix $A$ is calculated for each subpopulation at each time step, using first a growth function, then a mortality function, and finally a function for larval production. The growth rate function is built using in situ observations (MacDonald and Thompson 1985) applied to the Von Bertalanffy growth equation:

$$H_t = H_\infty \left[1 - e^{-k(t-t_0)}\right]$$

where $H_t$ = height at age $t$; $H_\infty$ = mean asymptotic height; $k$ = Von Bertalanffy growth coefficient; $t_0$ = a parameter representing time when $H_t$ = zero

The values for each of the terms in the Von Bertalanffy growth equation vary both geographically and with depth. These variations are undoubtedly due to a variety of factors, but depth is a reasonable proxy – encompassing differences in temperature and food availability. Of the three terms, $H_\infty$ is the only one that appears to vary consistently with depth. A rough approximation of the decrease in $H_\infty$ as a function of depth, as observed by MacDonald & Thompson (1985), is given by the equation
\[ H_\infty = H_{\text{max}} - .3z \]

*Where* \( z = \text{depth in meters}; H_{\text{max}} = \text{the maximum mean asymptotic height} *

For this application, the \( H_{\text{max}} \) parameter was set to 180 mm, \( k \) at 0.20, and \( t_0 \) at 0.56 – values typical of those measured *in situ*. Because the Von Bertalanffy equation results do not approach the origin with decreasing shell heights, we instead increase growth rates linearly during the first year, to the value calculated by the Von Bertalanffy equation at year 1. Beyond that time, growth rates are derived from the Von Bertalanffy equation directly.

Transition probabilities for \( A \) were calculated by first finding the shell heights achieved in 1 time step from the mid-point of each size class, then distributing transition probability between the two closest size classes relative to their distance from this value.

To incorporate mortality into \( A \), the transition probabilities were multiplied by survival coefficients, \( \text{surv}_{(sc,loc,t)} \), representing the fraction of individuals surviving to the next time step, given a particular size class, location, and year. Survival coefficients were a function of natural mortality, density-dependence, and bottom temperatures. Natural mortality was determined in the following way:

\[ M_{\text{nat,sc}} = e^{M_{\text{sc}}(t)} \]

*Where* \( M_{\text{sc}} \) *is the instantaneous mortality for size class* \( sc \), *and* \( t \) *is the model time step length*
$M_{sc}$ is derived by applying empirically-derived parameters (MacDonald and Thomson 1985) to the polynomial equation:

$$M_{sc} = a(SH_{sc}-110)^2 - b(SH_{sc}-110) + c$$

Where $SH_{sc} =$ mid shell height of size class sc; $a = 1.05e^{-4}$; $b = 5.0e^{-4}$; and $c = 7.9e^{-3}$

To prevent unbounded growth in subpopulations, a density-dependent component was added to the mortality function. Because the empirically-derived parameters used to calculate $M$ already bring any existing natural density-dependent mortality to the model, artificial density-dependent mortality is only invoked at high threshold densities. Because our model includes multiple size classes, density is sensitive to demographic distributions, making it a poor candidate variable for estimating mortality effects. Instead, we based our estimates of mortality on the total scallop biomass, approximated by a per scallop volume of $(1/5)\pi(shellheight/2)^3$. The threshold for density dependence, $k$, was the mass of a subpopulation with a mean shellheight of 180 mm and a density of 2 scallops·m$^{-2}$ – within the range reported by Caddy (1970). Where a subpopulation’s biomass $m$ exceeds $k$, a density-dependent mortality coefficient Mdd$_{sub}$ is calculated in this way:

$$Mdd_{sub} = k/m$$

Where $m$ was the subpopulation biomass integrated across all size classes, and $k=2.38e11$
Because sea scallops are known to be intolerant of temperatures beyond their preferred range of 5 to 20 degrees Celsius (Shumway and Parsons 2006), extremes in bottom temperature were also brought in to the calculation of survival fractions. This necessitated the creation of bottom temperature timelines for each subpopulation. A collection of hydrographic observations was assembled, using data from NOAA Fisheries, HydroBase, Fisheries Canada, and the South Atlantic Bight Recruitment Experiment (SABRE). Objective analysis was then used on 2-month subsets of the temperature data for each year from 1980 through 2003, resulting in a total of 150 bimonthly averages. For every point in each OA solution that was unreliable due to gaps in data coverage, the temperature was nudged towards the 1980-2003 mean for that point and bimonthly period, with the strength of the nudging inversely proportional to that point’s reliability. The bimonthly bottom temperature timelines extrapolated from the 3D bimonthly averages were then used to produce yearly minimum and maximum bottom temperature timelines.

As in density dependence, temperature-induced mortality is incorporated into the survivability fraction using a coefficient, $M_{bt_{loc,t}}$, specific to a particular location and year. Temperature-induced mortality is calculated in the following way:

$$M_{hot_{loc,t}} = 1 - \frac{(BT_{max_{loc,t}} - lim_{lower})}{lim_{upper} - lim_{lower}} \text{ for } lim_{lower} < BT_{max_{loc,t}} < lim_{upper}$$

$$or \ M_{hot_{loc,t}} = 0 \text{ for } BT_{max_{loc,t}} > lim_{upper}$$
Where $BT_{max,loc,t}$ = the maximum bottom temperature at location loc and year $t$,

$$lim_{lower} = 17.0c, \ limite_{upper} = 21.0c$$

$M_{cold,loc,t} = 1 - (lim_{upper} BT_{min,loc,t})/ (lim_{upper} - lim_{lower})$ for $lim_{lower} < BT_{min,loc,t} < lim_{upper}$

or $M_{cold,loc,t} = 0$ for $BT_{min,loc,t} < lim_{lower}$

Where $BT_{min,loc,t}$ = the minimum bottom temperature at location loc and year $t$,

$$lim_{lower} = 3.0c, \ limite_{upper} = 7.0c$$

$M_{bt,loc,t} = M_{hot,loc,t} \cdot M_{cold,loc,t}$

The final survival fraction incorporates natural, density dependent, and temperature-induced mortalities:

$$surv = Mnatsc \cdot M_{bt,loc,t} \cdot Mdd_{sub}$$

The survival fraction is calculated at each time step for every size class, in every subpopulation, then multiplied by the appropriate transition probabilities.

In the absence of clear stock-recruitment relationships for sea scallops, we use an empirically-derived function for egg production, and observations of recruit-eggs relationship. Fecundity is estimated using the method of Langton et al (1987) who subtracted post-spawn ($\log_{10}a=-8.13, b=4.19$) from pre-spawn ($\log_{10}a=-5.86, b=3.42$) gonadal mass regressions, then divided by the volume of a scallop egg 66.8 µm in
diameter (assuming a density of 1.0). The ratio of recruits to eggs is set at $10^{-7}$ (McGarvey et al 1993).

Fishing mortality was imposed on subpopulations by subtracting individuals from the population vector. The number of scallops harvested from each subpopulation was the difference between the total local number of scallops of all fishable size classes (>89 mm shell height) and a threshold parameter. Harvest was distributed evenly between fishable size classes (beyond excluding small individuals, the simulated trawl gear was not selective). Although simple, this method simulates the optimal-foraging behavior of fishermen by focusing fishing effort on the densest subpopulations. In other words, over the course of each year, the simulated fishery was able to locate and collectively harvest the densest subpopulations down to a density no longer practical to fish. This density threshold was set at 0.7 scallops·m$^{-2}$ – 5% of the density observed in the densest scallop beds (Caddy 1970).

