What Maintains the Western Gulf of Maine Cod Stock?

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Introduction

Maps of the distribution of cod, derived from National Marine Fisheries Service (NMFS) survey data, show distinct centers of cod population in the Gulf of Maine/Georges Bank region (Figure 1). Particularly high cod densities are consistently seen in the western Gulf of Maine, in the areas of Ipswich and Massachusetts Bay and Stellwagen Bank. The recent fish tagging studies of Howell et al. (2008) and Tallack et al. (2009) indicate that this western Gulf of Maine cod stock complex may be dominated by a "stay at home" group, characterized as "sedentary, resident" by Howell et al.

Genetic work of Wirgin et al. (2007) and Breton et al. (2009) has further indicated that this cod stock may be, in some respects, genetically distinct from the other cod groups in the region. The distinction, however, differs with spawning time. There are two major spawning events in the western Gulf of Maine: a spring spawning that generally occurs in May and June, and a winter spawning typically occurring over December and January. According to the genetic analysis noted above, a large fraction of the cod participating in the spring spawning genetically differ from the other spawning cod of the Gulf of Maine/Georges Bank region, whereas the winter spawning cod have genetic similarities with cod of other regions, particularly in Nantucket Shoals and the eastern New York Bight.

Although high fish densities are consistently seen in the Western Gulf of Maine, the success of cod recruitment in this area varies significantly. Population analysis conducted by the NMFS indicates that the recruitment success (ratio of newly recruited juveniles to the spawning stock biomass) of cod in the western Gulf of Maine has undergone significant variation over the past 2 1/2 decades, differing by more than a factor of 25 from a low in 2000 to a high in 2005 (Figure 2).

The spring-spawning cod population in the western Gulf of Maine thus appears to be a distinct group with limited reproductive connection with other regional cod groups. The study described here is focused on three fundamental questions regarding the cod stock of the western Gulf of Maine:

- What controls the variation in recruitment success?
- What maintains the western Gulf of Maine cod stock?
- How did it evolve?

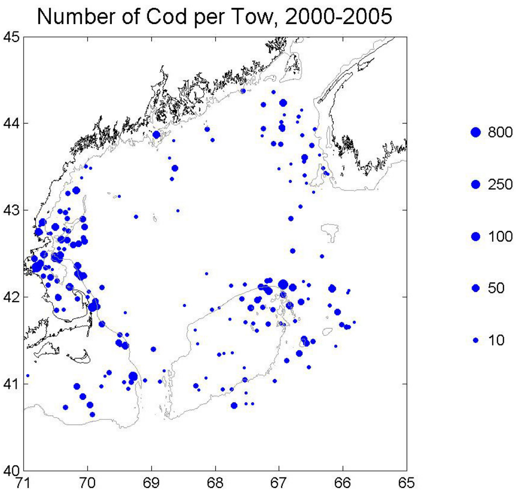

Figure 1. Distribution of cod, expressed as number of cod per tow, derived from National Marine Fisheries Service survey data acquired over 2000-2005. Note the particularly high concentration of cod in the western Gulf of Maine.

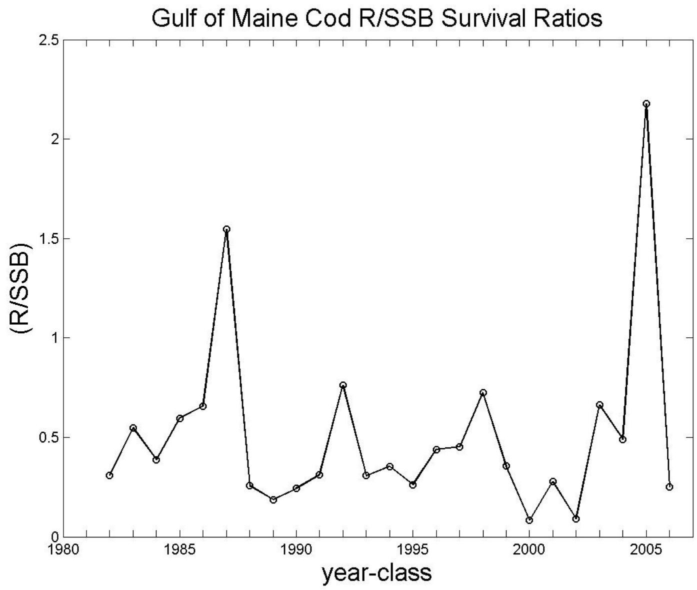

Figure 2. Year-to-year variation in survival ratios (juvenile recruits to spawning stock biomass) of Gulf of Maine cod as determine by NMSF assessments (values supplied by Loretta O'Brien, NEFSC/NMFS Woods Hole, MA)

