Understanding Climate Impacts on Recruitment and Spatial Dynamics of Atlantic Cod in the Gulf of Maine: Integration of Observations and Modeling

Jeffrey A. Runge

School of Marine Sciences, University of Maine and Gulf of Maine Research Institute, 350 Commercial Street, Portland, ME 04101 USA. Tel: 207-502-1652; Fax: 207-772-6855; Email: jeffrey.runge@maine.edu

Adrienne Kovach

Department of Natural Resources and the Environment, University of New Hampshire, 46 College Rd., Durham, NH 03824 USA. Tel: 603-862-1603; Fax: 603-862-4976; Email: akovach@unh.edu

James Churchill

Department of Physical Oceanography, Clark 304a, MS 21, Woods Hole Oceanographic Institution, Woods Hole, MA 02536 USA. Tel: 508-289-2536; Fax: 508-457-2181 Email: jchurchill@whoi.edu

Lisa Kerr,

School for Marine Science & Technology, University of Massachusetts Dartmouth 200 Mill Road, Suite 325, Fairhaven, MA 02719 USA. Tel: 508-910-6324; Fax: 508-910-6374; Email: lkerr@umassd.edu

John R. Morrison,

Executive Director, Northeastern Regional Association of Coastal Ocean Observing Systems (NERACOOS), Seacoast Science Center, 570 Ocean Blvd.,Rye, NH 03870, USA. Tel: (603) 319 1785; Fax: (603) 319 1799; Email: Ru.Morrison@neracoos.org

Robert Beardsley

Department of Physical Oceanography, Clark 343, MS 21, Woods Hole Oceanographic Institution, Woods Hole, MA 02536 USA, Tel: 508-289-2536 Fax: 508-457-2181; Email: rbeardsley@whoi.edu

David Berlinsky

Department of Biological Sciences, University of New Hampshire; 171 Spaulding Life Science Building, 38 College Rd., Durham, NH 03824 USA. Tel: 603-862-0007; Fax: 603-862-3784; Email: david.berlinsky@unh.edu

Changsheng Chen

School for Marine Science & Technology, University of Massachusetts Dartmouth 706 South Rodney French Boulevard, New Bedford, MA 02744 USA. Tel: 508-910-6388l Fax: 508-910-6371; Email: c1chen@umassd.edu

Steven Cadrin

NOAA/UMass Cooperative Marine Education and Research Program, 200 Mill Road, Suite 325 Fairhaven, MA 02719 USA. Tel: 508-910-6358; Fax: 508-910-6374;

Email: steven.cadrin@noaa.gov

Cabell Davis

Department of Biology, Redfield 2-20, MS 33, Woods Hole Oceanographic Institution Woods Hole, MA 02543 USA. Tel: 508-289-2333; Fax: 508-457-2134; Email: cdavis@whoi.edu

Kathryn Ford

Massachusetts Division of Marine Fisheries, 1213 Purchase St. 3rd Floor, New Bedford, MA 02740. Tel: (508) 990-2860 x145; Fax: (508) 990-0449; Email: kathryn.ford@state.ma.us

Jonathan H. Grabowski

School of Marine Science, University of Maine and Gulf of Maine Research Institute, 350 Commercial Street, Portland, ME 04101. Tel: 207-228-1628; Fax: 207-772-6855; Email; jgrabowski@gmri.org

W. Hunting Howell

Dept. of Biological Sciences, University of New Hampshire, Spaulding Life Sciences Bldg., Durham, NH 03824. Tel: 603-862-2109; Fax: 603-862-3784; Email: whh@unh.edu

Rubao Ji

Department of Biology, Redfield 2-14, MS 33, Woods Hole Oceanographic Institution Woods Hole, MA 02543 USA. Tel: 508-289-2986 Fax: 508-457-2134;

Email: rji@whoi.edu

Rebecca Jones

School of Marine Sciences, University of Maine and Gulf of Maine Research Institute, 350 Commercial Street, Portland, ME 04101 USA. Tel: 207-502-1652; Fax: 207-772-6855;

Email: rjones@gmri.org

Andrew Pershing

School of Marine Sciences, University of Maine and Gulf of Maine Research Institute, 350 Commercial Street, Portland, ME 04101 USA. Tel: 207-228-1656; Fax: 207-772-6855;

Email: andrew.pershing@maine.edu

Nicholas Record

School of Marine Sciences, University of Maine and Gulf of Maine Research Institute, 350 Commercial Street, Portland, ME 04101 USA. Tel: 207-228-1670; Fax: 207-772-6855;

Email: nrecord@gmri.org

Andrew Thomas

School of Marine Sciences, University of Maine, Orono, ME 04469 USA. Tel: 207-581-4335; Fax: 207-772-6855; Email: thomas@maine.edu