The model runs use Tuljapurkar’s method (Tuljapurkar and Orzack 1980), performing iterative multiplications of the population vector with a series of transition matrices until equilibrium is reached. The control run for the model applied environmental data to the transition matrices chronologically, so the emergent impacts of regime shifts could be evaluated. To eliminate the effects of the initial conditions, the set of chronological environmental data were used iteratively until the population responses stabilized. Stability was defined using a normalized root mean square deviation (NRMSD) value of 0.01 between the last two complete environmental cycles.

Two scenarios were explored using the completed model, one evaluating the value of connectivity when establishing the location of fishery closure areas, and another
demonstrating the impacts of climate on scallop populations. For the earlier, a Monte Carlo approach was used to place identically-sized but randomly located fishery closures (similar in size to Georges Bank closures in the 1990s) in a series of serial simulations. The effects of particular climate regimes were explored by forcing runs using either the highest or lowest shelfwater volume years (Mountain 2003) – a metric that is inversely correlated with NAO (Dickson et al. 1996). Each of these simulations applied the same set of environmental forcings iteratively, over the same number of cycles used in the control runs.

RESULTS

Controls

Unfished populations: The equilibrium condition in the control run was met after 11 iterations of the 1980 to 2003 environmental conditions, yielding a scallop distribution with several notable features. Adult scallops (defined as having a shell height greater than 45 mm) showed their greatest densities on the southeastern shore of Nova Scotia, and along the shelfbreak near Hudson Canyon (Fig. 18). In those regions the densities were approximately 10/m². Mid-level adult scallop densities, about 5/m², were generated throughout the nearshore regions of Brown’s Bank, the Bay of Fundy, and the Mid-Atlantic shelf including up-shelf extensions north of the Hudson and Delaware shelf valleys, and a small finger off the mouth of Chesapeake Bay. Lower adult densities, about 2/m², were found on the southern and especially the northwestern flanks of Georges Bank, between Nantucket Shoals and Long Island, and the nearshore regions of the shelf between Long Island and Delaware Bay.
Fished populations

With fishing pressure imposed upon the entire population, maximum densities of about 2 scallops/m² developed around the southern coastline of Nova Scotia (Fig. 19), on the northwestern flank of Georges Bank, most of the shelf between Nantucket Shoals and the Hudson shelf valley, and the outer shelf from the Hudson to the Delaware shelf valleys. Densities about 1 adult scallop/m² are found just off the southern end of Nova Scotia, throughout the Bay of Fundy to Jeffreys Bank, the western side of Georges Bank including the Great Southern Channel, and a small patch on the eastern flank,

Fishery yields

The spatial distribution of fishery yield – the biomass removed through simulated fishing activity – roughly mirrors the population densities established under the fished simulations (Fig. 20). A notable exception is the Mid-Atlantic shelf break between Delaware and Chesapeake Bays, where yields are higher than anywhere else south of Nova Scotia.

Simulation and Verification

The simulation period from 1980 to 1991 demonstrates a slow and consistent increase in adult densities centered on the northwestern flank of Georges Bank, and the Mid-Atlantic Bight (Fig. 21). In 1992 the adult densities on Georges Bank were substantially reduced, recovered slightly in the next year, then dropped even further in 1993 in all areas outside of the closed areas. From 1993 to 2001, the patch of high density
adults in Closed Area 1 experienced a consistent decline, with the beginning of a recovery in 2002 and 2003. The local high-density patch in closed Area 2 remained at a relatively high density from 1993 to 2000, then quickly declined through 2003. The Nantucket Lightship Closed Area developed high density populations in its southwest corner from 1993 to 1998. This population was reduced by half in 1994, then slowly redeveloped along with neighboring populations along the entire southern boundary until the end of the simulation. In contrast to the Georges Bank populations, the populations between Nantucket Shoals and Cape Hatteras maintained relatively high densities until 1995, when the higher density regions were reduced to the areas north of Hudson Shelf Valley, and a thin strip along the shelf break to the south. The populations looked similar in 1996, but experienced a high degree of recruitment throughout the entire Mid-Atlantic region in 1997. The Hudson Canyon and Delmarva closures were imposed on the 1998 simulation, which resulted in locally high densities in both closed areas. The Hudson Canyon closed area densities were rather uniform, while the Virginia Beach closed area densities were higher in the northern part of the closed area. These distributions were consistent until 2000, when the entire shelf south of the Delaware Shelf Valley saw dramatic declines in scallop densities that remained until the end of the simulation. The regions north of the Delaware Shelf Valley continued to display high densities – especially in the Hudson Canyon closed area.

The impacts of the closed areas can be evaluated through a comparison with a simulation run that does not implement fishery closures. Although the density differences within the Mid-Atlantic Bight closure areas are locally high, density differences are slight to non-existent outside the closed areas themselves for the length of the simulation runs
After the closures on Georges Bank, high density differences develop in the southern limits of Closed Area 1 and the eastern corner of Closed Area 2, but are absent from the Nantucket Shoals Closed Area. In 1997 the closure simulations produce slightly higher density differences along the northern extent of the Great Southern Channel and up along the northwestern flank of Georges Bank, as well as the Nantucket Lightship Closed Area. That year also saw the beginning of the development of locally high closure density differences in the southern region of the Nantucket Lightship Closed Area, that were sustained until the end of the simulation. In other areas, the closure density differences remained relatively consistent, with the exception of 1998, which saw the highest density differences in Closed Area 1.

Spatial Fishery Closures

In all of the 100 randomly situated closure simulations, the scallop populations and fishery yields increased to some extent. There was, however, significant variability in the magnitude and character of response (Fig. 22). The juvenile components of the metapopulations benefitted slightly more from closures than adults, as demonstrated by the linear trend in Figure 22, which is greater than 1. Generally, however, the relative increases in adults, juveniles and yields were mostly constant. The most efficacious closures, generating increases in adult and juvenile populations over the control by as much as 1.9 and 2.2 times respectively, as well as increasing yields by about 1.8 times, were all located on the northwestern flank of Georges Bank, near the Great South Channel (Fig. 23). Although the Hudson Shelf Valley closures saw only modest increases in population numbers (about 1.25 times), the yields approached those generated by
closures at the southwest flank of Georges Bank. The shelf areas between the Delaware Shelf Valley and Cape Hatteras were unusual for generating strong adult populations, but low juvenile populations and yields.

Climate Regime Simulation

Both the high and low shelfwater volume regime simulations generated adult scallop densities an order of magnitude lower than the control, nevertheless, a difference between the simulations was clearly apparent. Low shelfwater volume years, associated with a stronger Georges Bank gyre and a shoreward migration of the shelf-slope front in the Mid-Atlantic Bight, produced the greatest densities (Fig. 24) around the Great South Channel and the highest yields just downstream of Nantucket Shoals (Fig. 25). High shelfwater volume years produced the greatest densities (Fig. 26) and yields (Fig. 27) in the Mid-Atlantic Bight, where a seaward migration of the shelf-slope front increased self-seeding potentials.

DISCUSSION

The mean scallop densities (1980 through 2003) produced by the model display varying levels of success when compared with actual scallop distributions. The density values themselves are difficult to compare with NOAA-Fisheries survey data, as their methods are sensitive to the heterogeneity created by spatially-discrete scallop beds. The model resolution used in this analysis is too coarse to resolve smaller scallop beds, but because we are interested in maximum observable densities, the model calibration was done using these values. As a result, the total modeled population biomass – when the
region is considered as a whole – is much higher than the biomass estimates generated by NOAA-Fisheries sea scallop surveys.

