Processes controlling retention of spring-spawned Atlantic cod (*Gadus morhus*) in the western Gulf of Maine and their relationship to an index of recruitment success

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ABSTRACT

The Gulf of Maine cod stock is concentrated in coastal areas west of 70 ^{o}W. As revealed by population analysis conducted by the US National Marine Fisheries Service, the success of age-1 recruitment to this cod stock has varied considerably over the past 2 ½ decades. To explore how this variation may be related to ocean circulation, we carried out simulations of the movement of developing cod eggs and larvae spawned within the western Gulf of Maine during the well documented spring spawning event. Results of the modeling, which encompassed spring spawning events from 1995-2005, indicate that the likelihood that cod spawned in the spring be retained in the western Gulf of Maine, and carried to areas suitable for early stage juvenile development, is strongly related to the local wind conditions. Larval cod retention is favored during times of downwelling favorable winds and is least likely during times of upwelling favorable winds. In times of upwelling circulation, buoyant cod eggs and early stage larvae tend to be transported offshore to the Western Maine Coastal Current and subsequently carried out of the Gulf of Maine. Our analysis also indicates that diel vertical migration during the advanced stage of larval development tends to enhance the likelihood of larval retention within the western Gulf of Maine. A mean northward (downwelling favorable) wind velocity during May is found to be a viable indicator for strong recruitment success of age-1 cod to the Gulf of Maine cod stock.

Key words: Gulf of Maine cod, cod recruitment, recruitment success index

INTRODUCTION

The harvest of Atlantic cod (*Gadus morhus*) from the Gulf of Maine (Fig. 1) is an important part of the overall commercial fishing economy of the northeast US. In 2004, roughly 3.8 x 10^3 mt of cod were taken from the Gulf of Maine, only slightly less than the 4.6 x 10^3 mt cod harvest from Georges Bank and southern New England (O'Brien et al., 2006; Mayo and Col, 2006). However the yearly cod harvest from the Gulf of Maine has declined considerably since its peak of 17.8 mt in 1991, prompting concern about the future commercial viability of Gulf of Maine cod.

In forming management decisions aimed at rebuilding or maintaining a regional fish stock, it is important to understand what controls the recruitment to the year-1 population. For many species, recruitment is a highly variable process as evidenced by large year-to-year variation in the ratio of the number of year-1 recruits to the previous year's spawning stock biomass, often referred to as the survival ratio or the recruitment success. Such variation is particularly large for the Gulf of Maine cod stock. Since they were first tabulated by the U.S. National Marine Fisheries Service (NMFS) in 1982, recruitment success estimates for Gulf of Maine cod have varied by more than a factor of 25 (Fig. 2).

Undoubtedly, this variation in recruitment success is the product of a number of factors, including food availability, predation on young cod and cod mortality. A factor at play in controlling the fate of newly spawned cod is ocean circulation. Like many pelagic fish species, Gulf of Maine cod tend to spawn in distinct areas and time periods. The developing eggs and larvae are carried by ocean currents before reaching a stage where they are capable of colonizing a benthic habitat. Recruitment success of Gulf of Maine cod thus depends in part on the extent to which larvae are carried to regions of the gulf suitable for early stage cod development. Inter-annual variations in Gulf of Maine currents could thus be in part responsible for the large variation in recruitment success of year-1 cod to the gulf.

As revealed by data from trawl surveys conducted by the NMFS, a large fraction of the Gulf of Maine cod stock is concentrated within the western Gulf of Maine (Fig. 1). Recent evidence has indicated that spawning by this western Gulf of Maine cod stock is largely confined to two distinct events: a spring spawning with locations principally in Ipswich Bay (Fig. 3), and a winter spawning with locations spread over the western Gulf of Maine.

The focus of this study is on the fate of cod eggs/larvae released in the spring spawning event. As will be more fully explained below, this event was chosen because it occurs in a distinct area and at a time when the water column is vertically stratified, allowing us to specify the depth of cod eggs. Our work is aimed at understanding how variations in western Gulf of Maine circulation impacts the extent to which larvae spawned in Ipswich Bay are retained within the western Gulf of Maine and successfully delivered to areas suitable for early-stage juvenile development. A practical goal is to identify a readily determined index of recruitment success to the western Gulf of Maine cod stock. Perhaps more importantly, we view our study as an initial step in understanding how this cod stock is maintained and how it interacts with other regional cod stocks.

Our approach is to simulate the movement of developing cod eggs/larvae spawned in Ipswich Bay using an 11-yr series of high resolution velocity fields derived from a hydrodynamic model of Georges Bank and the Gulf of Maine. We examine how the transport and ultimate fate of cod larvae are impacted by wind-driven circulation, the large-scale regional flow and larval behavior.

In the sections to follow, we first present background information on the Gulf of Maine cod stock and the physical setting in the western Gulf of Maine   This is followed by a description of the numerical model used to generate the velocity fields employed in our study and the numerical techniques used to simulate particle motion from the spawning region. Presentation of the results will concentrate on factors that control the interannual variation in cod transport to areas in the western Gulf of Maine suitable for early-stage juvenile development. In the Discussion, we review our findings consider some of their broader implications.

BACKGROUND

Western Gulf of Maine cod stock

As readily seen in maps of fish distribution derived from NMFS survey data, the western Gulf of Maine cod stock is primarily contained in the areas of Ipswich and Massachusetts Bay (including Cape Cod Bay) and Stellwagen Bank. It appears to be geographically isolated from other regional cod stocks, such as those found on the flanks of Georges Bank and on the shelf region west of Nova Scotia (Fig. 1, also see Fig. 2 of Hunt et al., 1999). Evidence is accumulating that the western Gulf of Maine cod stock may be largely sustained through self-recruitment and have limited communication, via fish migration, with other regional cod stocks.

Movements of cod within the western Gulf of Maine were recently examined by Howell et al. (2008) using the data from a fish tagging and recapture study. They found that recoveries of fish tagged in the western Gulf of Maine were mostly (>73 %) within 30 km of their point of release, and only a small proportion (3 %) were > 100 km from their release point. Based on these and other recapture statistics, Howell et al. characterized the western Gulf of Maine cod population as "sedentary resident". This characterization is consistent with the data of a larger-scale fish tagging program reported by Tallack et al. (2009), which showed little movement of cod out of the inshore waters of the western Gulf of Maine.

Information on cod spawning activity in the Ipswich Bay area has been compiled by Howell et al. (2008) on the basis of fish captured in closure area 133, which includes Ipswich Bay. A larger scale view of spawning activity in the western Gulf of Maine has been provided by analysis of data from the Massachusetts Division of Marine Fisheries industry based surveys of Gulf of Maine cod, which included 9 cruises conducted over 2004-2007 (Hoffman et al., 2006; 2007). Based on these two sources, and numerous conversations with local fishermen, we have concluded that although cod spawning may occur intermittently in the western Gulf of Maine throughout the year, the appearance of large spawning aggregations in the western gulf is confined to winter and spring "spawning events". Winter spawning typically extends from November through February and is broadly distributed over the western gulf. Spawning in the spring is concentrated in the area of Ipswich Bay and near Cape Ann. The most intensive spawning of the spring event extends over April through June, with peak activity tending to occur in May.

The study of Howell et al. (2008) also indicated that spawning cod may return to the Ipswich Bay spawning area every spring, exhibiting a natal homing behavior. The mean distance of recapture relative to release location of cod set out in Ipswich Bay during April and May significantly declined every spring for the three years of their study.

At 2-3 months following spawning, cod larvae metamorphose into juveniles capable of bottom settlement (Lough, 2004). As noted by Huret et al. (2007), the bottom habitat in the western Gulf of Maine suitable for early stage settlement of juvenile cod may be inferred from the distribution of age-0 cod reported by Howe et al. (2002). Based on 22 years of data from trawl surveys off the Massachusetts coast, Howe et al. found that newly settled cod tend to be concentrated within distinct depth zones. Data from spring surveys show age-0 cod predominately within near-shore waters with depths shallower than 30 m. Newly settled cod found in the autumn surveys appear over a somewhat deeper swath, but are nonetheless largely confined to depths of less than 60-m. Howe et al. concluded that the near-shore region of Massachusetts and Ipswich Bay constitute a critical habitat for newly settled cod.

Gulf of Maine circulation

Our model results on larval transport and settlement need to be viewed in the context of the general circulation of the Gulf of Maine. Numerous studies have shown that the basin-scale circulation in the Gulf of Maine tends to be cyclonic and is principally driven by the pressure gradient associated with the density contrast between the relatively buoyant coastal water and the more saline water occupying the various basins of the Gulf (Bigelow, 1927; Brooks, 1985; Lynch et al., 1997; Pettigrew et al., 1998, 2005; Manning et al., 2009). An important part of this circulation is a current flowing near the coasts of northern New England and Nova Scotia (see Fig. 3 of Pettigrew et al, 2005). This is often referred to as the Gulf of Maine Coastal Current, although the name is somewhat misleading as it is not bound to the coast. In many observations, the maximum flow of Gulf of Maine Coastal Current is seen a considerable distance from the coast, often centered near the 100 m isobath (Churchill et al., 2005; Keafer et al., 2005; Pettigrew et al., 2005). Furthermore, the Gulf of Maine Coastal Current cannot be viewed as a single continuous flow. Rather, it consists of multiple branches with varying degree of flow from one to another (Lynch et al., 1997; Pettigrew et al., 1998, 2005). The branch flowing within our area of interest is referred to as the Western Maine Coastal Current (Vermusch et al., 1979; Churchill et al., 2005).