Graham Sherwood

School of Marine Science, University of Maine and Gulf of Maine Research Institute, 350 Commercial Street, Portland, ME 04101 USA. Tel: 207-228-1644; Fax: 207-772-6855; Email; gsherwood@gmri.org

Shelly Tallack

School of Marine Science, Gulf of Maine Research Institute, 350 Commercial Street, Portland, ME 04101 USA. Tel: 207-228-1639; Fax: 207-772-6855; Email; stallack@gmri.org

David Townsend

School of Marine Sciences, University of Maine, Orono, ME 04469 USA. Tel: 207-581-4367; Fax: 207-772-6855; Email: davidt@maine.edu

Abstract

We put forward a combined observing and modeling strategy for forecasting effects of climate change on the dynamics of spatially structured cod populations spawning in the western Gulf of Maine. Recent work indicates at least two genetically differentiated complexes in this region: a late spring spawning, coastal population centered in Ipswich Bay, and a population that spawns in winter inshore and on nearshore banks in the Gulf of Maine and off southern New England. The two populations likely differ in trophic interactions and in physiological and behavioral responses to different winter and spring environments. Coupled physical - biological modeling has advanced to the point where forecasting of environmental conditions for recruitment to each of the two populations is feasible. However, the modeling needs to be supported by hydrographic, primary production and zooplankton data collected by buoys, and by data from remote sensing and fixed station sampling. Forecasts of environmentally driven dispersal and growth of planktonic early life stages, combined with an understanding of possible population-specific usage of coastal habitat by juveniles and differential resident and migratory patterns of adults, can be used to develop scenarios for spatially explicit population responses to multiple forcings, including climate change, anthropogenic impacts on nearshore juvenile habitat, connectivity among populations and management interventions such as regional fisheries closures.

1. Introduction

One objective of recent initiatives to establish observing systems for the coastal ocean (e.g. Malone et al. IOOS document) is acquisition of observing data for application in ecosystem approaches to fisheries management. The 2006 Magnuson Stevens Fishery Conservation and Management Reauthorization Act (Section 406) calls for a study of the “state of the science for advancing the concepts and integration of ecosystem considerations in regional fishery management”. While the need for including environmental change (and by implication, climate change) in management decision making has been identified, the integration and interpretation of environmental data into useful products for fisheries managers has remained an elusive goal (NMFS Tech Memo 2009).

A major pathway through which environmental change influences fish population dynamics links bottom-up forcing to recruitment processes (Cushing 1982; Runge 1988). Evidence indicates that environmental forcing has a large influence on recruitment variability in groundfish and pelagic fish stocks in the northwest Atlantic, implying that such forcing is an important factor to incorporate into regional fishery management (Fig. 1). For example, Castonguay et al. (2008) report that mackerel recruitment in the southern Gulf of St. Lawrence is significantly related to copepod egg production rate (Fig. 1a), a proxy for availability of nauplius stages to the planktonic mackerel larvae. Using available satellite ocean color data, Platt et al. (2003) estimated the timing of the spring phytoplankton bloom on the Nova Scotia shelf. They found that the highest recruit per spawner indices for Scotian Shelf haddock, including the exceptional years of 1981 and 1999, occurred when the spring bloom was initiated unusually early (Fig. 1b). These observations are consistent with the match-mismatch (Cushing 1990) and growth-mortality hypotheses (Anderson 1988; Cushing and Horwood 1994). The common theme of both hypotheses is that food availability during the period of planktonic larval feeding determines how many and how quickly larvae pass through the window of high mortality rates. These hypotheses imply that variability of relative year class strength is usually determined in the larval phase for marine demersal species (Myers and Cadigan 1993). For both the Scotian Shelf haddock and southern Gulf mackerel populations, auspicious conditions for planktonic food availability were linked to the formation of exceptional year classes, which can sustain fisheries for many subsequent years.

While prey availability may be a necessary condition for determining larval survival, recruitment to any fish population involves complex processes that may either counteract or enhance the link of prey production with growth and survival of planktonic larvae. The recent strong year classes of Georges Bank haddock, including the exceptional 2003 year class, are strongly correlated with the magnitude of the fall phytoplankton bloom preceding the successful year class (Fig. 1c, from Friedland et al. 2008). This correlation is consistent with a hypothesis that high and prolonged fall blooms sustain benthic food production (brittle starfish, amphipods and polychaetes) for adult haddock, which in turn enhances adult condition, fecundity and egg quality, leading to higher larval survival. Alternatively, increases in copepod egg production driven by the higher fall-winter primary production (e.g. Durbin et al. 2003, Greene and Pershing 2007) may have contributed to higher growth and enhanced survival of planktonic haddock larvae. In either case, the evidence indicates that relative year-class strength can be determined by the end of the larval phase and forced by climatic variability acting on bottom-up processes.