The distributions generated by the model, in contrast to the densities, are more easily compared with observations (Hart and Chute 2004). In general, the model is better at predicting distributions in the Mid-Atlantic Bight than it is on Georges Bank. The model fails to capture any of the populations on the northwest side of the Great South Channel. On Georges Bank, the model predicts higher densities on the east side of the Great South Channel, which is consistent with observation, but the second location of high modeled densities, the shallowest region of Georges Bank, is the only part of the bank in which high scallop densities are not commonly observed. The model captures higher densities along the Georges Bank shelfbreak, especially the higher densities found on the eastern flank in the vicinity of the EEZ, but fails to reproduce the high densities on the northeastern tip. Scallop distributions on the shelf regions between the Great South Channel and Long Island match observation, but the densities appear to be even more greatly overestimated than on those on Georges Bank.

The simulations do not take into account several important factors, such as sediment type, the persistence of overlying fronts, or the productivity of overlying waters, both of which play a role in successful recruitment (Naidu and Anderson 1984), but we believe the failures of the model in the Georges Bank region are primarily due to deficiencies in the circulation model. In particular, an inability to fully represent the high flow rates of the Georges Bank and Gulf of Maine gyres. A superposition of Argos drifter paths on particle pathways used to generate the dispersal kernels showed similar trajectories, but speeds of lesser magnitude. The lack of significant densities off Cape
Cod does not appear to be attributable to a lack of larval supply, as many of the dispersal kernels generated from the Great South Channel region extend to (but not past) the tip of Cape Cod. It seems more likely that those populations are reduced due to bottom water temperatures dropping below the 3.0 celsius limit.

Modeled scallop distributions in the Mid-Atlantic Bight match observed distributions fairly well, capturing many qualitative patterns. The most obvious similarity is the divide at the Hudson Shelf Valley between the northern populations that extend along the entire shelf, and the southern populations that are centered closer to the shelfbreak. Also notable is the southern extent of the population, which closely matches known distributions. Other similarities include a point of higher densities extending along the Long Island shore towards Rhode Island, higher densities along the axes of the Hudson, Delaware and Albemarle Shelf Valleys, and a peculiar point of higher densities extending across the entire shelf at a latitude of about 36.5 degrees.

Fishery closure simulations

The results of the fishery closure simulations suggest that the location of a closure can have a significant impact on its success, ranging from no change to a doubling of annual yields. Some of the poorest responses were generated by closures situated in the Nantucket Shoals area, as well as the regions south of the Delaware Shelf Valley, regions where actual fishery closures in the ’90’s did not appear to produce significant impacts on scallop populations (NEFSC 2007). The higher simulated yields produced by closures on Georges Bank and the Hudson Shelf Valley are also consistent with scallop population responses to historical closures. The closure simulations on Georges Bank and the
Hudson Shelf Valley both performed well, but the patterns of connectivity in those regions are very different, suggesting they be analyzed individually. The dispersal kernels associated with Georges Bank demonstrate scallop habitat with relatively higher levels of self-seeding, providing a linkage between strong adult populations and recruitment rates. These characteristics helped Georges Bank closure simulations develop strong populations in the juvenile and adult size classes, and the highest yield increases of all the simulations. Additionally, the presence of large downstream habitats reduces the likelihood that larval propagules will be advected offshore, enhancing the influence of these spawning stocks on the metapopulation. Unlike the Georges Bank dispersal kernels, the Hudson Shelf Valley dispersal kernels demonstrated shifts between generally self-seeding periods, and periods of strong connectivity with upstream source populations. These patterns produced smaller increases in the already high juvenile and adult populations, but in some instances yield increases comparable to the GB closures. The increases in adult populations generated by closures in the southern portion of the MAB were constrained to the closure areas themselves, and almost entirely driven by the supply of recruits generated by upstream populations. These closures produced minimal, if any, increases in yields.

The difference in response between the GB, HSV, and southern MAB closures suggests that in practice, closure outcomes may be improved by specifically tuning the harvest strategies to capitalize on a closure’s specific properties. For GB closures, higher yields appear to be driven by increases in the adult populations in regions that frequently act as larval sources to large areas. Maintaining these populations is best achieved through the use of relatively permanent fishery closure areas. Furthermore, reducing the
catch limits on the Georges Bank scallop fishery, or establishing a maximum harvestable shell height, may also help enhance the efficacy of these closures. The HSV closures likely function in a way similar to the GB closures, establishing large adult populations that provide recruits to downstream populations. However, the recruitment potential provided by upstream source populations, along with the potential loss of propagules due to cross-shelf advection in the MAB, suggest that a different harvest strategy may be appropriate for these closures. The HSV may be an appropriate location for rotating closures, protecting cohorts as they grow to harvestable size, then opening them to the scallop fishery. The large upstream source area, coupled with recruits generated from other HSV closed areas would facilitate a relatively quick recovery of fished populations. Furthermore, more traditional catch-size limits would be appropriate in these areas, reducing density-dependent mortality effects on new recruits. Closures in the southern portion of the MAB did not produce notable increases in yields, but they did increase the numbers of adult scallops. This suggests the practice of using closures to protect specific recruitment events as they occur, then harvesting them once they reach a large enough size. Permissive catch-size limits in this region are unlikely to impose deleterious effects on the broader scallop populations.

Climate Regime Simulation

The results of the climate regime simulation demonstrate a qualitative shift in population distributions and yields with changes in climate, primarily as a result of changes in larval transport dynamics. Specifically, the highest densities during high shelfwater years (Mountain 2003) develop along the Mid-Atlantic Bight. This is due to a
combination of 2 factors – a relative weakening of the Georges Bank gyre that reduces self-seeding in that region, and a seaward migration of the shelf-slope front (Fratantoni and Pickart 2003) in the Mid-Atlantic Bight that increases self-seeding in that region. These effects are more easily visualized by plotting the spatial differences in densities (Fig. 28) and yields (Fig. 29) between the high shelfwater and low shelfwater simulations, which suggest a general shift in distribution from the Georges Bank area to the Mid-Atlantic Bight area with increases in shelfwater volume.

Linking a measurable environmental variable such as shelfwater volume to population dynamics through a known mechanism can help us anticipate the impacts of future climatic shifts. The establishment of a link between sea scallop populations and the physical environment is especially valuable, as most of the predictions generated by climate change research are generally limited to physical variables. A common characteristic of many atmosphere-ocean coupled predictive models (IPCC 1997) is an increased freshening of water in the Labrador sea – the source of cold, relatively fresh water that feeds into the shelfwater system. Similar variations in Labrador Water salinity have been observed and correlated with NAO (Dickson et al. 1996), and as demonstrated by our models, may play a significant role in the transport of larval sea scallops. This simulation suggests that as climate change progresses through the 21st century, scallop populations, along with the fisheries they support, may shift southward towards the Mid-Atlantic Bight.

With this population model we have addressed two questions – the impacts of shelfwater variability on scallop populations, and how the larval transport dynamics of a region may impact the function of closed areas. The model also demonstrates its potential
in predicting short-term dynamics. Although comparisons between the model and scallop fishery data are encouraging, they highlight the need for better representation of circulation features in the underlying physical models. With increasing model skills and computational power, the significance of these limitations will become increasingly reduced. More development is needed, but the preliminary results are encouraging, and certainly of use to sea scallop managers.
SPATIAL MANAGEMENT OF THE SEA SCALLOP FISHERY: USING
BIOPHYSICALLY-COUPLED MODELS TO UNDERSTAND THE RELATIONSHIP
BETWEEN NATURAL HISTORY AND ENVIRONMENTAL VARIABILITY

INTRODUCTION

In the world of marine resource management, the sea scallop (*Placopecten magellanicus*) stands out as a true success story, rebounding from dangerously low numbers over the last two decades (NEFSC 2007). Although a tremendous achievement, this success was in fact a lucky accident, being attributable to actions taken to protect dwindling cod stocks. To help bolster the cod populations, managers established a series of areas on Georges Bank closed to trawling, in hopes that those regions might serve as refuges, providing cod stock to the rest of the region. Because the sea scallop fishery also utilizes trawls, they were unintentionally barred from regions they had been fishing for decades. Ironically, the cod populations did not appear to benefit from the closures anywhere near as well as the sea scallops.