A recent study by Manning et al. (2009) included Lagrangian observations of the Western Maine Coastal Current that are particularly relevant to our study. Their study employed 227 drifter tracks acquired over 20 years. Analysis of the tracks passing through the western Gulf of Maine reveals the presence of a strong current that flows to the SSE and is not attached to the coast. Specifically, the mean velocity of drifters that passed through their "Stellwagen Bank" region, which extends from Ipswich Bay to the outer arm of Cape Cod, was directed to 139 ^{o}T with a magnitude of 14 cm s^{-1}. The mean isobath over which these drifters passed while transiting the region, taken as an indicator of the mean core of the coastal current by Manning et al, was 67 m.

Vertical Stratification during spring spawning

Also of interest to our study is the vertical stratification of waters in the western Gulf of Maine during the time of spring spawning (May-June). Density stratification will strongly influence where developing eggs and larvae tend to reside in the water column. In examining the density structure in the western Gulf of Maine, we have drawn from three data sources. One is a set of 163 conductivity temperature and depth (CTD) profiles acquired over 7 cruises carried out as part of a Massachusetts Water Resource Authority study during May-June of 2000 and 2001 (Anderson et al., 2002). The second is a series of 87 CTD profiles acquired during May and June as part of the NMFS survey cruises conducted from 1978 to 2007. The third is a set of CTD data acquired from Dec. 1989 through Nov. 2002 from a mooring deployed in western Massachusetts Bay (Anderson et al., 2007). Analyses of all of these data sets indicate strong and persistent vertical density stratification in the Ipswich and Massachusetts Bay region throughout May and June. In the majority of CTD profiles from this period, the surface to bottom density difference exceeds 1.5 kg m^{-3}, and is due to a combination of vertical temperature and salinity stratification (Fig. 4). The surface density seen in most profiles is in the range of 1023-1025 kg m^{-3}. Occasionally lower surface densities are seen near the coast and are associated with a thin (typically <5 m) low salinity plume, presumably due to local river discharge.

Vertical positioning of cod eggs and larvae

After spawning, cod progress through an egg and an early larval stage before becoming capable of active swimming, at a body length of 6-9 mm (Lough and Potter, 1993). Once swimming capable, larval cod exhibit a tendency for diel vertical migration, occupying deep and dimly lit water during daylight hours and residing near the surface at night (Bailey, 1975; Lough and Potter, 1993; Lough et al., 1996).

Duration of the egg stage and early larval stages (till swimming capability) is highly temperature dependent (Page and Frank, 1989; Otterlei et al., 1999; Folkvord, 2005, and references contained therein). Using a function relating egg stage duration to ambient temperature, derived from historical laboratory data, Page and Frank (1989) determined that cod eggs spawned over Georges Bank should hatch at an age of 10-20 d. Using this same function and the expected near-surface springtime temperatures in the western Gulf of Maine, we determined that eggs spawned in Ipswich Bay during spring should be expected to hatch in roughly 10 days. Based on analysis of larval growth rates presented by Bolz and Lough (1988) and Otterlei et al. (2005), we further determined that cod larvae spawned in Ipswich Bay during spring should become swimming capable 10-30 days after hatching.

In a stratified water column, the vertical position of cod eggs and early stage larvae will depend principally on egg and larval density. To our knowledge, there have been no measurements of the density of cod eggs and larvae spawned in the western Gulf of Maine. In a relevant study on the density of eggs and early stage larvae spawned by cod captured over Newfoundland Shelf and Grand Banks, Anderson and de Young (1994) found that egg density varies considerably depending on spawning stock and the properties of the water in which spawning occurs. Most applicable to cod eggs spawned in Ipswich Bay were their measurements of the density of eggs spawned by cod captured over the inner Newfoundland Shelf and held in tanks containing inshore surface water. Notably, the density declined with egg age, and mean densities for all ages were in the 1020-1023 kg m^{-3} range. Based on this result and the measured density distributions in western Gulf of Maine during May and June, we have assumed that eggs spawned in Ipswich Bay during spring are predominately situated in the near-surface layer subject to direct wind forcing.

METHODS

Our work follows an earlier study of larval cod transport in the western Gulf of Maine by Huret et al. (2007). Using velocity fields from a hydrographic model, Huret et al. tracked particles from identified spawning areas and used the results to derive estimates of transport success to areas suitable for settlement and early stage juvenile cod development. Their analysis was confined to simulations of a single year (1995) and did not include the effect of vertical migration of larvae. Our methodology is essentially an extension of that developed by Huret et al. (2007). In the subsections below, we describe the model used for generating the velocity fields and the method for tracking particles within theses fields.

Generation of velocities fields

For our study, we used velocity fields spanning the period of 1995-2005 and generated by the Finite Volume Coastal Ocean Model of the Gulf of Maine and Georges Bank (GoM/GB FVCOM). Developed by the Marine Ecosystems Dynamics Modeling group at the University of Massachusetts Dartmouth, this is an unstructured grid, free-surface, fully 3-dimensional primitive equation model that solves the governing equations through computation of fluxes between triangular control volumes of an unstructured grid (Chen et al., 2003, 2006, 2007). The model grid encompasses the Gulf of Maine and Georges Bank, as well as the Scotian Shelf and the New York Bight. It extends offshore to roughly the 3000-m isobath. Within the Gulf of Maine, the horizontal grid resolution is 2-10 km in the basins and 0.5-2 km in coastal regions. In the vertical, the grid is divided into 30 equally spaced sigma layers, giving a 1-m resolution at 30-m depth.

Forcing of the model at the lateral boundary is applied in the form of tidal elevations, imposed at the open boundary, and freshwater influx from all major rivers in the model domain. Forcing at the surface is derived from the fifth generation mesoscale meteorological model (MM5) run at 10-km resolution (Chen et al., 2005). The surface forcing terms include atmospheric heat fluxes, precipitation/evaporation and wind stress. At the upstream boundary, the time-varying influx of Scotian shelf and slope water is imposed. During model execution, satellite-derived sea surface temperature fields are assimilated to adjust the modeled surface temperature.

Particle tracking

The larval tracking simulations were done in the “off-line” mode using hourly-averaged velocity fields generated by GoM/GB FVCOM. Larval movement in the horizontal plane was assumed to be passive. The larval trajectories were determined by integrating model velocities, linearly interpolated in space and time, using an explicit fourth order Runge-Kutta scheme with a 120 s time step.

In specifying the vertical position of larvae released into the model flow field, it was assumed that the early life history of cod, from spawning to settlement, consisted of a buoyant egg/larval stage followed by a larval stage capable of vertical migration. As alluded to earlier, the development of cod eggs and the subsequent migration behavior of cod larvae depend on a number of processes that are currently not well understood, particularly not in the Gulf of Maine where there is a dearth of data on cod eggs and larvae. For this reason, the vertical position of developing eggs and larvae was represented by a simple idealized function (Fig. 5). In the buoyant stage, cod eggs and early-stage larvae were assumed to maintain a constant depth. Based on the measurements of water and cod egg density reviewed above, this depth was set to

2.5 m to ensure that the modeled eggs would reside in the near-surface layer subject to direct wind forcing (i.e. predominately above the seasonal pycnocline). Because the duration of the passive buoyant stage may vary depending on a number of factors, we conducted transport simulations with the duration of the constant depth stage set to several different values. The results shown here were determined with the constant depth stage set to 21 d, a conservatively low estimate of the age to attain swimming capability. As detailed below, we also carried out transport simulations in which the developing eggs and larvae remained buoyant, maintaining a depth of 2.5 m, from spawning to settlement. The diel vertical migration was confined between two specified levels: a near surface level of 2.5 occupied during dark hours and a deep level occupied during daylight hours. We show results for two deep levels: 20 and 40 m. At bottom depths shallower than the specified deep level, the maximum decent was set to 1 m above the sea floor. Initiation of upward and downward migration were set to coincide with sunset and sunrise, respectively, and migration time was set to 4 h. Similar functions have been used to describe the vertical migration behavior of cod in other modeling studies (Werner et al., 1993; Vikebø et al., 2005, 2007)

Transport Success

Following Huret et al. (2007), transport success was defined as the likelihood that larvae will be over areas suitable for juvenile settlement during an age when they are settlement capable. Our method for estimating this quantity was identical to that employed by Huret et al. As a first step, ensembles of particles, representing spawned cod eggs, were released into the model flow field. The particles were evenly distributed over the region designated by Huret et al. as the Ipswich Bay spawning area (Fig. 3). Ensembles were set out at intervals of three days. This is shorter than the 8-30 day range of decorrelation times of currents within the western Gulf of Maine that we have computed from available current meter data. Each particle was tracked for 60-days, taken as the maximum age to larval settlement. The minimum age of settlement capability was set to 45 days. The transport success for a particular spawning period was then taken as the average fraction of time (expressed as a percentage) that the simulated egg/larval tracks initiated during this period were over areas suitable for settlement during the last 15 days of their 60 day drift. Based on the juvenile cod distributions reviewed above, the area suitable for larval settlement was taken as regions shallower than either 30- or 60-m. Here we show only those results derived by assuming a 30-m maximum depth for the settlement suitable region. Results determined assuming that the settlement region extended to 60-m were not significantly different.