In addition to factors influencing availability of planktonic prey to cod larvae during the winter and spring, recruitment success may be directly related to physical processes in the atmosphere and ocean. Eggs and larvae spawned along the coastal Gulf of Maine are subject to advection by the southwestward coastal Gulf of Maine current. There is significant potential for interannual to interdecadal variation in wind forcing, freshwater runoff, and hydrographic conditions external to the Gulf to affect dispersal of the planktonic cod eggs and larvae and successful transport to nursery areas. In the Gulf of Maine, Churchill et al. (Woods Hole Oceanographic Institution, unpublished manuscript) found a significant correlation between Atlantic cod recruitment success and mean velocity of northerly winds during the May spawning period (Fig. 1d), consistent with the hypothesis that wind-driven downwelling favors transport of buoyant planktonic larvae to nearshore nursery areas where juvenile survival is enhanced.

While there is empirical evidence that bottom-up forcing significantly influences recruitment success, the complex set of processes determining larval survival mandates the use of integrative models to better understand and predict the consequences of change in environmental conditions on recruitment success and connectivity among populations. An approach was developed in the GLOBEC (Global Ocean Ecosystem Dynamics: http://web.pml.ac.uk/globec/) program, in which physically-forced biological models of varying trophic level resolution were used to develop a mechanistic understanding of underlying correlations between environmental variability and fish productivity (GLOBEC, 1992, Wiebe et al. 2002, de Young et al. 2004). Runge et al. (2005) discuss the concept of an integrative system of linked, coupled physical-biological models (Fig. 2). They review the status of, and challenges confronting, each coupled physical biological component.

The GLOBEC Georges Bank/Northwest Atlantic program generated considerable advances in understanding the physical processes, nutrient dynamics, lower trophic level productivity, zooplankton population dynamics and larval cod and haddock ecology in the Georges Bank and the Gulf of Maine regions (e.g. Wiebe and Beardsley 1996; Wiebe et al. 2001, 2002; Wiebe et al. 2006 and articles therein; Ji et al. 2008a,b; Mountain et al. 2008; Ji et al. 2009). The integration of experimental and field observations into coupled, 3-D physical-biological models and their application to prediction of scenarios under climate change is presently ongoing as part of the final synthesis phase.

In this paper, we explore the feasibility of using coupled physical-biological models as an integrative tool for understanding climate forcing of fish populations in the Gulf of Maine, using the Gulf of Maine Atlantic cod stock as an example. We examine existing observing data and explore the potential for future observing systems to supply data needed for model development, operation and validation. We review the present status of coupled physical-biological modeling as it applies to Atlantic cod in the western Gulf of Maine ecosystem. Before considering the needs and potentials of integrative modeling, we first review the present understanding of the spatial structure of the Gulf of Maine Atlantic cod stock. As detailed below, there is evidence of genetically distinct populations within the Gulf of Maine cod stock, leading us to consider recruitment processes in the context of the broader spatial dynamics of Gulf of Maine Atlantic cod, including population-specific juvenile habitat and connectivity among populations.

In the following sections, we present a vision for implementation of observing activities and coupled physical-biological modeling to understand the consequences of environmental forcing on recruitment into, and connectivity among, local and genetically distinct Atlantic cod populations. Multidisciplinary integration of these efforts sets the stage for construction of predictive models of climate-forced impacts on fish population dynamics.

2. The structure of Atlantic cod in the Gulf of Maine

Recently, a paradigm shift has occurred in the conceptualization of population structure of marine species (Hauser & Carvalho 2008). Populations of many marine species traditionally viewed as panmictic, with high connectivity, have now been shown to exhibit population structure on fine geographic and temporal scales. Population subdivision on small spatial scales has been well documented for Atlantic cod across its range. For example, along the Norwegian Skaggerak coast, genetically distinct resident populations of cod have been detected within distances of < 50 km (e.g. Jorde et al. 2007). Furthermore, there is now evidence of four genetically distinct populations of Atlantic cod in the North Sea (Hutchinson et al. 2001), and of at least two distinct spawning components occurring in waters surrounding Iceland (e.g. Pampoulie et al. 2006). The findings of these, and other, genetic studies show Atlantic cod to be a population-rich species (Sinclair 1988).

Atlantic cod in U.S. waters are currently managed by a two-stock model, consisting of a Gulf of Maine stock and a stock residing over Georges Bank and adjacent areas to the south, extending from southern New England to the mid-Atlantic coast. Recent evidence from tagging studies suggests that cod movements do not conform to the two-stock model (Tallack 2009). This is supported by the analysis of recent genetic data, which reveal fine-scale genetic differentiation among spatially and temporally divergent spawning populations in the Gulf of Maine/Georges Bank region, a result also inconsistent with the 2-stock management model (Lage et al. 2004, Wirgin et al. 2007, Kovach et al. University of New Hampshire, unpublished manuscript). The locations of spawning adults and their genetic composition are shown in Fig. 3.