Obviously, something about the life history of sea scallops sets them apart from codfish in such a way as to make regional closures a more efficacious means of bolstering their stocks. Perhaps the most obvious difference between cod and scallops is that scallops are relatively sedentary as adults – once the pelagic larvae settle, they are unlikely to move more than a few kilometers from that spot over the course of their lives (Stokesbury and Himmelman 1996). Any ability for scallop populations to move from
place to place – utilizing newly opened habitat, or recolonizing fished out areas – must primarily be achieved through the transport of their pelagic larvae. Although it may seem a rather passive affair, floating through the sea in the plankton has tremendous potential to move larvae great distances. Georges Bank and the Mid Atlantic Bight, both develop strong current systems during the times of sea scallop spawning (Aretxabaleta et al. 2008) that could certainly facilitate larval transport. Studies of larval settlement on Georges Bank have shown strong correlations between the strength of its clockwise-rotating gyre and the retention of larvae (NEFSC 2007). This suggests two things: that ocean currents may be an important factor in the ability for Georges Bank sea scallops to replace their populations’ dying members, and that in weak gyre years, large numbers of scallop larvae may be settling in new regions – reinforcing the scallop numbers in established beds, or establishing entirely new ones.

Although the mechanisms responsible for the successes of the Georges Bank closures are not immediately clear, there may be useful lessons to be gained from these events. Developing a better sense for why sea scallops benefited so well from these closures, understanding what it is about scallop life history that makes closed areas work for them, and recognizing how the interplay between physical and biological forces influences scallop populations, will aid managers in the creation of better tools for managing all species. So what approach should we as researchers take when trying to elucidate the factors responsible for these increases in sea scallop population? The primary factor of importance is to quantify how various regions connect to others through larval transport – and to know how connections vary from year to year. If these processes are, as hypothesized, driven by environmental factors, this knowledge may also help us
predict how climate change may influence the distribution of sea scallops over the next century.

The most direct way to identify the connections scallop larval transport provides between regions would involve the release of tagged scallop larvae from particular locations, and then sampling downstream regions to identify settlers (Arnold et al. 2005). While technically possible, the extremely large areas involved would be impractical to sample adequately, and the number of specific release locations would require extremely large numbers of larvae and ship days, making this approach logistically impossible at a useful scale.

When faced with these sorts of difficulties, researchers turn to models as a means of testing hypotheses. Many useful models are already being used to explore the dynamics of ocean circulation, larval transport, and sea scallop population dynamics (Cowen et al. 2000; Cowen et al. 2006; Guizen et al. 2006), but few efforts to tie these models together have been undertaken. Models are only as good as the observational data used to evaluate their accuracy, and limited field data on the larval portion of sea scallop life history exists (Tremblay and Sinclair 1990). Nevertheless, modeling provides our best chance of addressing our hypothesis, so appropriate compromises need to be identified.

Models allow us to create the same sorts of experiments we would like to perform in the field, and as such, can often be set up using the same (albeit virtual) protocols that would be used by field researchers. Certainly a virtual larva can be introduced into a circulation model and tracked through time to see where it might end up. However, computers do have their limitations, and where a single release of tagged scallop larvae
might include millions of individuals (Arnold et al. 2005), a computer simulation is realistically unable to track a large enough number of individuals to create an equivalent simulation (at least using today’s technologies).

These limitations can be addressed by dropping the more intuitive view of these particles as virtual larvae, and instead thinking of them as aggregations of larvae, transported as a coherent group through the virtual seas. This approach introduces a few complications – most notably, in our ability to resolve the downstream spread of a cloud of scallop larvae. Large numbers of real scallop larvae released from a common location will spread out as the group travels through the seas, primarily through the effects of swirls and eddies present along the travel path. A large enough release of larvae can capture this variability, but a virtual larval group represented by a single particle will have but one final destination. Interpreting spatial distributions from these pathways requires a bit of artifice.

Of course, before any virtual larvae can be released, some decisions need to be made on which circulation model to use. The regions we are interested in – including the Scotian Shelf, Gulf of Maine, Georges Bank and the Mid-Atlantic Bight – are extremely dynamic, possessing complex coastlines and bathymetry. These qualities make them a challenge to model accurately, so we decided to adopt a model that had already been calibrated and used for these regions – Quoddy (Lynch and Werner 1991).

Utilizing a preexisting circulation model saves a considerable amount of development time, but every run still needs a significant amount of data and processing to establish the starting conditions of the model. We need to generate salinity and temperature values for all regions and depths of the model domain before we begin the
simulations. Rather than simply create estimates or idealizations of what we expect these values to be, and to build year to year differences in ocean conditions into our simulations, we archived a large collection of direct measurements from which to estimate these initial conditions. The temperature and salinity observations we found were primarily generated by NOAA oceanographic vessels. We also received data from Fisheries and Ocean Canada, and were able to incorporate data archives created for projects undertaken in the South-Atlantic Bight. The total archive gave us good coverage throughout our target regions, from 1977 to 2003. Of course, the spatial and temporal coverage was not complete – to initialize each model run, we needed a method for converting the few measurements made during each time period into 3-dimensional representations of salinity and temperature, effectively filling in the gaps in time and space between the observations stored in our archive. Objective Analysis provides a good tool for this task, weighting the data that go into the equations in a way that better represents physical realities. For example, let us say we want to know the salinity at a particular location, and we have two nearby salinity observations from which to infer a value: one 10 kilometers away at the same depth, and another 2 meters away but 100 meters deeper. Even though the latter observation is physically closer to our target location, because density differences cause the ocean to stratify in flat layers, the distant observation will provide a better estimate of salinity at our target point. Objective analysis incorporates a weighting scheme into the estimations that takes these physical realities into account, yielding more accurate 3D representations of ocean conditions.

Although little is known about the lives of sea scallop larvae as they pass their time in the plankton, numerous lab studies have demonstrated many consistent behaviors
that may play a significant role in transport. Scallop larvae are able to swim, and respond to external stimuli, such as light. During the daylight hours scallop larvae tend to concentrate in lower depths, rising towards the surface after the sun sets. In the course of these travels, scallop larvae are likely to encounter differences in ocean currents – driven both by fronts and tides. The timing, length and magnitude of these vertical excursions could play a role in where the larvae eventually settle. A study undertaken in the Georges Bank region has documented the vertical positions of sea scallop larvae during the day and night, giving us a good estimate of depths to which scallops migrate, along with mean swimming speeds (Tremblay & Sinclair 1990). With these values we added a simple behavioral model to the simulations that caused larvae to swim towards the surface at night and to their target depths in the day.

The issue of settlement is more complicated. Many of the cues scallop larvae respond to as they become ready to settle have been established through lab studies, most of these variables are not part of the circulation models we are using. Instead of modeling the development and final settlement of the sea scallop larvae, we have instead opted to keep the virtual larvae drifting in the plankton for a span of time that exceeds the typical pelagic larval duration. We are then left with the challenge of interpreting settlement locations using long, spaghetti-like pathways. More on that later.