Approach

To address these questions, we used the velocity fields generated by a hydrodynamic model of the Gulf of Maine/Georges Bank region to simulate the movement of developing cod eggs and larvae and to determine the likelihood that the larvae arrive at areas suitable for settlement as young juveniles. The model results were supplied by the Marine Ecosystem Dynamics Modeling group at U. Mass. Dartmouth (courtesy of C. Chen) and were generated by the FVCOM Gulf of Maine/Georges Bank model (http://fvcom.smast.umassd.edu/FVCOM/index.html). The velocity fields were of high resolution in both time (1 hour interval) and space (order 1 km cell size in the coastal zone).

Our focus was on cod spawned in Ipswich Bay (Figure 3) during the spring spawning event. In carrying out the modeling, the newly spawned cod eggs were assumed to be buoyant and to reside in the near surface layer of the stratified water column, subject to direct forcing by the surface wind stress. The manner in which larval transport is impacted by diel vertical migration of larvae was also examined, as detailed below. The age of settlement capability was assumed to be in the range of 45-60 d (e.g.

all cod were assumed to settle by an age of 60 days). Based on the distribution of age-0 juvenile cod reported by Howe (2002), the western Gulf of Maine region suitable as an early stage juvenile habitat was taken as the coastal area with depth of < 30 m.

In carrying out the transport simulations, ensembles of cod eggs distributed over the Ipswich Bay spawning region were released into the modeled flow field at intervals of 3 days over May and June. Each developing cod egg/larvae particle was tracked for 60 days. From the tracks, we determined the ensemble likelihood that the drifting cod arrive at a settlement suitable area at an age when settlement capable, a quantity defined as transport success by Huret et al. (2007). This was taken as the percent of time that particles (larvae) of the ensemble were over depths of less than 30 m (i.e. in a region suitable for settlement) during the last 15 days of their 60 day drift (i.e. the assumed age of settlement capability). The transport success was averaged over ensembles giving an expected success of transport to settlement areas for releases (spawns) during a given time period.

Transport simulations were carried out over 11 spring spawning events, from 1995 to 2005, and the resulting year-to-year variation in computed transport success was compared with the wind, measured at the NOAA 44013 weather buoy in Massachusetts Bay (Figure 3).

Understanding the relationship of wind to transport success requires knowledge of the large scale Gulf of Maine circulation. Numerous studies have shown that this circulation is dominated by a current that flows counterclockwise about the Gulf of Maine Basin. It is referred to as the Maine Coastal current, although this is somewhat of a misnomer as it is not bound to the coast but typically centered near the 80-m isobath. In the western Gulf of Maine, it takes the form of the Western Maine Coastal Current (WMCC), which flows southward off the coast of Massachusetts (Figure 4).

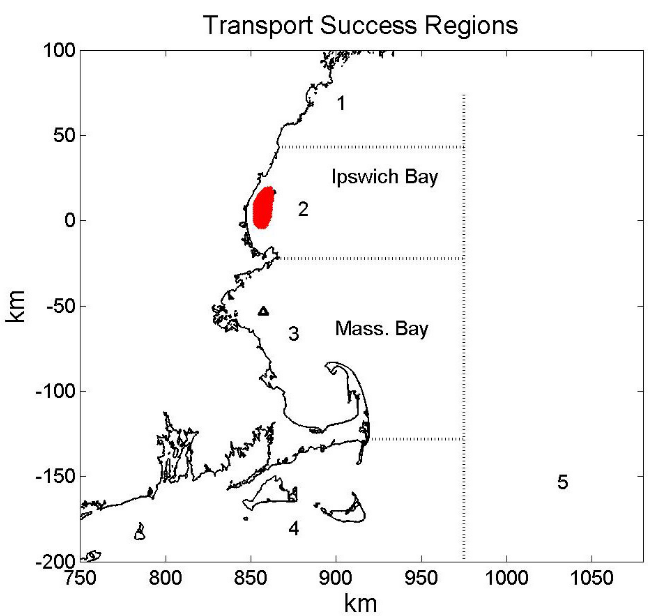

Figure 3. Our study region. The red area encompasses our representation of the Ipswich Bay spring spawning area from which ensembles of particles, representing developing eggs and larvae, were released into a modeled flow field. Success of larval transport to suitable settlement area of regions 1-5 was computed from the simulated egg/larvae tracks. Our focus is on transport success to regions 2 and 3. Because of the mean circulation in the Western Gulf of Maine, transport to region 1, north of the spawning area, was negligible. The triangle in region 3 marks the location of the NOAA 40013 weather buoy.