We computed transport success to three separate settlement regions in the western Gulf of Maine (Fig. 3): (1) a northern region off the Maine and New Hampshire coasts and north of the Ipswich Bay spawning area, (2) the Ipswich Bay region, encompassing the Ipswich Bay spawning area, and (3) the Massachusetts Bay region.

RESULTS

Model-generated flow in the Western Gulf of Maine

Before considering the results of the larval tracking simulations, it is useful to examine flows generated by the model in the near-absence of wind forcing. These are illustrated by the averaged modeled surface currents of May 1995 (Fig. 6), a time when the magnitude of the mean wind velocity measured at the NOAA/National Data Buoy Center (NDBC) buoy 44013 (Fig. 3) was less than 0.25 m s^{-1}. These mean currents clearly show the Western Maine Coastal Current, which takes the form of a strong flow directed westward along the Maine coast and southward along the outer arm of Cape Cod. Importantly, this current bypasses two of our regions of interest: the spawning area of Ipswich Bay the shallow areas of Massachusetts Bay where cod tend to settle. A focus of our analysis will be the extent to which the combination the Western Maine Coastal Current and wind-driven flow impacts the retention of Ipswich-spawned cod in the western Gulf of Maine.

Transport success for eggs/larvae maintaining a constant depth

In presenting the transport success results, our intentions are to demonstrate the effect that wind forcing has on the year-to-year variation in larval retention in the western Gulf of Maine and to quantify how vertical migration behavior impacts larval retention. For this reason, we will first present the results of transport simulations in which the developing eggs and larvae are maintained a constant depth of 2.5 m until settlement. We will then consider how the introduction of vertical migration affects cod movement and transport success.

Reflecting the mean southward flow in the western Gulf of Maine (Fig. 6), yearly averaged values of transport success of eggs/larvae fixed at 2.5 m to region 1 are negligible, never > 0.15 %, indicating little transmission of spawned cod from Ipswich Bay to the north (Fig. 7). Yearly averages values of transport success to region 2, encompassing Ipswich Bay, are modest, with a maximum of 5 % in 2001, indicating a relatively little local retention of larvae within Ipswich Bay. However, significant retention of larvae is indicated for region 3, Massachusetts Bay. Yearly-averaged transport success to region 3 is in excess of 10 % for 7 of the 11 simulation years. Hereafter, we consider only transport success to regions 2 and 3, the regions of Ipswich and Massachusetts, ignoring the negligible transport to the north.

To determine if transport success may vary with date of spawning, we averaged the transport success values for each release date (e.g. May 1, 4, 7 …) over all 11 years of the transport simulations. The results show a nearly monotonic decline in transport success with advancing date of release, from a high of 25-30 % for release dates in early May to a low of 2-5 % for release dates in late June (Fig. 8a).

Given this trend, we found it useful to separately consider transport success for May and June releases. Not surprisingly, for most years, the transport success for those particles released in May is significantly greater than the transport success of the particles set out in June (Fig. 9). The only exception is 1999, a year with low (<1.5 %) transport success for both May and June releases.

For both May and June releases, the yearly-averaged transport success series show considerable year-to-year variation. The analysis to follow is directed at the hypothesis that this variation, and the decline in transport success with release date (Fig. 8a), are largely due to the combination of wind-driven upwelling/downwelling circulation and the Western Maine Coastal Current. More specifically, we hypothesize that the likelihood that buoyant eggs/larvae released from Ipswich Bay spawning area be retained in the western Gulf of Maine may be relatively low during a time of predominately upwelling circulation, and may be relatively high during a period when the circulation is predominately downwelling. The reasoning is that upwelling circulation will tend to carry buoyant particles offshore to the Western Maine Coastal Current, which will in turn transport the particles out of the Gulf of Maine. By contrast, a downwelling circulation will tend to move buoyant particles onshore and away of the influence of the Western Maine Coastal Current.

In considering the possible impact of winds on upwelling/downwelling circulation is often convenient to view the influence of across-shore and alongshore winds separately. In the western Gulf of Maine, the across-shore axis is roughly oriented east-west. An eastward wind will tend to accelerate the surface water offshore and thus be upwelling favorable. By the same logic, a westward wind will be downwelling favorable. If north-south direction is taken as the alongshore axis, a northward wind would be considered upwelling favorable as this would generate, through the Coriolis effect, a cross-shore flow to the east. Conversely, a southward wind would be downwelling favorable.

The tendency for downwelling winds to favor retention of buoyant particles in the western Gulf of Maine is illustrated here by the positions (at 15 day intervals) of particles released from the Ipswich Bay spawning area on 1 May 2003 (Fig. 10). Their release was followed by a period of predominately downwelling favorable winds, as indicated by the wind record from NDBC buoy 44013 (Fig. 3). Over the first 15 days after release, winds were predominately westward, resulting in a downwelling circulation that kept the buoyant particles within the nearshore zone (Fig. 10a). Over the subsequent 15 days, winds were southward (also downwelling favorable) and the majority of particles were contained within Massachusetts Bay (Fig. 10b). Mean winds were close to zero for the next 15 days (Fig. 10c) and were directed to the ENE (downwelling favorable) over the final 15 days of the 60-day simulation (Fig. 10d). The result of this predominately downwelling favorable wind history is that the majority of the particles were confined to the Massachusetts Bay region over the last 15 days of their 60-day drift (the time when the developing cod are considered settlement capable). The transport success of these particles to the Massachusetts Bay region was 78 %.

The tendency for upwelling wind to favor the export of buoyant particles from the western Gulf of Maine is illustrated by the positions of particles released on 13 May 1999 (Fig. 11). The persistent upwelling circulation following their release carried the majority of particles offshore to the Western Maine Coastal Current. The result was low particle retention in the western Gulf of Maine as reflected by low transport success (<0.4 %) to all regions.

To explore how the decline in transport success with release date (Fig. 8a) may be related to the local wind forcing, we averaged the winds from buoy 44013 over 21-day intervals following each release date. As demonstrated later, the first 21 days of a particle's drift appears to be crucial in determining whether it is ultimately retained in the western Gulf of Maine. For each release date, the average extended over all 11 years of the simulations (1995-2005). These averages become progressively more upwelling favorable with advancing starting date (Fig. 8b). Averages for starting dates in early May are weakly downwelling favorable, whereas averages for starting dates in late June are strongly upwelling favorable. Plotting these averaged winds against the corresponding averages in transport success (matching release date with starting date of the wind average), clearly shows that transport success tends to decline as the wind over the first 21 day of egg/larval drift becomes more upwelling favorable (Fig. 8c). This trend is particularly strong for the comparison of transport success with averaged northward (alongshore) wind. The inference is that the decline in transport success with advancing release date during the spring spawning period is principally due to a shift in the wind pattern in the western Gulf of Maine, with winds becoming progressively more upwelling favorable (favoring export of particles out of the western Gulf of Maine) going from early May through June.

To investigate how the year-to-year variation in transport success may be related to wind forcing, we computed averaged winds for each May and June of the 1995-2005 simulation period. Averages of the east and north wind components for May tend to co-vary with regard to being upwelling or downwelling favorable. The average winds of June are all strongly upwelling favorable, consistent with the 21-d wind averages discussed above (Fig. 8b). Plotting transport success against the northward (alongshore) monthly averaged wind speed (Fig. 12) reveals a tendency for the highest transport successes to be associated with downwelling favorable winds. Notably, the highest yearly-averaged transport success for May releases occur for those years when the mean alongshore wind of May is directed to the south (downwelling favorable) with a magnitude of greater than 0.5 m/s (1998, 2003 and 2005).

The effect of vertical migration

The analysis reviewed thus far indicates that the tendency for buoyant eggs/larval spawned in Ipswich Bay during spring to be retained in the western Gulf of Maine is strongly tied to the upwelling/downwelling character of the local wind. The question remains as to how vertical migration in the larval stage may influence larval transport and retention in the western gulf. To address this, we carried out transport simulations with diel vertical migration imposed at a specified age after spawning (Fig. 5). As noted in Methods, sets of simulations were carried out with different ages of migration capability and differing maximum depth of migration. As illustrated by the representative results shown here (Fig. 13), the introduction of vertical migration did not significantly alter the year-to-year variation in transport success.

For nearly all years, transport success is marginally enhanced by the introduction of vertical migration, indicating that diel migration improves the likelihood of larval cod retention in the western Gulf of Maine during spring. Our examination of the larval tracks and the circulation fields indicates that this is an upshot of the manner in which the migration exposes the larvae to the cross-shore flow associated with upwelling/downwelling circulation. To understand the phenomenon, consider a particle, representing a developing cod larvae, which is at the end of its buoyant stage (when it becomes capable of migration) and is contained within the western Gulf of Maine. If this particle remains buoyant and is exposed to a lengthy period of upwelling circulation, it will likely be carried offshore to the Western Maine Coastal Current and subsequently exported out of the Gulf of Maine. However, if the particle executes vertical migration during a lengthy upwelling period, during the course of each day it will alternate between the offshore flow in the upper layer and the onshore flow in the lower layer and likely be spared offshore transport to the Western Maine Coastal Current.

The close comparison between the transport patterns determined from simulations with and without vertical migrations (Fig. 13) further suggests that transport in the initial buoyant egg-early larval stage may be critical in determining the ultimate settlement fate of cod spawned in Ipswich Bay.