Just like setting up field experiments, the computer simulations must be carefully defined and constructed to specifically address our hypotheses. This was especially true given the sophistication of the circulation model and the large number of runs necessary to resolve the year to year transport differences we are interested in. For example, sea scallops primarily spawn in the late summer, but there are populations that also spawn at
lower intensities in the spring. Generating circulation model runs spanning these time periods would have been prohibitively difficult, and introduce complications that would be difficult to resolve without significant structural changes to the circulation model itself. Instead, we chose to simulate the fall spawning event alone, for each of the years from 1980 through 2003, resulting in 24 separate spawning simulations. As the pelagic larval duration of sea scallops is about 6 weeks, we chose simulation runs of 3 months in length. We also needed to decide how to distribute release locations of the virtual larvae. Our primary limitation with regard to virtual larvae was numerical – computational limitations required that we hold the number down to approximately 10,000 individuals. When distributing release locations, we felt it was important to place them not only in regions with known populations, but also in those shelf regions that could support scallops, but for whatever reason do not. Sea scallops densities are relatively low in depths deeper than 150 meters (Hart and Chute, 2004), so those regions were not included in the releases. A series of evenly spaced stations was produced covering the shelf regions shallower than 150 meters, spanning the area between the Scotian Shelf and Cape Flattery. Each virtual larva release would include approximately 1100 individuals, yielding a large number of pathways. To better represent uncertainty in the timing of spawning events, and to capture the variability of pathways driven by environmental conditions at the precise times of release, a series of daily releases was made over 15 days, arranged around the target day itself. This brought the number of virtual larvae in each individual run up to about 17,000 individuals, within the limits we set for ourselves.

We created and ran the simulations, and were encouraged to find that the virtual larvae pathways varied greatly between runs, demonstrating clear year to year differences.
in connectivities between regions. Comparisons between our modeled pathways and GPS-fitted drifting oceanic buoys, showed qualitative consistency between the two. Transport velocities were more often under rather than overpredicted in the simulations, and all the major current and gyre systems were clearly visible.

The pathways traveled by the virtual larvae produced a thick tangle of spaghetti-like strands throughout the domain, forcing us to answer the question: how do you untangle this mess of information into something of actual use?

Our goal was to use these simulations to create settlement probability maps for all the areas that could potentially sustain scallop populations. In other words, we needed to know, for any point in the domain, where scallop larvae spawned at that point are like to settle.

As described earlier, the most intuitive way to accomplish this is to simply count how many virtual larvae arrive at each location, taking care to note from which locations they were generated.

Unfortunately, there are not enough virtual larvae in each release to generate a statistically valid spread of settlement locations. Instead, we used each virtual larva to represent the center of a larval aggregation, estimating the aggregations’ spread over the course of the run. However, there are many potential sources of variability in the transport distributions to account for, and little empirical data for determining which are most significant. As such, it falls upon us to anticipate and account for these sources based on what is currently understood about transport processes.

Many of the studies done on dispersal have focused on wind transport of seeds in terrestrial systems. Such studies have demonstrated a tendency for transport distances to
skew from simple bell-curve distributions towards the seed source, creating a long “tail” of individual seeds, falling far from their parents. Building a similar kurtosis (Pringle et al. 2009) into our model seemed important, but the direction of the skew – either towards or away from the source – could be different in the marine milieu. Such evidence was provided by a single study carried out in a Florida lagoon, that released and sampled a large number of tagged larvae (Arnold et al, 2005). While this study did not attempt to create a dispersal kernel similar in nature to the seed dispersal studies, preventing a direct comparison, they did note the retention of larvae along the pathway traveled by the aggregation. An observation that supports the hypothesis that marine dispersal kernels skew away from their sources, with longer tails on the source-side of the peak in distance distributions.

The method used to address this skew was primarily a function of how we defined settlement in the model. You will recall that the transport information saved from our model consisted of long pathways, encompassing a longer span of time than is likely for a sea scallop larva to remain in the plankton. To solve this problem we utilized a technique that was extended to the other sources of transport variability. Instead of focusing on a discrete settlement location, each virtual larva carried a uniquely identifiable weighting factor that was contributed, additively, to each location in the domain that it passed. Each location kept track of the total amount of “settlement” value contributed by source-specific virtual larva in the run. Once the run was complete, the settlement values associated with a release location were all normalized by the maximum total settlement possible from the locations. In this way, we converted the many pathways generated by the particle tracking program into probability of settlement values, by
location, from every source location in the grid. The total settlement percentages from any one source would usually sum to less than 1.0, due to the loss of some larvae carried to regions outside of appropriate settlement habitat.

To represent a nearfield skew, the virtual larvae were given time-varying weights, starting at zero and linearly increasing to 1.0 at the 42-day mark – a reasonable PLD for sea scallop larvae (Hart and Chute 2004).

In regions of our model domain possessing complex current patterns, relatively small differences in starting positions generated very different transport pathways. In some instances, the resultant pathways would fork off in wildly different locations. These forks were most noticeable on the Northeast Channel and at the Great South Channel, where slight cross-shelf velocity differences resulted in particles either entering or crossing the channels. The weighting method was also extended to help characterize these spatial variabilities in ocean flow by using multiple particles to carry settlement weight values. To accomplish this, the particles released from a location were given full value, and the six particles released from adjacent locations, arranged hexagonally around the main location, were each given 1/6 of the main particles’ value.

Settlement weighting can also be used to integrate the 15 daily releases described above in a way that emphasizes the central release. In this way the resultant dispersal kernels incorporate transport variations driven by daily changes in winds and tides.

After processing, we were left with a large number of 2D dispersal kernels – settlement probability footprints – showing the likely settlement locations of scallop larvae spawned throughout the Gulf of Maine, Georges Bank, and Mid-Atlantic Bight regions.
When viewed individually, these pathways showed many of the features we expected to see: long nearfield tails in the distance distributions, greater variability in along-shelf transport differences compared to cross-shelf, and significant year to year variations in transport pathways. The dispersal kernels also demonstrated characteristics consistent with known oceanographic processes, providing some qualitative confirmation of the underlying circulation model’s accuracy. In particular, the presence of gyres on Georges Bank and at the entrance of the Bay of Fundy (Aretxabaleta et al. 2009), Scotian Shelf crossover events (Smith et al 2003), and the Mid-Atlantic Bight’s shelf-slope front (Fratantoni and Pickart 2003).

The large number of dispersal kernels does present a challenge – how to summarize a large number of individual probabilities into information easier for the human brain to digest. A simple way to do this is by finding the total number of destinations each source location in the domain is connected to in a given year. These values can be interpreted as the value of each location as a source of larval propagules to downstream populations. Conversely, the total number of source sites supplying larvae to each destination location represents that point’s value as a larval sink. Generally speaking, a population of sea scallops living in a high source-value region may be most valuable to a fishery as standing stock – a strong and consistent source of larval propagules to the broader population. Populations in high sink-value regions may be more valuable as places to focus fishing activity – allowing higher recruitment rates to maintain consistent annual harvests.