Analysis of historical data by Ames (2004) indicates that there were once multiple sites of cod spawning along the Gulf of Maine coast, presumably supporting a number of subpopulations. The number of active spawning sites has contracted considerably over the past few decades. Currently, known sites of consistently active spawning within the Gulf of Maine/Georges Bank region are limited to Ipswich Bay, Massachusetts Bay, Nantucket Shoals/Chatham, Block Island/Cox Ledge, and the northeastern flank of Georges Bank (Lough 2005). Small spawning aggregates are also found on nearshore banks in the western Gulf of Maine, such as Stellwagen Bank and Jeffreys Ledge.

Recent research using microsatellite and single nucleotide polymorphism DNA markers reveal that the majority of the genetic variation among cod spawning populations in U.S. waters can be explained by three major groupings: 1) a northern spring coastal complex, 2) a southern complex, and 3) a population spawning over the northeast peak of Georges Bank (Breton 2008; A. Kovach et al. University of New Hampshire, unpublished manuscript; see also Fig. 3). The northern spring complex spawns in coastal Gulf of Maine waters from Massachusetts Bay to Bigelow Bight in the spring and summer. The southern complex spawns within the inshore Gulf of Maine in the winter, and also at different offshore locations and seasons within the Gulf of Maine and southern New England waters. Spawning on the northeast peak of Georges Bank occurs in the late winter. Fish within this spawning complex are differentiated from the southern complex, but only weakly differentiated or similar to fish of the northern spring complex.

One of the most significant findings in the above work is that of genetic differentiation among temporally divergent spawning groups that overlap spatially in the Gulf of Maine. Cod that spawn in Ipswich and Massachusetts Bays in the spring are genetically distinct from cod that spawn in the same bays in the winter. Evidence also exists for fine scale population structuring within the three complexes, including weak differentiation between populations in the offshore

Gulf of Maine and southern New England waters, as well as differentiation between populations within southern New England (e.g. Cox Ledge and Nantucket Shoals).

The development of modeling tools to understand and predict bottom-up forcing of recruitment processes in Gulf of Maine Atlantic cod must take into account the fine scale population structure. The environmental conditions influencing maternal condition as well as the transport and survival of planktonic early life stages are likely to be different among populations. Furthermore, it is clear that environmental conditions constitute only part of the processes that lead to successful recruitment; other factors, such as juvenile survival and population fidelity determining connectivity among populations, also contribute. In the following sections, we address the measurement and modeling of environmental conditions and cod life history.

3. Environmental forcing in the Gulf of Maine: components of an observing system

Strategies for long time series observations of the Gulf of Maine are presently evolving under the auspices of the Northeastern Regional Association for Coastal Ocean Observing Systems (NERACOOS). We review here components of observing data that can provide understanding of the environmental contrasts influencing cod recruitment along the coastal Gulf of Maine. Much of the hydrographic, nutrient, phytoplankton and zooplankton data time series collected in the coastal western Gulf of Maine originate from the GoMOOS (Gulf of Maine Ocean Observing System) buoy data and from sample collections by University of New Hampshire Coastal Observing Center and Northeast Consortium supported projects, all of which are precursors to the present NERACOOS.

3.1 Physical Dynamics

At present, the principal source of physical data within the Gulf of Maine is the NERACOOS Gulf of Maine Array. Essentially a successor to the GoMOOS buoy array (Pettigrew et al. 2008), which included instrumented buoys at as many as 11 locations, the NERACOOS array currently consists of 7 instrumented buoys distributed throughout the Gulf of Maine. Measurements of temperature, salinity and current velocity are acquired at each buoy site and made available to the public in near real time. The NERACOOS measurement suite also includes high resolution distributions of surface current derived from Coastal Ocean Dynamics Applications Radar (CODAR), a land-based high-frequency radar system for determining ocean surface velocity (Lipa and Barrick 1983; Chapman and Graber 1997; Kohut and Glenn 2003). At present, the University of Maine maintains three CODAR stations within the Gulf of Maine region. When fully operational, this array will provide surface current measurements over the coastal region extending from the Bay of Fundy to Casco Bay. Data from the Gulf of Maine CODAR and buoy arrays should be particularly useful in determining how the coastal circulation in the Gulf of Maine responds to variations in climatic forcing.