An Index of Recruitment Success

Our analysis strongly indicates that the extent to which buoyant cod eggs/larvae spawned in Ipswich Bay during spring are retained in the western Gulf of Maine, and transported to areas suitable for juvenile development, is tied to the dominant local wind direction during May. Retention is largest in those years when the winds during May are predominately downwelling favorable. In applying this result for fisheries management, it is clearly of interest to determine the extent to which recruitment success of cod are related to our estimates of transport success and to the mean winds during May.

A priori, a close comparison between recruitment success and transport success may not be expected. Our calculation of transport success does not include the winter spawning event, nor does it account for factors influencing larval survival, including predation and food supply. Nevertheless, cod recruitment to the Gulf of Maine appears to be weakly related to our estimates of transport success (Fig. 14). Most significant is that the three highest values of recruitment success of our analysis period (1995-2005) occur during those years (1998, 2003 and 2005) when the estimates of transport success are highest and mean wind of May (as recorded at buoy 44013) is most downwelling favorable (Figs. 9, 12 and 15). This leads to the hypothesis that unusually strong recruitment success of Gulf of Maine cod may be largely due to high retention of spring-spawned larvae and occur during those years when May winds are predominately downwelling favorable.

This hypothesis is supported by comparison of recruitment success with the mean northward wind component measured at buoy 44013 during May (Fig. 15). This shows a tendency for the highest recruitment success to occur during years when the May wind is strongly downwelling favorable. For the 20 years with both 44013 wind measurements and recruitment success estimates, the years with the highest recruitment success estimates are also the years when the mean north-south wind measured at buoy 44013 during May is most downwelling favorable. For each of these years the mean north-south wind is southward (downwelling favorable) with a magnitude of greater than 0.4 m/s (Fig. 15). The tentative conclusion is that the mean wind of May may be used as an index of unusually high age-1 cod recruitment to the Gulf of Maine.

DISCUSSION

Our analysis has indicated that a significant fraction of the cod larvae spawned in the Ipswich Bay is likely to be retained in the western Gulf of Maine. It is thus possible that the western Gulf of Maine cod population, described by Howell et al (2008) as sedentary-resident, may be largely sustained through self-recruitment. Also indicated by our analysis is that the retention of spring-spawned larvae in the western gulf is strongly tied to the local wind, with downwelling winds favoring retention. This is due to the tendency of upwelling circulation to transport buoyant eggs and larvae offshore to the Western Maine Coastal Current. Larval retention is somewhat enhanced through diel migration of drifting larvae, as this action forestalls lengthy offshore excursions during times of upwelling circulation.

The relative simplicity of our model and limited scope of our investigation leave a number of issues regarding the recruitment of cod to western Gulf of Maine unresolved. One is the manner in which early-stage cod survival is impacted by food availability, growth rate and predation.

Also unresolved is the impact of larvae exported from the western Gulf of Maine. Do these larvae significantly contribute to other cod stock, such as those over Georges Bank and Nantucket Shoals (Fig. 1)? Recent analysis of genetic markers by Wirgin et al. (2007) suggests that the extent to which cod spawned in the Gulf of Maine are incorporated into remote cod stocks may be different for the spring and winter spawning events. Their results show that spawning-condition cod found in Ipswich Bay during spring are genetically distinct from other regional cod stocks, whereas spawning-condition cod found 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. We have not reported on our simulations of the transport of cod spawned in the winter event primarily because of uncertainty in the vertical location of the buoyant eggs and early stage larvae. The water column is vertically mixed during the winter spawning event, making it difficult to ascribe a depth range over which cod eggs are likely to be found. Nevertheless, it is of interest to note that our preliminary simulations have indicated buoyant cod spawned during the winter event have a very low likelihood of retention within the western Gulf of Maine. This is because of the predominately upwelling favorable wind conditions prevailing throughout the winter spawning event, and because a sizeable fraction of the winter event spawning occurs close to the path of the Western Maine Coastal Current (Hoffman et al., 2006, 2007). Combining this tentative result with the findings of Wirgin et al. (2007) leads to the hypothesis that the winter and spring spawning events in the western Gulf of Maine may serve somewhat different functions in sustaining the cod stocks off the northeast US coast. The spring spawning event may principally sustain the local cod stock in the western Gulf of Maine, whereas the winter spawning may be more important in supplying recruits to other regional cod stocks.

Another unresolved issue of interest is the manner in which local circulation may affect egg/larval transport and recruitment of cod to other coastal areas in the Gulf of Maine. The Massachusetts Bay region is the largest coastal area onshore of the normal path of the Gulf of Maine Coastal Current (Pettigrew et al., 2005). It may thus constitute a zone more favorable to the retention of locally spawned larvae than other areas along Gulf of Maine coast. This may be partly the reason why a concentrated population of sedentary-resident cod is found in Massachusetts and Ipswich Bays, while cod populations elsewhere in the Gulf of Maine have become decimated (Ames, 2004).

Addressing these and related issues will require more sophisticated modeling, for example to account for variations in egg and larval growth and predation, as well as more detailed observations on cod spawning behavior, migration patterns and juvenile habitat distribution. Given the importance of cod to the northeast Atlantic ecosystem and to the fishing economy of the northeast US, further modeling and observational investigation of cod recruitment dynamics is in our view warranted.

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FIGURE CAPTIONS

Figure 1. The distribution of cod in the Gulf of Maine/Georges Bank region as determined from US National Marine Fisheries Service (NMFS) trawl data from 2000-2004. The circles show the number of fish per 30 minute tow, whereas the gray x's indicate locations where less than 2 cod were taken in a tow. The dashed line marks the boundary of the area enclosing Gulf of Maine cod stock as defined by the NMFS. Roughly 90 % of the total number of cod taken from this area during the 2000-2004 NMFS surveys was captured in the western Gulf of Maine (west of 70^{o}W).

Figure 2. Estimates of recruitment success of the Gulf of Maine cod (residing in the areas shown in Fig. 1) determined from the analysis of trawl survey data by the US National Marine Fisheries Service (Mayo and O'Brien, 2006). Recruitment success (or survival ratio) is defined at the ratio of spawning stock biomass (SSB, in kg) for a given year to the age-1 recruits (R, in numbers of individuals) of the subsequent year. Points appear at the year of the SSB estimate.

Figure 3. The western Gulf of Maine. The region shaded red is our representation of the Ipswich Bay spawning area from which particles, representing developing cod eggs and larvae, were released into a modeled flow field. Transport success of larval transport to the three regions enclosed by the dotted lines was computed from the simulated particle tracks. Also shown is the location of NOAA meteorological buoy 44013 (triangle) at which wind measurements used in our study were recorded.

Figure 4. Fields of temperature, salinity and density (sigma-T) representative of water properties seen in the western Gulf of Maine during May and June. The fields were derived from data acquired on 30 May 2002 at stations (indicated by the "V"s at the top of each panel) orientated along a line extending through Massachusetts Bay, roughly intercepting the location of buoy 44013 as shown in Fig. 3.

Figure 5. Sample function describing the vertical position of developing eggs and larvae as a function of age. In this example, it is assumed that the eggs and early-stage larvae are buoyant and reside at 2.5-m depth for the first 21 days after spawning, and then execute diel vertical migration for the remainder of their pelagic stage.

Figure 6. Means of model generated surface currents for May 1995. These currents approximate mean flows not driven by the local wind stress, as the mean wind of this period, measured at buoy 44013 (Fig. 3), was < 0.25 m/s in magnitude. The area shaded yellow is the modeled region of egg release in Ipswich Bay.

Figure 7. Mean transport success to regions 1, 2 and 3 for fixed depth (at 2.5 m) particles released from the Ipswich Bay spawning area (Fig. 3).

Figure 8. (a) Transport success, averaged over 1995-2005, as a function of release date.
(b) 21-day averages of wind velocities from 1995-2005 plotted as a function of the starting date of each average. Note that with advancing release date, the transport success tends to decline while the average wind experienced during the early-stage egg-larval drift becomes more

upwelling favorable. This trend is clearly seen in (c), a plot of transport success against 21-day wind average.

Figure 9. Averaged values of transport success to regions 2 and 3 (Fig. 3) for fixed depth (at 2.5 m) particles released in May and June.

Figure 10. Tracks of fixed depth (at 2.5 m) particles released from the Ipswich Bay spawning area (shaded red) on 1 May 2003. Tracks are shown in 15-day increments with the mean wind measured at NOAA buoy 44013 (Fig. 3) during each increment also shown (magnitude of the first increment's mean wind is shown in (a)). The numbers in (d) are the values of transport success to each of the target sub-regions of the western Gulf of Maine. During the first 30 days of the simulation, the winds are highly downwelling favorable resulting in significant particle retention in the western Gulf of Maine and high values of transport success.

Figure 11. Same as Fig. 10, except showing the tracks of particles released on 13 May 1999, at the beginning of a period with predominately upwelling favorable winds. The upwelling transport carries the buoyant particles offshore to the western Maine Coastal Current, which transports the majority of particles out of the Gulf of Maine.