Source and sink areas are useful when evaluating the large set of dispersal kernels, but clearly there is much more information in the full measures of connectivity to
be exploited. The dynamics of connected systems – networks – have been modeled extensively (Roberts 1976), but more often to address technical problems, such as power supply in electrical grids. The underlying mathematics, however, are easily adapted to address connections in scallop populations. By organizing the dispersal kernel data in matrix form, a whole host of analytical methods become available, allowing us, for instance, to trace the impacts of a recruitment event as it pulses through the rest of the population. An extremely applicable concept from network theory is “strong” connectivity. Two points in the domain are defined as being strongly connected if each is a source to the other. Furthermore, if you connected a strongly connected pair of points with the other points they connect strongly to, you define a strongly connected subset of the domain. This concept roughly parallels the idea of fishery management units – subpopulations of a managed species whose dynamics tend to respond coherently. Traditionally, the boundaries of management units are established using a variety of data, but sea scallop populations are harder to break down in this manner. Ocean currents appear to connect sea scallops throughout their range, and genetic differences are dampened by frequent mixing between source stocks. If network theory can provide a tool for converting the sets of dispersal kernels into strongly connected subsets, they may prove to be a powerful, objective means of establishing management units for sea scallops. With this knowledge, scallop fishery managers could allocate fishing efforts to take best advantage of the natural transport dynamics of the broader population.

This method (known in the network theory world as “condensation”) applied to the average dispersal kernels for the set of runs (1980-2003), highlights 9 separate regions in the domain, most of which overlap known scallop distributions. The fact that
some of these subsets include regions where scallops do not occur should not concern us at this point, as the analyses utilize nothing more than physical transport. Nevertheless, where existing populations do overlap these strongly connected regions, these analyses suggest that they may function ecologically as coherent subpopulations.

When condensations are carried out on dispersal kernels from individual years, a great deal of interannual variability becomes apparent. The year in which connectivities were highest, 1996, produced only 6 strongly connected subsets, entirely dominated by one large region extending from the MAB up around Georges Bank and into the Gulf of Maine. During the 1998, the most poorly geographically-connected year in the series, condensation produced 13 strongly connected regions, all of comparable size. These interannual changes could be a potential source of population variability in sea scallops, but a direct comparison with observed changes in scallop distributions may not be appropriate, as the layers of analyses create errors that can mask correlations. Instead, we attempted to identify the environmental mechanisms driving these interannual variations, in hopes of finding a better-observed variable to use in correlation analyses.

The most numerous ocean observations in our study region are temperatures and salinities. The data archive we assembled for initializing the circulation model runs contained large amounts of these data, providing a useful tool for these explorations. To facilitate our investigation, we again used objective analysis to build 3D snapshots of ocean salinities and temperatures for our study region. For each analysis, we utilized 2 months worth of observational data, providing average temperatures and salinities for each of those 2-month periods. The 24 years from 1980 to 2003 produced 144 separate bimonthly averages. When the bimonthly averages for the fall scallop spawning months
were compared with the others, one the most notable features was a cold pool of relatively fresh seawater on the MAB shelf in the summer months, bordered by sun-warmed water on the inshore side, and warmer but salty deep water edging up along the shelfbreak on the seaward side. What’s more, the size and temperature of this “cold pool” appeared to vary significantly from year to year. Could these variabilities somehow relate to variations in transport in our transport models?

Detailed examination of the climatology set helped identify the processes driving the cold pool, sometimes referred to as the “residual cold pool” for reasons that will be apparent. All the water on the shelf north of Cape Hatteras, has some history in the Gulf of St. Lawrence, where cold temperatures, high precipitation, and glacial melt all contribute to the generation of cold, relatively fresh seawater. Because of its freshness, this shelfwater (Mountain 2003) floats above the salty surface waters of the Atlantic. This creates an unusual condition in which cold water rests atop warmer water – an arrangement that is usually reversed in most seas. Through a combination of buoyancy and the Coriolis effect, the shelfwater slowly moves southward, adhering closely to the coastline. The chemical identity of the shelfwater remains relatively stable as it moves down around Nova Scotia, but once it enters the Gulf of Maine, high levels of tidal energy stir up the underlying warm water into the shelfwater mass. The source of the warmer water is the Northeast Channel, which is deep enough to permit deep water to flow into the Gulf of Maine, constantly exposing new bottom water to mixing forces. The newly altered shelfwater is driven by the same forces around Georges Bank, and down into the Mid-Atlantic Bight, where significant portions of its volume are leaked off in response to the decreasing width of the shelf. Any shelfwater that makes it to Cape
Hatteras is carried into the Gulf Stream. Although the residual cold pool appears superficially like a distinct water mass adhering to the shelf seafloor, it is in fact simply the deep portion of shelfwater that retains its temperature, effectively insulated from the influences of solar warming.

Although velocities are not captured in these bimonthly averages, the presence of strong horizontal density gradients, fronts that drive currents, can be inferred from the temperatures and salinities. The seaward edge of the cold pool is one such density gradient that has long been associated with a current near the shelf-slope boundary – one that has been observed to migrate to various cross-shelf positions from year to year (Fratantoni and Pickart 2003). Could the position of this shelf-slope front play a role in interannual variability in transport potentials?

To make comparisons between variability in the cold pool and transport patterns, we needed a single measure of the shelfwater’s character upon which to make comparisons. Because there are so many dynamics involved in the creation and propagation of shelfwater, we wanted a value that integrated all the myriad processes discussed above. There has been work done to identify the actual volume of shelfwater (Mountain 2003) and to observe how that value changes over time, which would suit our needs well, but the data used for this work were not extensive enough to provide a complete time series. The bimonthly averages however, being 3D, did contain the information we needed, at a scale appropriate for comparisons with transport data. Generating a time series of shelfwater volumes from our bimonthly averages of hydrographic data was a simple task, and was quickly done. The resulting time series showed clear interannual differences, but more significantly, a sort of flip-flop between
high and low stages, oscillating at a frequency suggestive of atmospheric forces such as the North Atlantic Oscillation (NAO) and the Atlantic Multidecadal Oscillation (AMO).

The apparent similarity between shelfwater volume variability and climate regime shifts inspired us to perform a simple correlation analysis on the two timelines to look for patterns. The results showed weak correlations that although somewhat apparent to the eye, were not mathematically significant. However, correlations are often confounded when many process are integrated in the analysis. Our measure of shelfwater volume included values observed over an extremely wide area, so the likelihood of this being a problem were relatively high. To better resolve the variabilities in shelfwater volume, we tried the correlation analyses using shelfwater volume variabilities at every point of the objective analysis results in the domain. The results completely eliminated the confounding effects of integrating volumes throughout the domain, demonstrating regions along the shelf with clear and mathematically significant direct correlations with climate patterns – especially the AMO. Interestingly, the regions of higher correlation appeared to progress southward along the shelf over the course of a year, starting on the seaward edge of Georges Bank in the January-February averages, and moving to the southern extent of the MAB by the September-October averages. The results suggest a bolus of shelfwater propagating along the shelf at a measurable rate. This process has been observed by investigators working on the shelfwater system in the MAB, who estimated a rate of advection virtually identical to our observations (Mountain 2003).

Finding a correlation between shelfwater volume and AMO is extremely useful, in that the historical record of shelfwater volume is extremely limited, but AMO values exist since 1948. If a mechanistic relationship can be drawn between transport
variabilities and shelfwater volume, AMO may provide a way of loosely reconstructing a larval transport history for sea scallop populations. In fact, an inverse correlation between total connectivity and total shelfwater volume is apparent (albeit just under statistical significance). Comparing the individual dispersal kernels between high connectivity and low connectivity years suggests that the position of the shelf-slope front is the main mechanism driving this variability. During high shelfwater years, the shelf-slope front is forced offshore, focusing the highest velocities over shelf regions too deep for successful scallop populations. Consequently, scallop habitats are overlain by relatively slow moving water that doesn’t move propagules as far as normal, reducing connectivity and enhancing rates of self-seeding. During high-connectivity years, the shelf-slope front moves inshore, sweeping scallop larvae long distances along the shelf, increasing connections between regions and feeding recruitment in other scallop subpopulations. Taken together, these result suggest a clear relationship between physical properties of the environment and transport dynamics in populations that disperse larvae via ocean currents. Recent efforts by scallop managers have demonstrated concurrent variations in scallop settlement that are partially explained by these changes in connectivity (NEFSC 2007), producing a limited, but encouraging, objective validation of our results.