Of particular interest to the study of cod larvae transport is the extent to which the various branches of the Gulf of Maine Coastal Current (GMCC) are connected. Despite its name, the GMCC is not bound to the coast but is often observed centered near the 100-m isobath (Churchill et al. 2005; Keafer et al. 2005; Pettigrew et al. 2005). Flowing clockwise around the perimeter of the Gulf of Maine, it consists of multiple branches with varying degree of flow from one to another (Lynch et al. 1997; Pettigrew et al. 1998, 2005; Manning et al. 2009). Also of importance to larval cod recruitment is the extent to which the Gulf of Maine coastal plume, flowing shoreward of the GMCC (Churchill et al. 2005; Keafer et al. 2005), is impacted by changes in climatic forcing.

Another important source of physical data in the Gulf of Maine is the Environmental Monitors on Lobster Traps (eMOLT) program (Manning and Pelletier 2009). Established in 2001, eMOLT is a collaboration of ocean scientists and lobster industry participants. The publically available eMOLT data base currently consists of more than 3.5 million hourly records of temperature, 80 thousand hourly records of salinity, and 260 thousand satellite drifter fixes. The relative low cost required to deploy and maintain the eMOLT sensor array, and the sustained interest of the fishing community, make it an ideal means of acquiring a long-term data base for assessing the impact of climatic variations on water properties in the Gulf of Maine.

3.2 Nutrients and primary production

Nutrient-rich, deep Slope Waters that enter the Gulf of Maine through the Northeast Channel are the primary source of dissolved inorganic nutrients that support the relatively high rates of primary production in the Gulf (Ramp et al. 1985; Schlitz and Cohen 1984; Townsend et al. 1987; Townsend 1991; Townsend 1998; Townsend et al. 2006; Townsend and Ellis 2009). Over the last four decades, the nutrient regime in the Gulf of Maine has been changing. Townsend et al. (University of Maine, unpublished manuscript) provide evidence that since the 1970s, the deeper waters in the interior Gulf of Maine (>100m) have become fresher and cooler, with lower nitrate but higher silicate concentrations. They argue that these changes are related to accelerated melting in the Arctic, influencing the relative proportions of shelf and slope waters in the Gulf, with implications for the timing, magnitude and species composition of future phytoplankton production.

Since 1998, surface nutrients have been observed in the Gulf of Maine, on a semi-monthly to monthly frequency between late spring and early autumn, as part of the Gulf of Maine North Atlantic Time Series (GNATS: Balch et al. 2008). This time series is derived from samples collected at 1-2 m along a transect between Portland, Maine and Yarmouth, Nova Scotia. A long term (9 yr to date) time series of nutrients has also been collected in Casco Bay by D. Townsend (http://grampus.umeoce.maine.edu/dave/homepage.htm).

The most temporally and geographically complete record of changing phytoplankton biomass within the Gulf of Maine is derived from bio-optical properties and calculated chlorophyll concentrations from satellite-derived ocean color data. At present, two operational satellites (SeaWiFS and MODIS) cover the Gulf of Maine each day. Satellite-derived chlorophyll time series begin in late 1997, providing quantification of climatological seasonal patterns (e.g. Thomas et al. 2003) and interannual variability (e.g. Thomas et al. 2003; Ji et al. 2008). These chlorophyll time series show that the dominant events of primary productivity in most regions of the Gulf of Maine are the spring and fall blooms. The chlorophyll time series reveal strong interannual variability in both the timing and the spatial pattern of the blooms (Fig. 4). In regions close to shore, and in shallow regions of episodic resuspension events, colored dissolved organic material (CDOM) and suspended sediment potentially bias the satellite-measured chlorophyll. Continued research into bio-optics in these regions, as well as in-situ sampling programs to validate satellite signals and provide vertical structure, are required.

3.3 Secondary production

The planktonic early life stages of Atlantic cod feed primarily on copepod eggs and nauplii (Heath and Lough 2007). Time series observations of copepod and other zooplankton species in the Gulf of Maine (see C. Johnson, Bedford Institute of Oceanography, unpublished manuscript, this volume) are being acquired by the U.S. National Marine Fisheries Service using the Continuous Plankton Recorder (CPR) and seasonal net surveys (ECOMON), and by the Canadian Department of Fisheries and Oceans under the Atlantic Zonal Monitoring Program (AZMP). These time series have shown interdecadal shifts in zooplankton community structure (Pershing et al. 2005; Kane 2007). These shifts are hypothesized to be primarily the result of increased stratification in fall, driven by surface freshening from the Scotian Current, which leads to more intense and longer duration fall phytoplankton productivity and subsequent increases in relative abundance of small copepod species (Pershing et al. 2005; Greene and Pershing 2007).