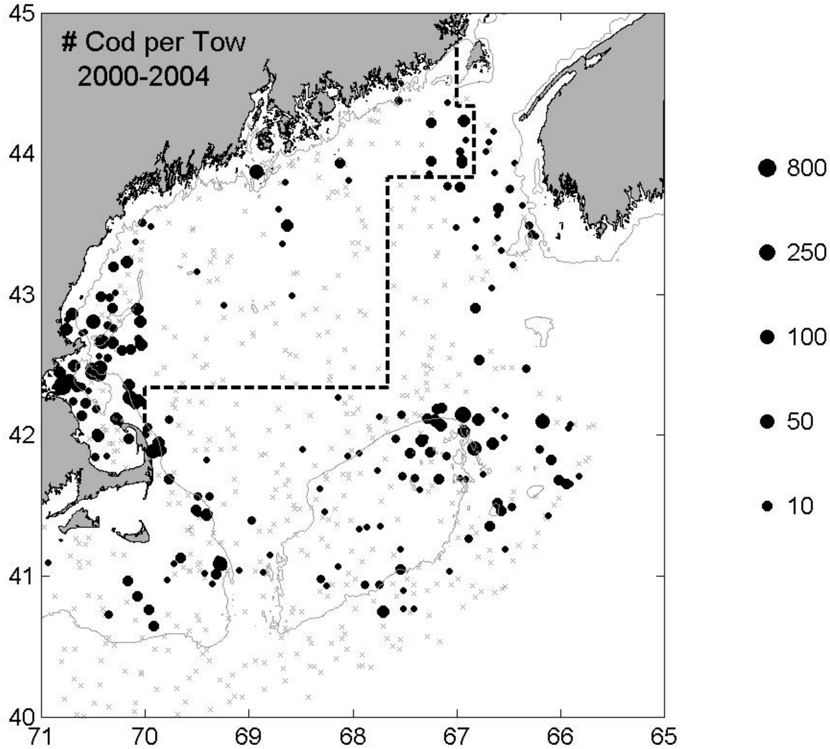
Figure 12. Averaged transport success for May and June releases against monthly mean northward wind of May and June.

Figure 13. Comparison of transport success determined from simulations of fixed depth particles (solid line) and of particles executing vertical migration after 21 days (Fig. 5). Migration limits were between 2.5 and 20 m (dashed line) and between 2.5 and 40 m (dotted line).

Figure 14. A comparison of age-1 recruitment success to the Gulf of Maine cod stock with estimates of transport success of May releases, computed assuming constant depth through the larval phase. Note that the three highest estimates of transport success correspond with the three highest estimates of recruitment success.

Figure 15. A comparison of cod recruitment success to the Gulf of Maine with the mean northward wind measured at buoy 44013 (Fig. 3) during May. Note that the five highest recruitment success estimates are for those years with the May wind is most downwelling favorable.

FIGURES



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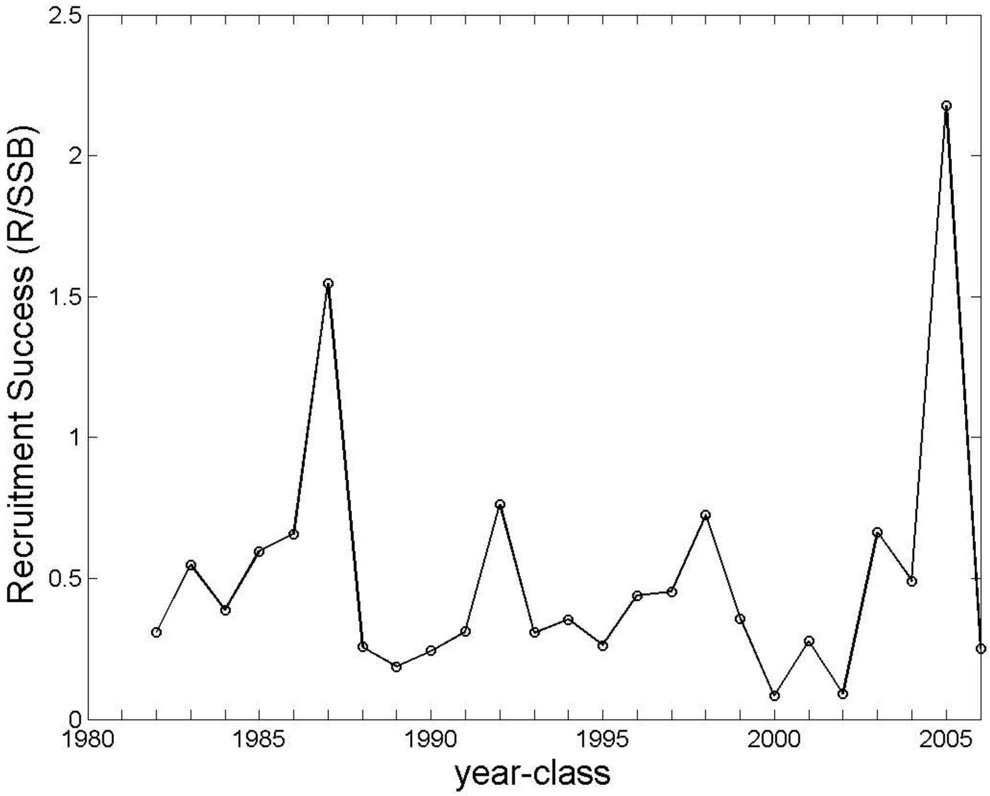

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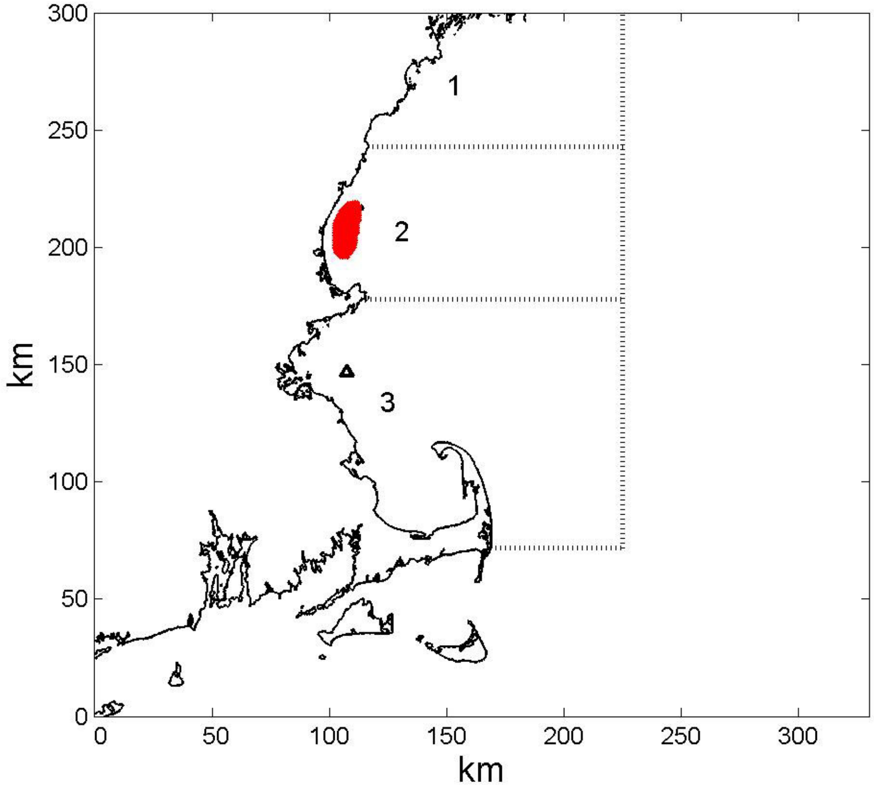

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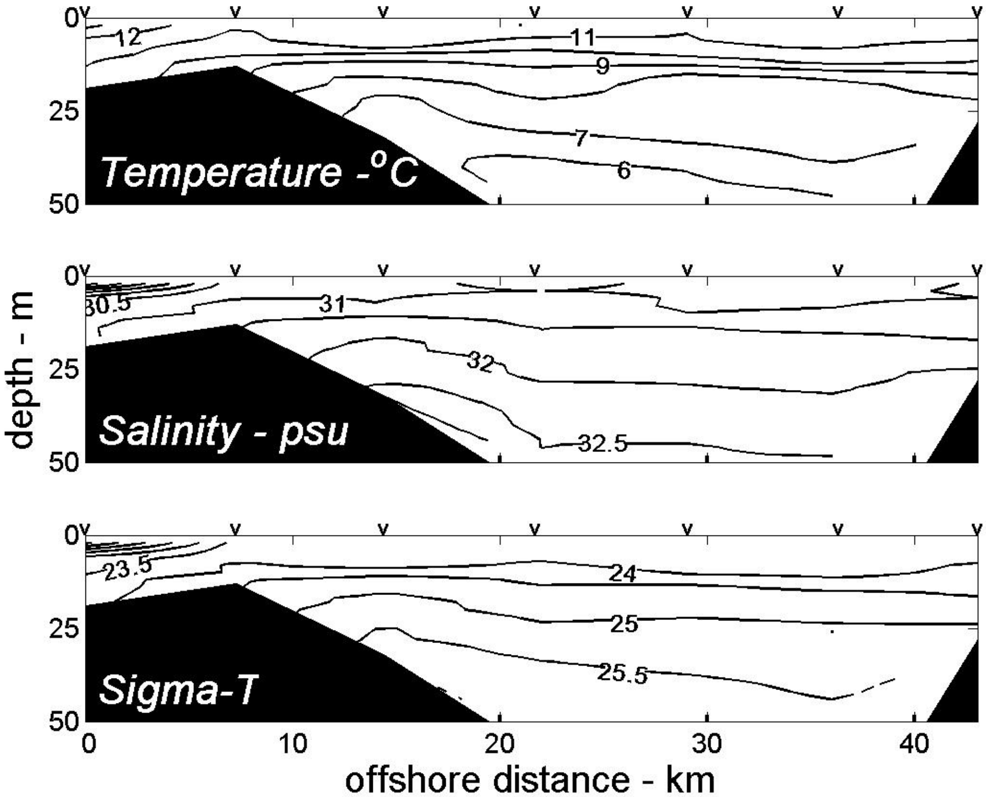