Although we have established that larval transport may play an important role in scallop population dynamics, many other aspects of their life history and environment undoubtedly impose their own influences. To evaluate these impacts, we needed a means of integrating biological patterns into our transport models, bridging the gap between settlement and subsequent spawning activities. Population models for sea scallop populations have been utilized by fishery managers for many years, but the spatial
resolution of these efforts have been too course for our purposes. Additionally, the
variables utilized by these models tend to focus on the demographics of previous years,
instead of environmental variables. This is understandable given both the difficulty of
observing important environmental variables, and the ambiguity surrounding how those
factors influence biology. The information gained in this study opens certain
opportunities, but a robust, spatially-explicit population model for scallops needed to be
developed.

We embarked on this effort knowing that many parameters of the model would be
difficult to calibrate. Being a commercially important species, much work has been done
on scallop physiology in the lab (MacDonald and Thompson 1985), but population-level
responses of scallops to environmental variability is poorly known. To accommodate
these limitations, we built a model utilizing the physiological and ecological data we had.
This required certain inferences – for example, without an empirical measure of the
relationship between scallop larvae abundances in the plankton and the abundances of
spawning adults, we relied on knowledge of gonad mass in adults, and the sizes of
scallop eggs. Simple products of the two values produce an estimate of how many larvae
are produced at each location. Unfortunately, many of these larvae do not survive long
enough to settle, producing a strong difference between predicted spawning potential and
actual settlement densities. In the absence of empirical data describing these losses, these
values become tunable parameters. In other words, when comparing predicted and
observed settlement densities, we alter the larval mortality factor to tune the model to
produce results consistent with observation. These methods, although ubiquitous in
modeling studies, require us to carefully interpret our results.
Once completed, our population model featured over 600 individual subpopulation models, all connected to each other using our circulation model derived dispersal kernels. Each subpopulation model featured 10 distinct size classes, each with their own size-specific rates of metabolism, growth, mortality, and fecundity. In addition to the transport data included in the runs, bottom temperatures were extracted from the objective analyses utilized in the transport runs and applied to the subpopulations, increasing adult mortality where temperatures exceeded known tolerance thresholds.

Because fishing induces a significant amount of mortality on scallop populations, we felt it important to include harvesting in the model. Such estimates are difficult because scallop trawlers alter their behaviors to maximize yield per effort. Behaviors are notoriously difficult to model accurately. Instead of developing a complex behavior model to represent fishing mortality, we opted for a more simplistic approach based on certain assumptions. First, we assumed that fishermen would focus their trawling activities in the regions of highest density. Second, we assumed that as those regions’ densities decreased, fishing vessels would move to the surrounding regions possessing similar densities. Thirdly, we assumed that the fishery would continue taking scallops until a threshold density – one at which the yield would not justify the expenses of the effort – were reached. Such assumptions are not unreasonable (although many other factors may matter), and they are easy to implement in our model. All assumptions can be imposed on our model using a simple cap on population densities – removing all scallops in excess of the threshold density from each subpopulation (distributed among harvestable size classes), and integrating them into the total harvest for that time period. Building fishing activity in the model also created another opportunity to evaluate the
accuracy of the model, providing the last piece necessary to simulate the effects of closed
areas on scallop distributions. The results of these simulations showed several patterns
consistent with those observed in sea scallop populations during the same time period. In
particular, the relatively consistently positive effectiveness of the Georges Bank closures
in contrast to the MAB closed areas (NEFSC 2007). The MAB closures also performed
well, replicating the high levels of recruitment that spurred the establishment of the
closures, and the subsequent successes and failures of the Hudson Shelf and Virginia
Beach closed areas respectively.

The creation of our bio-physically linked model opened up an interesting
possibility – to simulate a series of spatial closures in various regions and evaluate the
broader population response. Such a simulation was generated, imposing a spatial closure
to the fishery at a randomly-situated, but consistently sized location. The experiment was
repeated for 100 different locations, and the results were saved. Generally, all closures
increased fishery yields, but there was a wide range of variation in the final results, with
some closures producing increases in yield up to 180 percent. The impacts on standing
stock also saw interesting variabilities which proved to be dependent on the locations of
the closed areas. When evaluated in this light, The effect of closures on scallop
populations demonstrated three categories of response: significant increases in yield with
demographically-distributed population increases, such as were seen in Georges Bank
closure simulations; low increases in yield with demographically-distributed population
increases, such as produced by Hudson Shelf Valley closure simulations; and low
increases in yield with population increases limited to adult stages, such as produced by
closure simulations placed in the southern half of the MAB. These results suggest a few
guidelines that might help scallop fishery managers improve the effectiveness of future closed areas. There are two distinctly different ways of managing closed areas: establishing them as permanent refuges, or keeping them closed long enough for the scallops to reach harvestable sizes and then making them available to the scallop fishery. A good site for a sea scallop refuge is one that maintains consistent densities and frequently provides larvae to downstream areas. Such a refuge should increase the yields of the fishery by quickly replacing scallops taken in fished regions. This is the pattern clearly shown in our models by closure simulations in the Georges Bank region. For these closures to achieve their full potential, they should be maintained as permanent refuges, blocking all fishing activity for as long as the closed area is deemed to be useful. Closures in the Hudson Shelf Valley area appear to function similarly to Georges Bank closures, excepting that the magnitudes of response appear lower. As such, their primary value is as a refuge. If the total area that can be protected is limited, however, it may be more efficient to distribute those closures in the Georges Bank region. Closures implemented in the southern half of the MAB do not appear to provide recruits to the broader populations. This is not surprising given that the prevailing currents in that region tend to transport larvae offshore into the Gulf Stream. It may be argued that many of these larvae may find their way back to the shelf, carried by warm-core rings peeling off from the Gulf Stream, but these events are quite episodic (Campana et al. 1989; Hannah et al. 2000; Brickman et al. 2001). Additionally, the relatively oligotrophic waters of the warm Gulf Stream may be hard for scallop larvae to feed successfully and survive, given their dependence on phytoplankton forage (Hart and Chute 2004).
The biophysically coupled scallop model also provides an opportunity to examine how climate change impacts might influence scallop populations. This is achieved by running special scenarios where the environmental forcings are tuned to represent future conditions under many decades of global climate change. In an effort to keep as much of our modeling system consistent with our other simulations, we opted to avoid using the climate change models produced by the IPCC for forcing data, and instead organize our existing environmental dataset to represent climate extremes. This was done by identifying the highest and lowest shelfwater years in our environmental dataset (1991 and 2002 respectively), and then iteratively applying these forcings to two separate simulation runs. A simple comparison of the results can then be used to make qualitative predictions on how scallop distributions may change with climate. In both cases, the simulations were consistent with our earlier analyses. The simulation based on the low-shelfwater volume environmental data demonstrated a development of high scallop densities in the Georges Bank area, where increases in gyre strength led to retention of virtual larvae near their source populations. Populations in the MAB were virtually non-existent, unable to maintain densities under low self-seeding rates. The highest yields in this simulation were produced in the MAB, between the Great South Channel and the region just south of the Hudson Shelf Valley. These higher yields were likely the result of higher rates of recruitment south of the main population centers on Georges Bank, producing high recovery rates in the face of simulated fishing pressures.