The present long-term zooplankton sampling series do not necessarily represent zooplankton variability in the near coastal regions. Measurements of shorter duration (two to six years) time series of zooplankton abundance and composition, employing sampling protocols similar to the AZMP time series, have been carried out between 2003-2008 as part of the University of New Hampshire Coastal Observing Center and Northeast Consortium PULSE programs. Collection with vertical, ring net casts were made at fixed stations located in the planktonic feeding habitat of the western Gulf of Maine Atlantic cod populations (Fig. 3). The time series includes data from 2004-2006, among the wettest years on record for the western Gulf of Maine. The results (Jones and Runge, University of Maine, unpublished manuscript, this volume) show dominance of a few species of planktonic copepods, including *Pseudocalanus* spp, *Centropages typicus* and *Calanus finmarchicus,* as well as an order of magnitude interannual change in coastal abundance. The correlation of these coastal time series with the NMFS time series of zooplankton abundance and composition acquired further offshore has not been determined. These coastal time series can be used to calculate the production rate of the copepod prey field, similar to Castonguay et al. (2008: Fig. 1a) for validation of the output of the copepod life cycle models described below.

3.4. Juvenile habitat

Young-of-year (YOY) cod (0 age class) typically settle, after dispersal during the planktonic life stages, in relatively shallow water and move to deeper water with age (Swain 1993, Linehan et al. 2001). They are thought to settle indiscriminately and suffer disproportionate mortality in relatively featureless habitats (Gotceitas & Brown 1993). Laboratory investigations of habitat usage by YOY cod in the northwest Atlantic showed that they prefer structured habitats (i.e. cobble, sea grass, kelp, and sponge habitats) when predators are present (Gotceitas and Brown 1993, Gotceitas et al. 1995, Lindholm et al. 1999). Field surveys from inshore sites in the Canadian maritime provinces have confirmed that YOY cod associate with structured habitats such as sea grass beds and cobble/boulder habitat with high relief, suggesting that predation risk is high during early life-history (Keats et al. 1987, Tupper and Boutilier 1995, Gregory and Anderson 1997, Cote et al. 2001). In most cases, habitats with protective cover promote higher cod recruitment, and coastal cod probably recruit to habitats that are both highly heterogeneous and the same color of recruiting cod (Gregory & Anderson 1997). YOY cod also survive better at shallower depths, suggesting why they typically settle there (Linehan et al. 2001).

Time series observations of juvenile cod are conducted by the National Marine Fisheries Service, the Maine Department of Marine Resources and the Massachusetts Division of Marine Fisheries. Ongoing since 2000 and 1978, respectively, the Maine-New Hampshire and

Massachusetts Inshore Trawl Surveys provide data on the density and size-frequency distribution of juvenile cod from coastal regions of the Gulf of Maine in the spring and fall. These data can be used to examine how the habitat and depth preferences differ for YOY fish from different spawning periods, because the YOY (i.e., <10 cm fish) caught in the spring likely originate from winter spawners, whereas those captured in the fall likely originate from spring spawners. Information on juvenile cod provided by the NMFS Trawl Survey covers a much longer timer period, beginning in 1950, but is limited in inshore waters. These time series can be used to assess habitat associations for juvenile cod by superimposing trawl data onto substrate maps of the Gulf of Maine and Georges Bank.

Spatially continuous high-resolution substrate data collected via acoustic surveys are integral for monitoring cod nursery habitat. The state of Massachusetts recently completed multibeam acoustic surveys of the waters of coastal Massachusetts, and are in the process of developing substrate maps. Efforts focused on using remote physical measurements such as rugosity as a proxy for seafloor substrate and complexity are available in some areas. Because these studies are often not ground-truthed to determine actual seafloor composition or biological associations, they fall short of being true habitat maps. Collection of spatial high resolution data every 5 to 10 years will permit monitoring of anthropogenic impacts such as global climate change and environmental degradation on the distribution and abundance of essential fish habitats in the nearshore environment.

4. Coupled physical-biological modeling

In this section we review present status of modeling bottom-up forcing of the western Gulf of Maine ecosystem and cod recruitment dynamics, as outlined in Fig. 2.