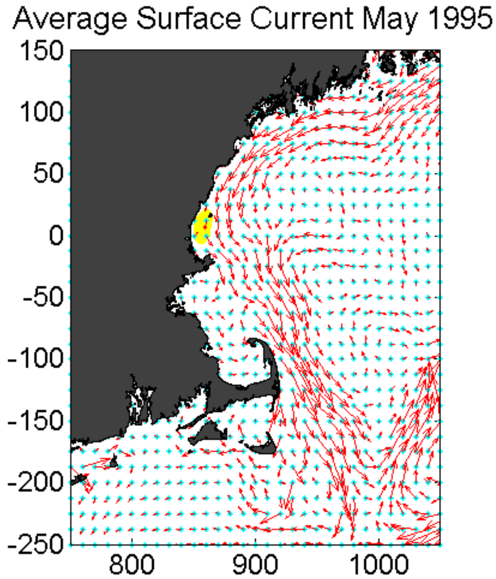

Figure 4. An example of the modeled flow field generated by the Gulf of Maine/Georges Bank FVCOM model. The vectors are average surface currents for May 1995. As the mean wind in May 1995 (measured at buoy 44013) was nearly zero, these currents are the modeled representation of the non-wind driven flow field in the western Gulf of Maine. They show the strong southward flow of the Western Maine Coastal Current bypassing Ipswich and Massachusetts Bays.

Results

To best understand the effect of wind on egg/larval transport, we first consider the movement of particles released at the Ipswich Bay spawning site and confined to the near-surface (wind-driven) layer (i.e. ignoring diel vertical migration in the larval stage). The yearly-averaged transport success of such particles to the Massachusetts and Ipswich Bay regions (regions 2 and 3 in Figure 3) shows considerable year-to-year variation (Figure 5).

To explore how wind forcing of the ocean surface layer may be responsible for this variation, it is necessary to understand the manner in which wind affects the surface layer current in terms of upwelling (with the surface layer flow directed offshore) and downwelling (with onshore surface flow). In Massachusetts and Ipswich Bay, a westward wind (from the east) will tend to generate on onshore flow and is thus downwelling favorable. Conversely, an eastward wind is upwelling favorable. Because of the effect of the earth's rotation, a southward wind in Massachusetts and Ipswich Bay region will force the surface layer westward and is downwelling favorable, whereas a northward wind tends to force upwelling.

Comparing the transport success of fixed-depth particles with the wind velocity averaged over each May (Figure 6) shows that the transport success to Massachusetts and Ipswich Bay tends to be high for those years when the averaged May winds are downwelling favorable. The reason for this is simple. Upwelling circulation tends to carry buoyant particles originating in Ipswich Bay offshore towards the WMCC, which transports the particles rapidly out of the region. Conversely, downwelling circulation tends carry particles onshore, allowing them to remain in the Ipswich Massachusetts Bay region, isolated from the WMCC. This same mechanism is responsible for a difference in the transport success of May vs June particle releases, with the transport success of the May releases being significantly higher than the transport success of the June releases (not shown). This is the result of a May-to-June shift in the wind pattern in the Western Gulf of Maine which results in predominantly upwelling favorable winds during each June of the years considered in our modeling (1995-2005).

Surprisingly, the introduction of diel vertical migration during the larval stage (migration to the surface at night for feeding and to depth during the day to avoid predators) has only moderate effect on the year-to-year variation in transport success to Ipswich and Massachusetts Bay as determined by our simulations. In general, the yearly-mean transport success is increased slightly with the introduction of vertical migration in the larval stage (Figure 7). The reason for this enhancement relates to the impact of upwelling circulation on those larvae that are within Ipswich and Massachusetts when they become capable of migration (at 3 weeks after spawning in our simulations). If these larvae remain fixed at the surface during an upwelling event, they will tend to be carried offshore towards the WMCC. However, with vertical migration, the larvae will be at sometimes within the lower layer and carried onshore. The net effect will be compensating onshore and offshore jogs for the vertical migrating larvae during the course of a day, as opposed to the persistent offshore movement that larvae confined to the surface layer will experience during upwelling circulation.