The high shelfwater volume simulation produced its highest population densities in the MAB, primarily between the Hudson Shelf Valley and the Delaware Shelf Valley – a region much smaller in areal extent than the high-density regions in the low-shelfwater
simulations. The lack of high population densities on Georges Bank appears to be the result of weakened gyre dynamics, reducing self-seeding rates there. The MAB, however, seemed to do much better under these conditions, as a seaward movement of the Shelf-Slope Front reduced transport potentials and increased self-seeding rates. Like the previously described simulation, this one also showed its highest yields in the regions just downstream from the high-density centers. In this case, that meant the highest yields were found in the region from the Hudson Shelf Valley to the shelf area off Chesapeake Bay.

Most of the climate change simulations created by the IPCC suggest that the future Labrador Sea will experience freshening, increasing the primary source of shelfwater in the GOM, GB, and MAB regions (IPCC 1997), suggesting a physical-biological link between the climate models and sea scallop populations through transport dynamics. In other words, under most accepted climate change scenarios, we expect to see a shift in sea scallop densities towards the south. We also expect a concurrent shift in the scallop fishery yields towards the south. Changes in the dynamics of the shelfwater system are likely to impact many other species as well. The presence of warmer bottom water at the shelfbreak – the result of slopewater slipping up slope under the shelfwater – is driven by the volume of shelfwater. When shelfwater volumes increase, as is expected under climate change conditions, this warmer water will be driven down to deeper waters along the continental slope. Such changes in bottom temperatures have been associated with large-scale die-offs of benthic species, such as the tilefish kill of 1882 (Marsh et al. 2001), and may eliminate a recognized refuge for overwintering MAB fishes.
When we initiated this work, our goal was to understand how larval transport influenced sea scallop populations at various locations throughout their range. After solving a series of technical challenges, we succeeded in characterizing these patterns, and most importantly, expressed them in simple, intuitive formats useful to scallop fishery managers. More broadly, however, this work helps us understand some of the important mechanisms that link environmental and ecological dynamics in the region. By identifying the impacts of shelfwater volume variability on the population dynamics of one species – driven through variations in larval connectivity – our ability to anticipate the impacts of environmental changes on all shelf species is greatly facilitated. Whether the question is where to position a marine protected area; if a recovered scallop bed should be opened to fishing activity; if rotational closed areas are more beneficial than permanent closures; how widely should a series of closed areas be spaced; or what can we expect as a result of climate change, these tools will facilitate informed decisions and help prepare for future environmental changes. What’s more, although our results offer immediate benefits, future increases in modeling accuracy and efficiency will continuously enhance the value of our methods. In the face of great ecological uncertainty, it is important for us to develop an understanding of the mechanisms driving change throughout the world’s oceans. It is our hope that this work helps fill one small but significant niche in these efforts.
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Figure 1 – Results from the 2006 NOAA-Fisheries sea scallop survey, showing distribution of sea scallop biomass in kg/tow (from NEFSC, 2007).
Figure 2 – A plot of the domain used in the Quoddy simulations, showing the positions of nodes and bathymetry. Contours are plotted at 50m, 100m, 300m, 500m, and 1500m. The red contour is drawn along the 150m isobath. The depth of the model grid is constrained to 2000m.
Figure 3 – Demonstration of the development of a dispersal kernel originating from the northwestern flank of Georges Bank. The larger particles above are released directly from the location, and the smaller particles originate from 6 points around the primary release location. The larger particles are weighted more heavily than the smaller. The auras around the particles show the range each particle searches when assigning current weight values. The purple shading is the total weight value accumulated at each point throughout the run.
Figure 4 – Dispersal kernels show the probabilities that a given particle will move from one part of the shelf to another. Sources are represented by small circles located at the upstream limit of the dispersal kernels and the transparency of the color scales with the probability of transport. The values have been log transformed to better resolve areas of low probability.
Figure 5 – Self-seeding potential is the probability that a larva will settle back into the population that created it. In this case, the means of all location-specific self-seeding probabilities from 1980 to 2003 is log transformed and plotted.
Figure 6 – The coefficient of variation of selfseeding potentials for the 1980-2003 simulations.
Figure 7 – In this context, a source is a region of the model domain that provides larvae to others. Source area is the total number of connections between a source site and the set of sites receiving larvae. This figure shows the spatial means of source area from 1980 through 2003.
Figure 8 – The spatial standard deviations in source area for all simulations from 1980 through 2003.
Figure 9 – In this context, a sink is a region of the model domain that receives larvae from others. Sink area is the total number of connections between a sink site and the set of sources providing larvae. This figure shows the spatial means of sink area from 1980 through 2003.
Figure 10 – The spatial standard deviations in sink area for all simulations from 1980 through 2003.
Figure 11 – The shelfwater volume timeline compared to the total connectivity timeline. Shelfwater is defined as having a salinity less than or equal to 34 psu. Total connectivity is the total number of elements in a connectivity matrix that are greater than zero. Bold lines (running means of the faded lines) are used in the correlation analysis.
Figure 12 – Condensation results using a threshold of 0.03 on the mean dispersal kernel. Subsets made up of less than 4 vertices are omitted for clarity. Paths between subsets are drawn as arrows.
Figure 13 – The condensation of the dispersal kernel generated for the fall 1999 spawning simulation. This year was notable for relatively high shelfwater volumes.
Figure 14 - The condensation of the dispersal kernel generated for the fall 1996 spawning simulation. This year was notable for relatively low shelfwater volumes.
Figure 15 – Temperature transects from bimonthly climatologies, generated using objective analyses on the hydrodynamic data archive. (CH – Cape Hatteras, MAB – Mid-Atlantic Bight, NS – Nantucket Shoals, GB – Georges Bank, COM – Gulf of Maine, SS – Scotian Shelf).
Figure 16 – Correlations between bimonthly shelf-water thicknesses and the AMO.
Figure 17 – A diagram showing the basic structure of the population model. The growth function is modified by depth, mortality by temperature and density. Fecundity is simply a function of shell height, but is indirectly affected by depth. Fecundities are distributed along the column of the full population matrix using that year’s dispersal kernel.
Figure 18 - The mean density (scallops/meter$^2$) of adult scallops generated by the population model in the absence of fishery-induced mortality.
Figure 19 - The mean density (scallops/meter$^2$) of adult scallops generated by the population model in the presence of fishery-induced mortality.
Figure 20 - The mean yield (k/m²) of scallops generated by the simulated fishery produced in the model.
Figure 21 - The mean density (scallops/meter$^2$) of fished adult scallops generated by the population model with the implementation of closed areas similar in magnitude and timing to historical closures.
Figure 22 - A scatterplot based on the results of the Monte Carlo simulation of randomly situated closures. The axes reflect the factor of increase in demographic subsets resulting from the closure simulation, while the color represents the factor of increase in the total simulated fishery yield. The locations of the closures breakdown well by region.
Figure 23 - The extent of areas included in closure simulations represented in Fig. 5.
Figure 24 - Mean adult scallop densities generated by simulations using only low shelfwater year environmental data
Figure 25 - Mean scallop yields generated by simulations using only low shelfwater year environmental data
Figure 26 - Mean adult scallop densities generated by simulations using only high shelfwater year environmental data
Figure 27 - Mean scallop yields generated by simulations using only high shelfwater year environmental data
Figure 28 - Spatial differences in scallop density means generated by low and high shelfwater year simulations. The color ranges from blue to red, indicating populations whose densities decrease or increase, respectively, with higher shelfwater volumes.
Figure 29 - Spatial differences in scallop yield means generated by low and high shelfwater year simulations. The color ranges from blue to red, indicating regions where yields decrease or increase, respectively, with higher shelfwater volumes.