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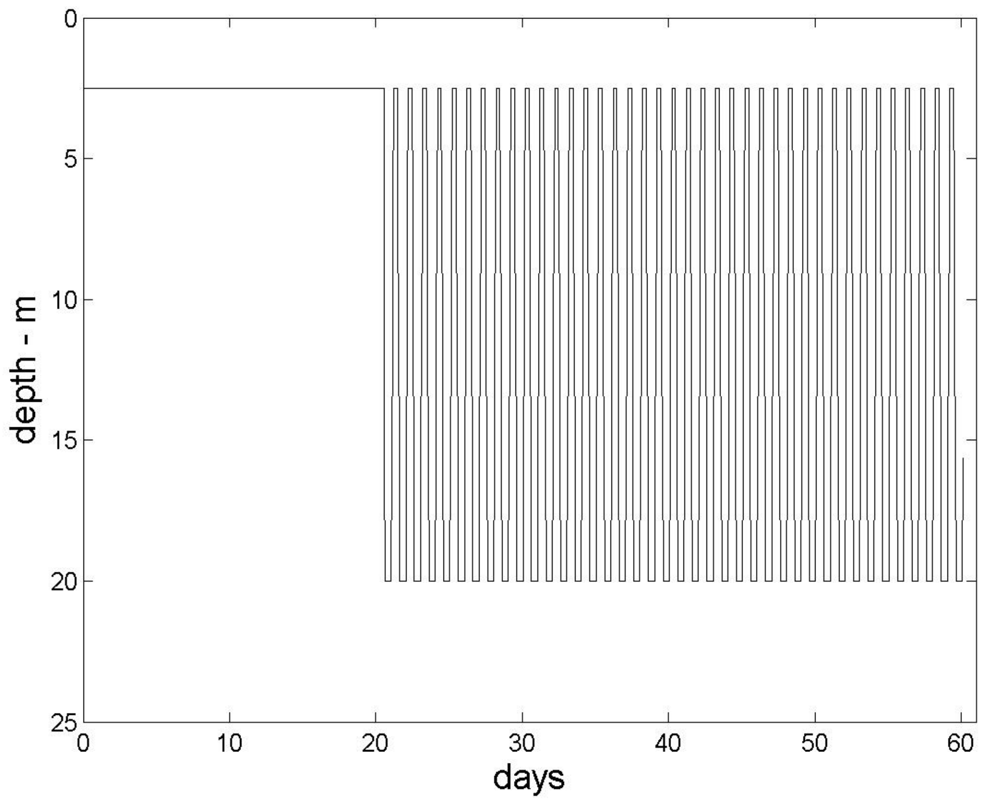

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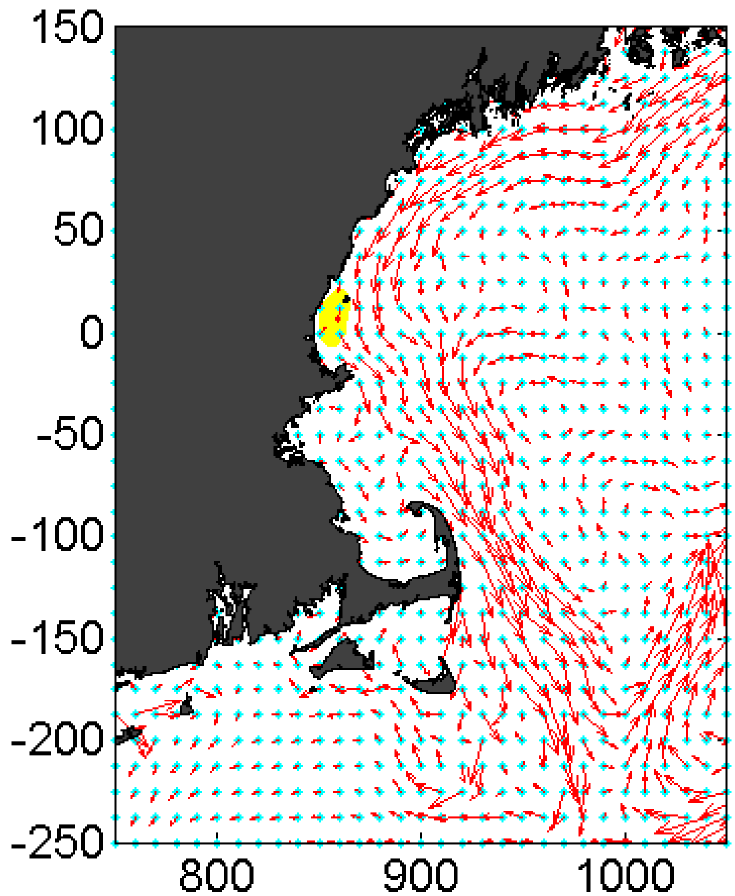

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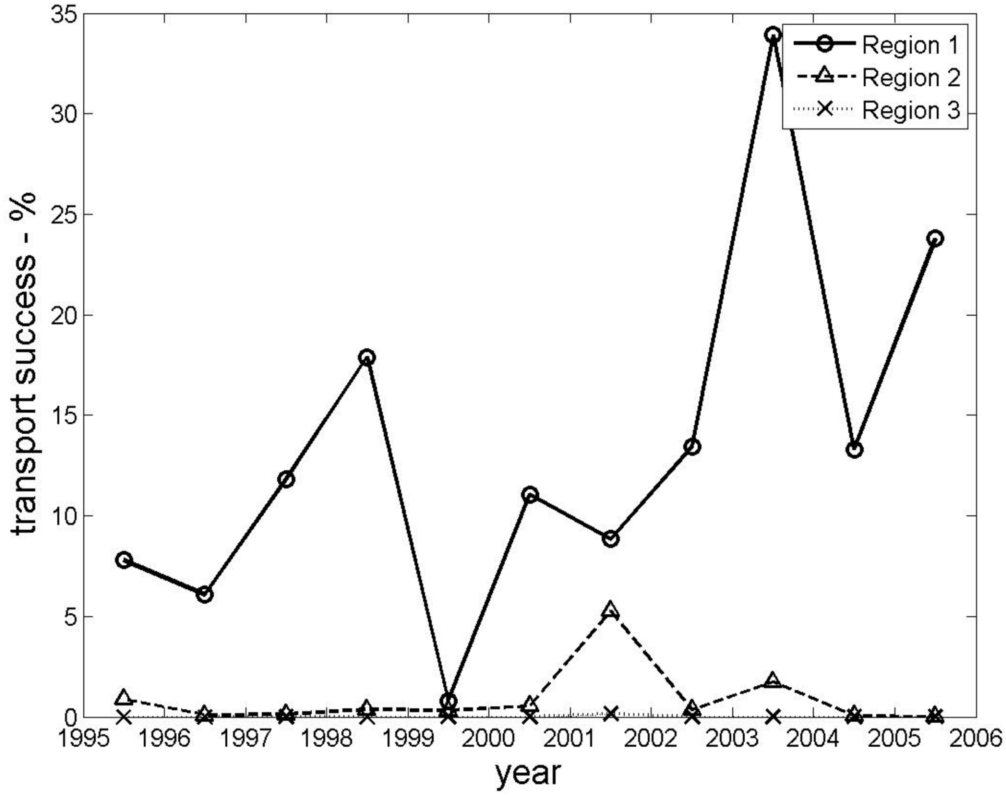

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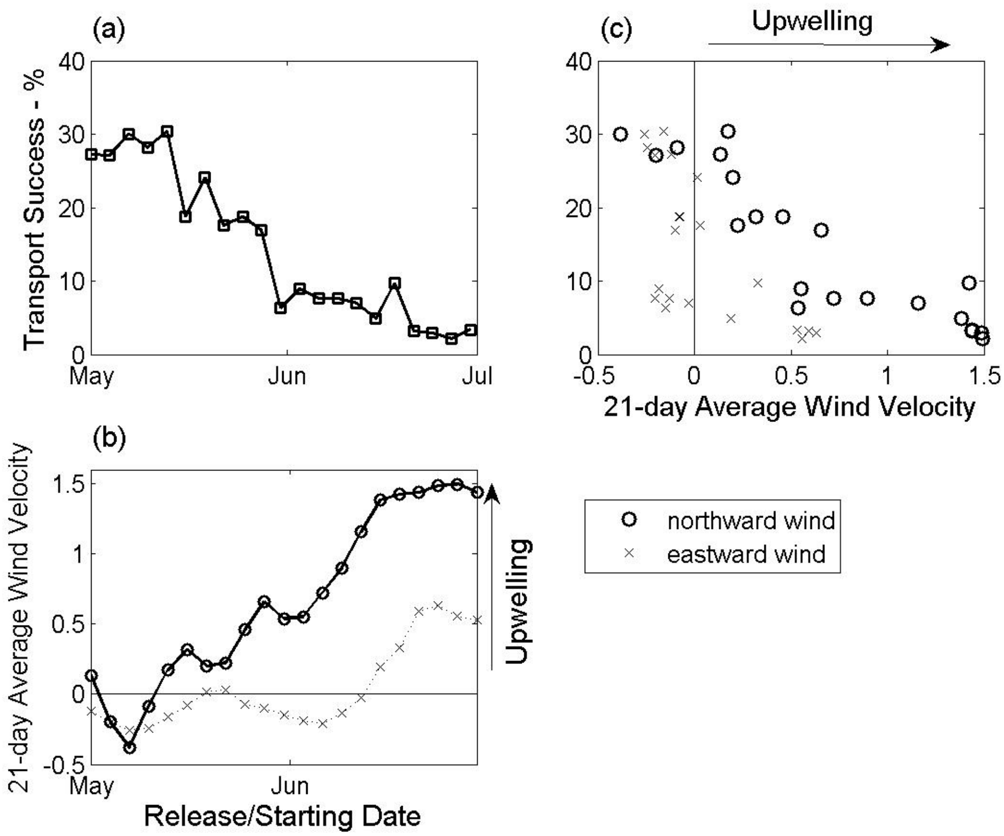