With or without diel migration included in the transport simulations, the estimated success of larval transport to settlement suitable area of Massachusetts and Ipswich Bay is fairly well related to the cod recruitment success for the western Gulf of Maine as estimated by the NMFS (Figure 5). In particular, years of high recruitment success (1998 and 2003) are also years of high transport success according to our simulations.

The results of our simulations suggest that the mean wind of May may be used as a predictor of recruitment success of cod in the western Gulf of Maine, specifically that an average May wind which is downwelling favorable might indicate conditions favorable for recruitment. Comparing the mean May north-south wind with the estimated recruitment success for the 1985-2005 period indeed indicate such a relationship. Recruitment success is particularly high in those years in which the mean May wind (measured at buoy 44013) is downwelling favorable (Figure 8). Most notable is 2005, which has both the highest recruitment success and the most strongly downwelling favorable wind during May for the 1985-2005 period.

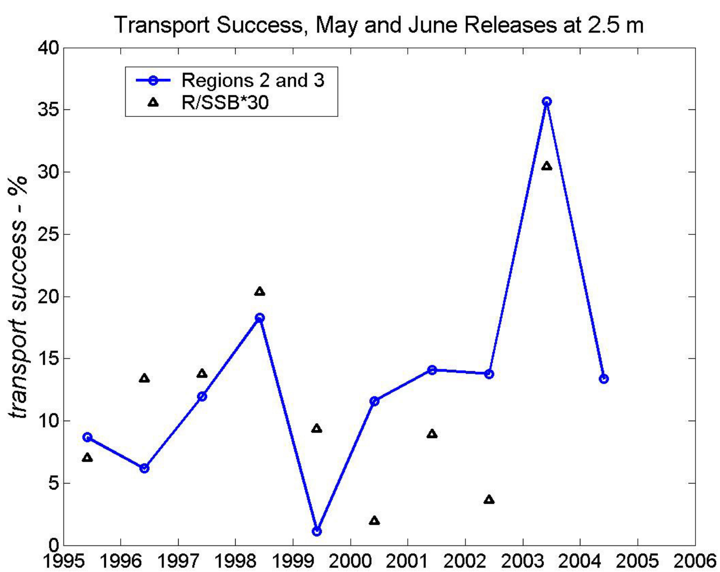

Figure 5. A comparison of recruitment success of Gulf of Maine cod determined from catch and survey data by the NMFS (triangles) with the success with which spring-spawned cod are transported from the Ipswich Bay spawning area to settlement suitable areas in Ipswich and Massachusetts Bay (blue line). The transport successes are for the case in which the developing eggs and larvae are held at a fixed depth during the transport simulations. Note a fair correlation between the transport and recruitment success values.

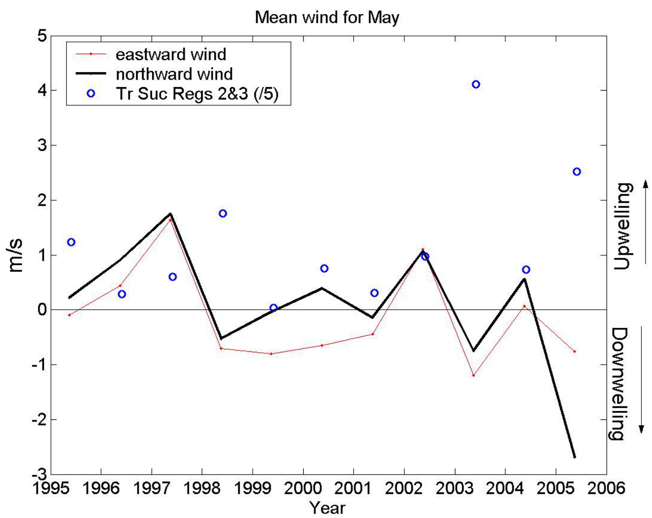

Figure 6. Comparison of the estimates of transport success to the Ipswich and Massachusetts Bay regions with the mean wind velocity of May measured at NOAA buoy 44013 (Figure 3). Note that the estimated transport success is always high when the mean wind of May is downwelling favorable.