4.1. Physical modeling

There are a number of individual groups actively modeling the circulation of the Gulf of Maine/Georges Bank region. The Marine Ecosystem Dynamics Modeling Laboratory at U. Mass. Dartmouth (http://fvcom.smast.umassd.edu/, Chen et al. 2007) utilizes the Finite Volume Coastal Ocean Model (FVCOM) to model the regional dynamics for a number of applications, including larval tracking studies (e.g. Huret et al. 2007). The Oceanographic Modeling and Analysis Laboratory (http://www.smast.umassd.edu/modeling/; also at U. Mass Dartmouth) employs the Harvard Ocean Prediction System in a model of Gulf of Maine dynamics (Brown et al. 2007a,b). As part of the Gulf of Maine Ocean Observing System (GoMOOS), the Ocean Modeling Group at the University of Maine has developed a regional hydrodynamic model (based on the Princeton Ocean Model) for hindcast and forecast studies (http://rocky.umeoce.maine.edu/GoMPOM/). The model was recently applied to examine connectivity among lobster populations in the Gulf of Maine (Xue et al. 2008). The Ocean Observing and Modeling Group at N.C. State Univ. (http://www4.ncsu.edu/~rhe/) has developed a Regional Ocean Model System (ROMS)-based model of the Gulf of Maine for studying, and predicting, the transport of harmful algal blooms (He et al. 2008). To promote easy and standardized access to the output from these various circulation models R. Signell of United States Geological Survey Woods Hole Science Center has recently launched the “Gulf of Maine Interoperability Pilot Project” ” (http://www.necodp.org/committees/modeling-committee/gulf-of-maine-model-interoperability-pilot-project) as part of the Northeast Coastal and Ocean Data Partnership (www.necodp.org), formerly the Gulf of Maine Ocean Data Partnership.

4.2. NPZD modeling

Considerable progress has been made in developing coupled physical and Nutrient-Phytoplankton-Zooplankton-Detritus (NPZD) component models for the Gulf of Maine/Georges Bank region. Ji et al. (2008a) developed an NPZD model coupled to a high resolution 3-D coastal ocean circulation model (FVCOM) to run continuous simulations for the Gulf of Maine – Georges Bank system on an annual basis (e.g. Fig. 5). They used the model to examine local and external processes that control nitrogen and phytoplankton dynamics on Georges Bank. In addition to the potential to simulate the spring bloom and chlorophyll fields to force copepod egg production on Georges Bank and elsewhere in the Gulf of Maine, the model can be used to investigate the potential influence of nutrient-poor Labrador Slope Water, driven by climate forced events in the Arctic (Greene and Pershing 2007) on the timing and magnitude of the fall bloom, connecting a mechanistic analysis of the fall bloom to Georges Bank haddock recruitment (Friedland et al. 2008). Three-dimensional physical-biological models have also been developed to estimate the spatial and temporal variations of phytoplankton biomass in the western Gulf of Maine (e.g. Liu et al. 2008; Ji et al. 2008b).

4.3. Copepod life cycle modeling

In addition to the NPZD models, a number of recent advances in the modeling of copepod population dynamics (e.g. Gentleman et al. 2008; Record and Pershing 2008; Hu et al. 2008; Neuheimer et al. 2009; Ji et al. 2009; A. Leising, Southwest Fisheries Science Center, NOAA, unpublished manuscript) allow for the possibility of simulating the abundance and production of the dominant copepods in the in the Gulf of Maine/Georges Bank region. R. Ji and colleagues at the Woods Hole Oceanographic Institution (WHOI) and the University of

Massachusetts, Dartmouth have developed a continuous, whole year model simulating abundance, egg production and distribution of *Pseudocalanus* spp. in the Gulf of Maine (Ji et al. 2009: Fig. 6a-d). A. Pershing (University of Maine) and colleagues have developed a coupled, 2-D life cycle model of *Calanus finmarchicus,* and applied it with forcing from satellite temperature and surface chlorophyll to predict arrival date of the northern right whale, which feeds primarily on *Calanus*, in the western Gulf of Maine in spring (Pershing et al. 2009: Fig. 6e-f;). A mechanistic hypothesis explaining diapause of *Calanus* has been put forward (Johnson et al. 2008) and successfully applied to reproduce *Calanus* demography (F. Maps, University of Maine, unpublished manuscript). These coupled physical life cycle models can be used not only to predict larval cod prey fields in the western Gulf of Maine, but also to evaluate potential distributional shifts in dominant copepod species, such as the lipid rich *Calanus finmarchicus,* under climate change scenarios (C. Johnson, Bedford Institute of Oceanography, unpublished manuscript).

4.4 Larval fish trophodynamic modeling

A critical element in modeling cod recruitment dynamics is the coupled, Individual-Based Model (IBM) that simulates transport of egg and larval stages to nursery areas, accounting for cod mortality as well as the feeding and growth rates of larval cod. The dispersion of cod eggs and larvae from the western Gulf of Maine spawning areas has been simulated using flow fields generated by FVCOM (Chen et al. 2006 a,b). The initial study (Huret et al. 2007) was confined to the 1995 spawning period. More recently Churchill et al. (Woods Hole Oceanographic Institution, unpublished manuscript) have expanded on this work to investigate factors influencing the year-to-year variation in transport of larvae spawned during spring within the Ipswich Bay spawning area. They found that the successful transport of buoyant eggs and early-stage larvae to suitable juvenile habitats was strongly influence by the interaction of the wind-driven transport with the larger-scale Gulf of Maine circulation, which includes a strong coastal current that tends to bypass Ipswich and Massachusetts Bays (Fig. 7). Eggs released during times of northward winds tend to be transported eastward by the surface Ekman flow into the coastal current, which carries them rapidly out of the western Gulf. In contrast, eggs released during times of southward (downwelling favorable) winds tend to be carried westward by the surface Ekman flow into coastal nursery areas of Ipswich and Massachusetts Bays (Fig. 7).