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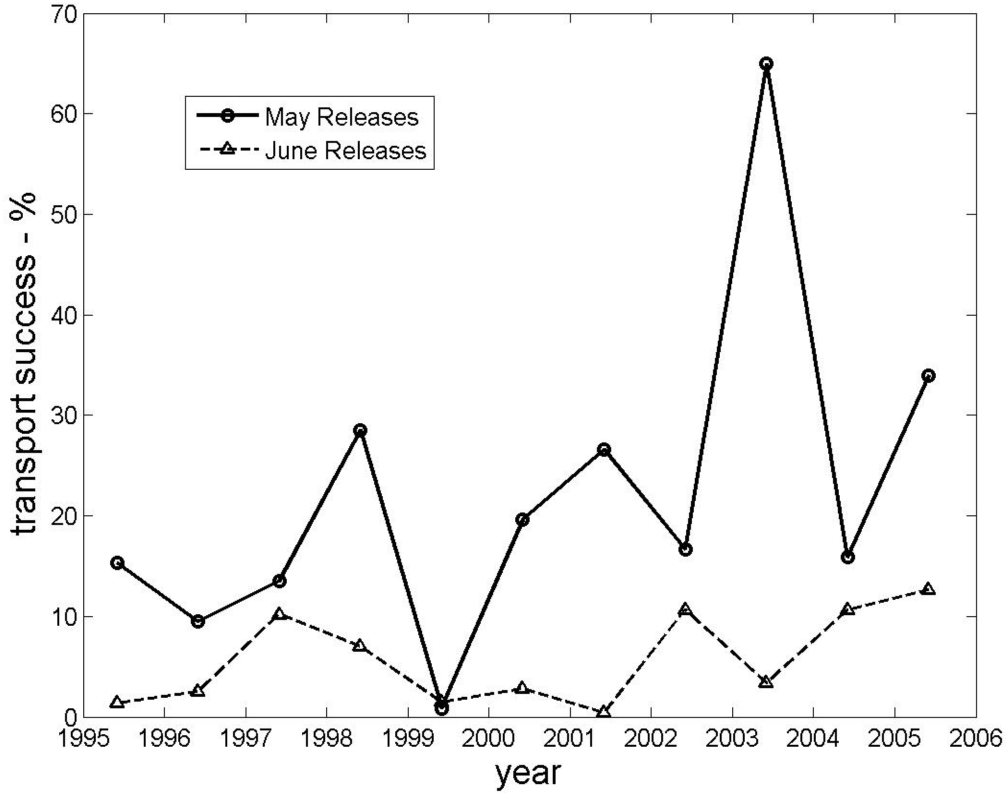

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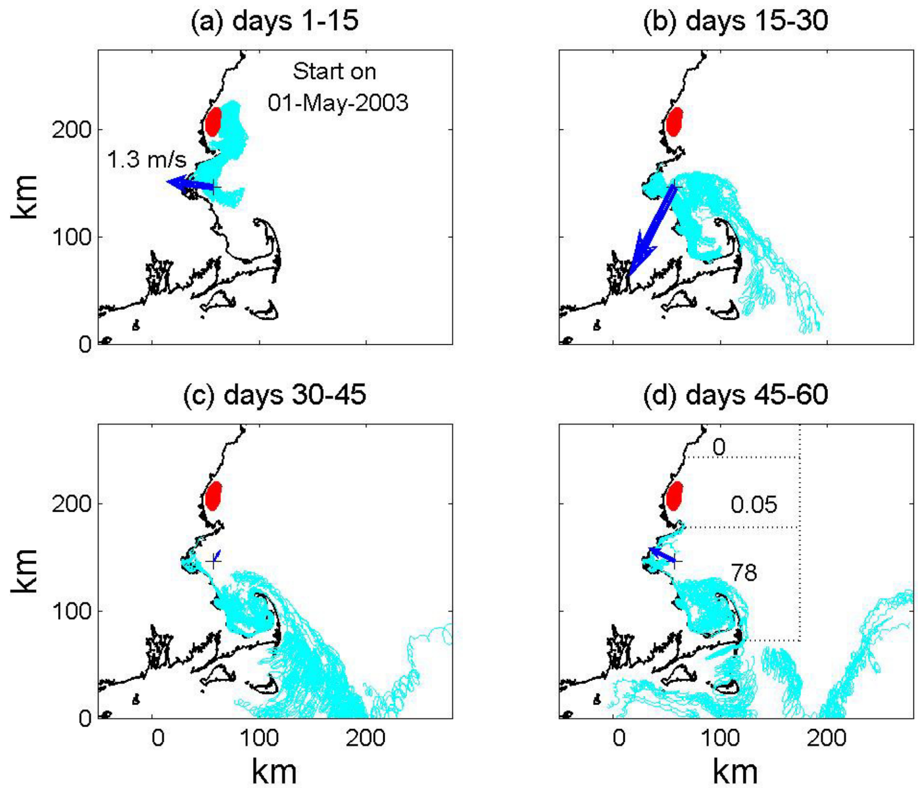

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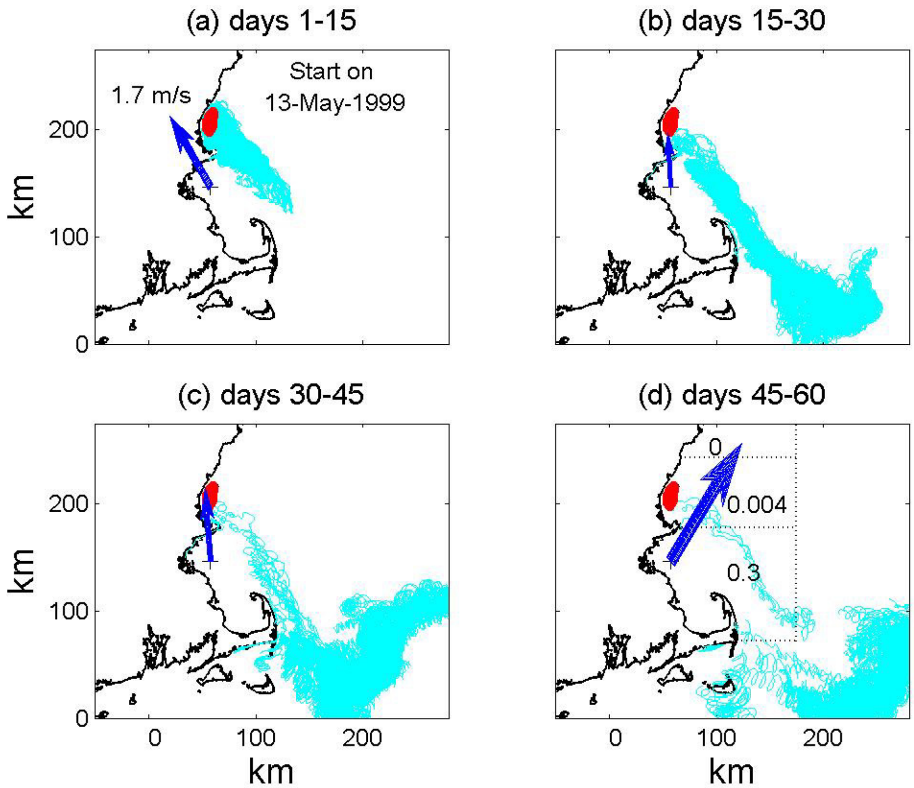