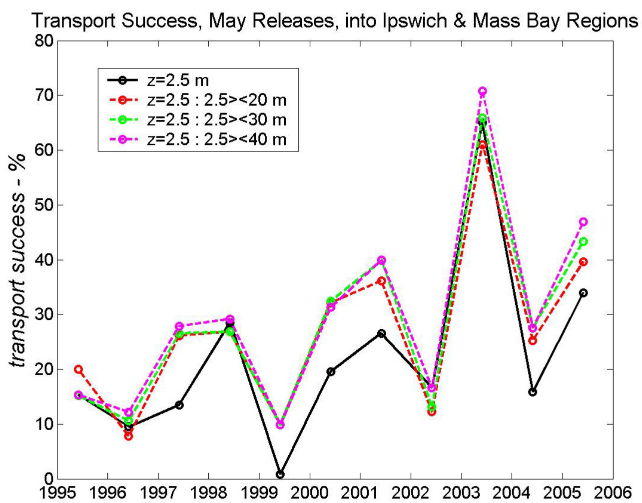

Figure 7. Comparison of the success of larval transport to settlement suitable area in Ipswich and Massachusetts for particles fixed at 2.5 m depth (black line) and particles which undergo diel vertical migration in the larval stage (colored lines). The depth limits of the migration are indicated in the legend.

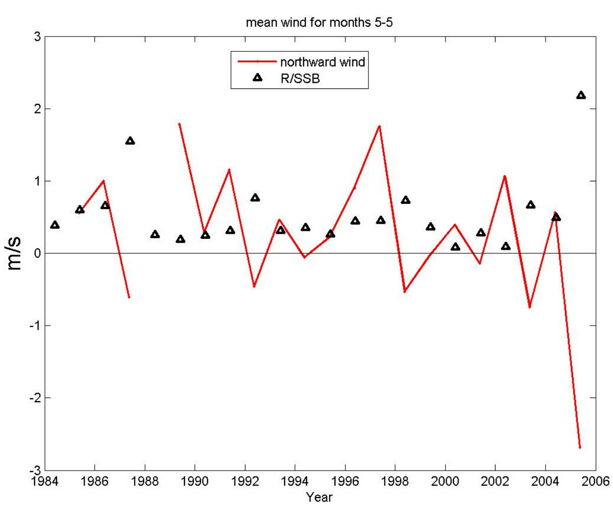

Figure 8. Comparison of the recruitment success of cod in the western Gulf of Maine with the mean north-south wind velocity of May measured at NOAA buoy 44013 (Figure 3). Note that the recruitment success is largest during those years when the mean wind of May is downwelling favorable (directed to the south)

Summary

The analysis reviewed above supports the following conclusions:

1. Coupling of wind-driven near-surface transport with the larger-scale Gulf of Maine "Coastal Current" controls whether Ipswich-spawned cod eggs and larvae are retained in the western Gulf of Maine or broadcast to distant areas (downwelling winds are larval retentive; upwelling winds are larval broadcasting).
2. The fate of the larvae is largely cast by the wind-driven transport in the buoyant egg stage, with diel vertical migration marginally enhancing retention.
3. Recruitment success in the western Gulf of Maine may be largely tied to the retention of the May-spawned population

Hypotheses

Coupled with the recent findings of the genetic and tagging studies mentioned in the Introduction, the results presented here also lead to some interesting hypotheses regarding the impact of cod spawning in the western Gulf of Maine. Three hypotheses, which may be particularly useful in guiding future studies, are:

1. *The two spawning times strategy*. It is possible that two spawning events in the western Gulf of Maine be part of different population strategies. The spring spawning may principally serve in sustaining the local western Gulf of Maine cod population, characterized as resident, sedentary by Howell et al. (2008). By contrast, the winter spawning may be important in supplying recruits to a more broadly dispersed cod complex, including Nantucket Shoals and the eastern New York Bight. This is consistent with the analysis of genetic markers by Wirgin et al. (2007) and Breton et al. (2009), which indicates that the cod spawning in Ipswich Bay during spring are genetically distinct from other regional cod stocks, whereas cod spawning in the western Gulf of Maine in winter are genetically similar to cod of other regions, particularly in Nantucket Shoals and the eastern New York Bight
2. *The sedentary-resident population is sustained in Massachusetts Bay because it's a pocket isolated from the WMCC.* The stay-at-home cod population of Massachusetts and Ipswich Bays may be maintained partly because these areas are largely isolated from the WMCC and thus are zones of larval cod retention.
3. *Ipswich Bay evolved as a prime spawning local because it is upstream of the Mass Bay pocket.* The aggregation of spawning cod in Ipswich Bay during spring may have evolved because of two factors. Ipswich Bay is uniquely situated at the "upstream" extreme of a larval retentive area, isolated from the WMCC, and the wind and water column stratification conditions during spring (particularly May) are ideal for retaining eggs and larvae in this region.

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