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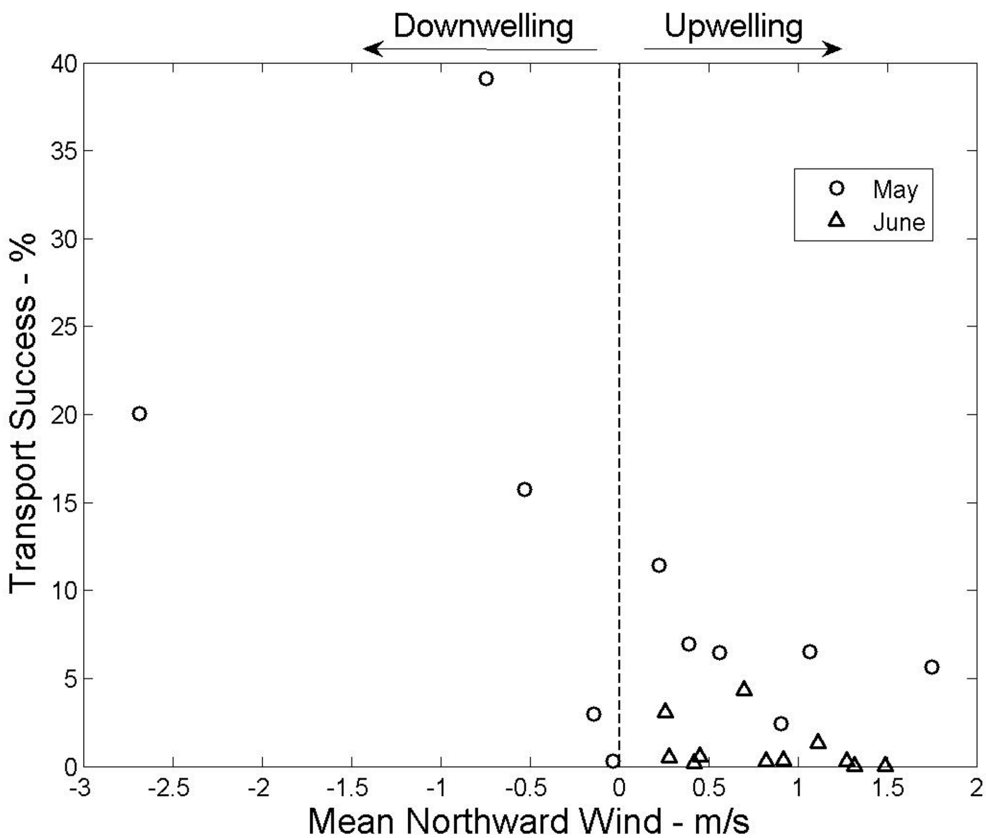

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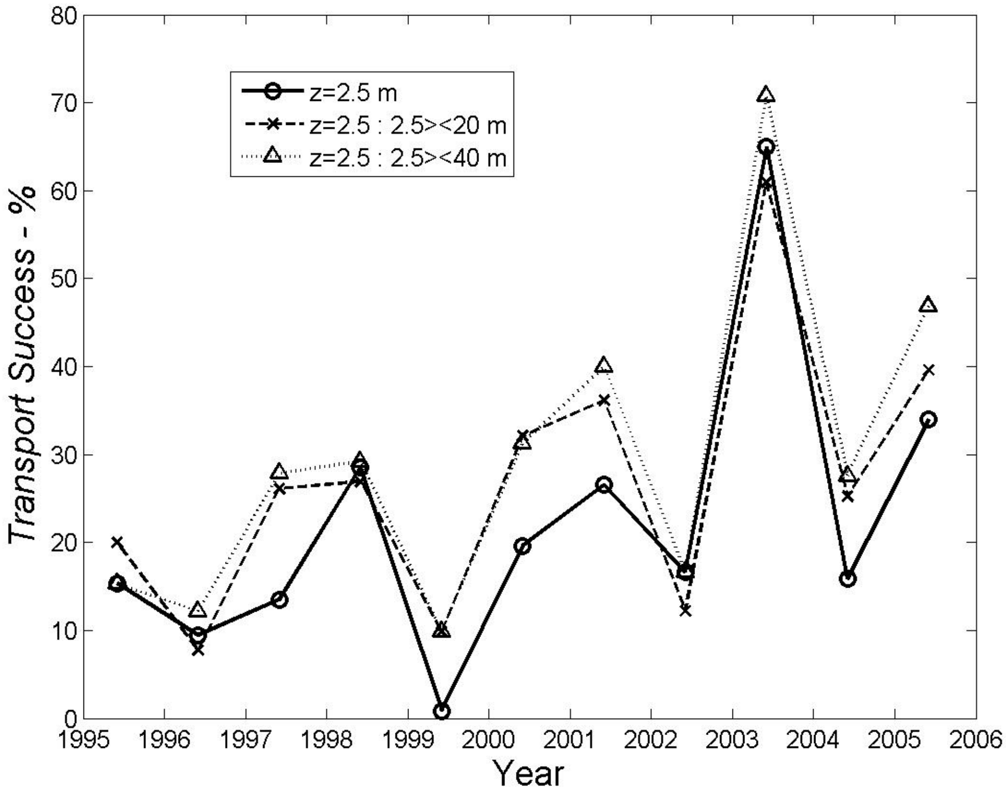

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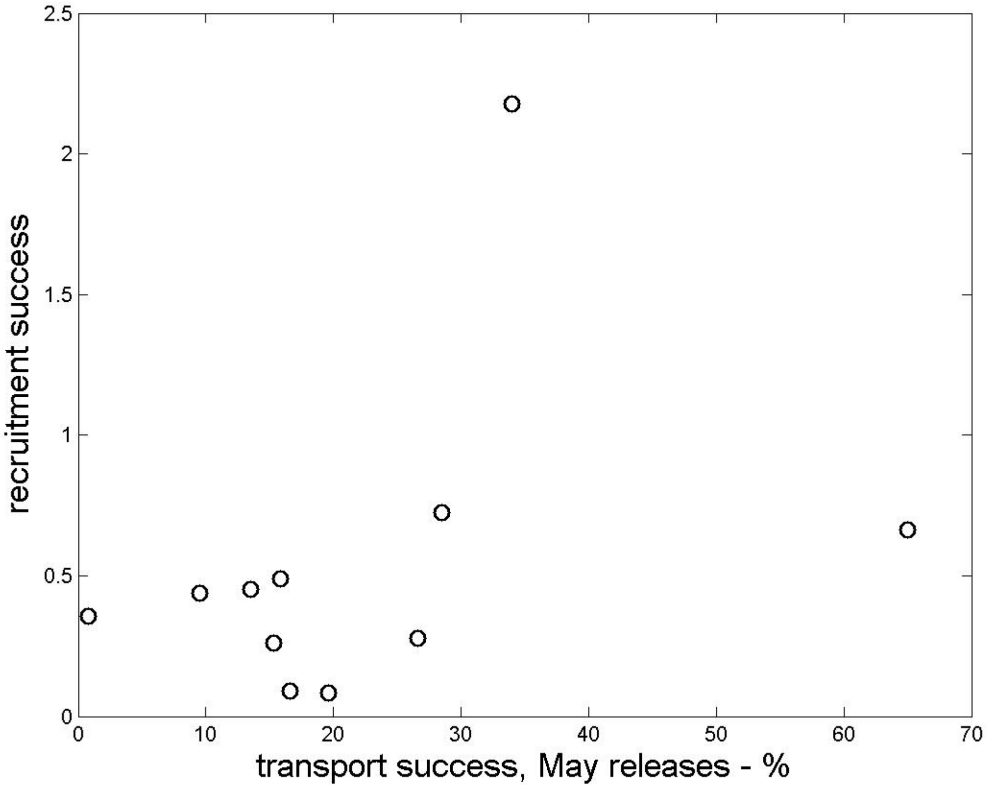

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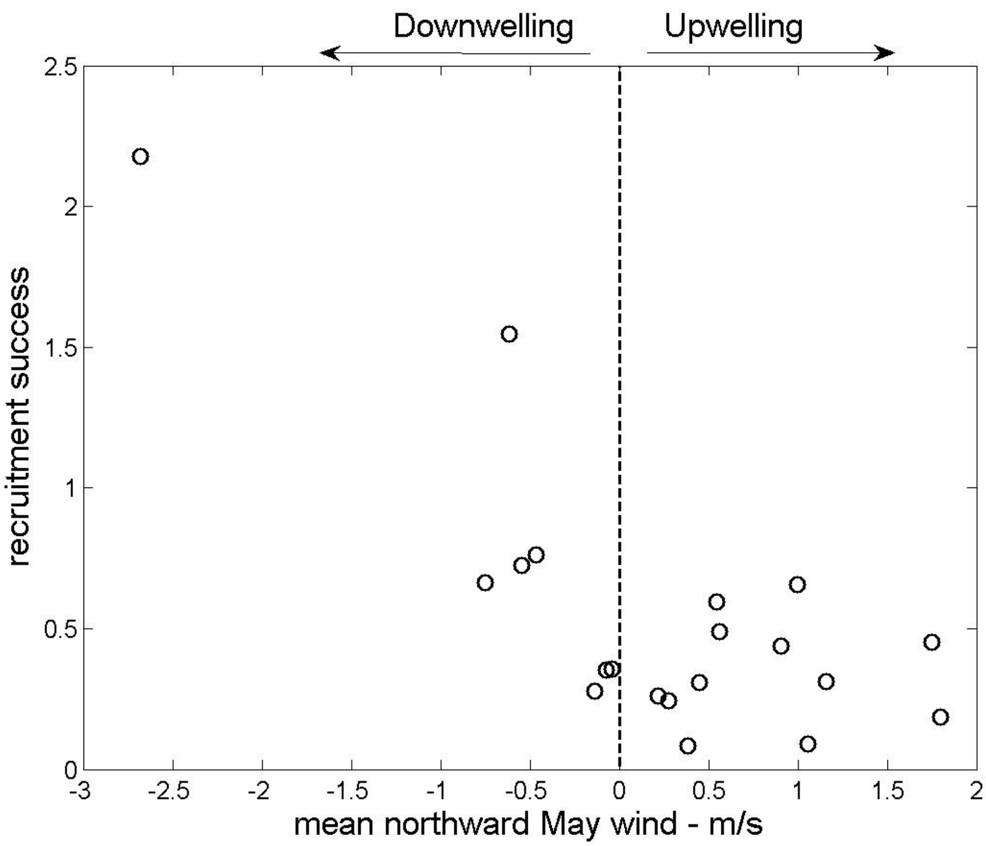

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