A working model of cod feeding and growth has been developed by G. Lough and colleagues (Lough et al. 2005; Petrik et al. 2009), and variations of the original model (e.g. Kristiansen et al. 2009) have been applied to Georges Bank and off coastal Norway (Vikebø, 2007). The core of the trophodynamic model is the standard bioenergetic supply-demand function, in which growth is represented as the difference between the amount of food absorbed by a larva and the metabolic costs of its daily activities. The formulation includes: (i) variable composition of prey fields; (ii) effect of turbulence, swimming behavior and satiation on encounters and ingestion of larval fish and their prey; (iii) light limitation on ingestion rates at low and at high light intensities and (iv) effects of temperature on metabolic costs, ingestion rates and growth. These models may be supplied with forecasts of the copepod prey fields to indicate environmental conditions for growth and survival of the early cod life history stages.

5. Achieving a synthesis: Application to Atlantic Cod in the Gulf of Maine

Our brief overview has attempted to outline the state of understanding of several components needed to understand potential climate change influences on population rich species such as Atlantic cod. We have shown that these components have now been developed and may be applied towards understanding the spatial dynamics of recruitment variability in the coastal and bank systems of the Gulf of Maine. We believe that a multidisciplinary synthesis effort, involving oceanographers, fisheries scientists and those involved in fisheries management decisions, is now warranted in order to assess how the research advances can be translated into useful information for management. Synthesis activities should address questions such as: Which aspects of the modeling and observing systems might be made operational into decision/ information support tools in the near term? Which research directions need to be encouraged to support development of information support tools in the longer term? What data time series that support fisheries management should be sustained or established as part of the emerging regional observing system?

While we are not aware of a Linked Coupled Model (LCM: Fig. 2) system that has been fully implemented, some modeling efforts are coming close to this goal (e.g. Hermann et al. 2001; Ji et al. 2008a; 2009). We believe that the components are now in place to develop LCMs for both the coastal Gulf of Maine and Georges Bank in order to understand spatial dynamics of recruitment variability in cod. This application to Atlantic cod would serve as a model and proof of concept for understanding spatial recruitment dynamics for other population rich species, such as herring and other forage and groundfish populations. The coupled model components need not be linked together to be useful; each coupled modeling component has value as an information support tool in its own right.

5.1. Needs for developing coupled modeling capacity in the Gulf of Maine region

Coupled multidisciplinary models serve to integrate multiple data sets in the analysis and interpretation of physical and ecological processes, and can provide valuable insight and information for ecosystem approaches to management. Over the past three decades, a number of regional workshops have addressed the need to develop and coordinate regional modeling activities to support the detection and understanding of changes in the Gulf of Maine ecosystem. The results of these workshops are summarized in a report of a meeting convened in 2005 by the Regional Association for Research on the Gulf of Maine (RARGOM), which was focused on modeling needs related to the regional observing system (Runge and Braasch 2005). In addition to identifying specific research priorities for advancement of modeling capabilities, three critical issues were emphasized for development of a regional modeling capacity to analyze and interpret observing data: (1) a regional infrastructure that will facilitate regional coordination; (2) advancement of models and model systems (such as the LCM envisioned here) that have experimental forecasts as products and (3) regional coordination of model assessment (e.g. model skill assessment, evaluation of uncertainty, model ensemble approaches to predictions). The recommendations from that meeting included the need to establish a Regional Modeling Center and/or a Gulf of Maine Experimental Environment Forecast Center (Runge and Braasch 2005). It is expected that experimental environmental forecasting will be an iterative process in which model forecasts are improved by new data, against which predictions can be compared, and from managers using forecast products.

Models may also enhance observing system design through simulations aimed at maximizing return on observing investment for various infrastructure scenarios. A recent study used the model output, together with the Variance QuadTree (VQT) optimization algorithm, to minimize the root mean square sampling error in plankton survey designs (Lin et al. Woods Hole Oceanographic Institution, unpublished manuscript). The model was used in an observation system simulation experiment (OSSE) to determine the optimal plankton sampling locations. More generally, numerical models can be used to gain insights into optimal temporal and spatial sampling of biological and physical variables. The models also can be used to examine which variables and parameters are most important to measure. Once the observing system is in place, the 3D coupled model can then interact with the observing system, assimilating the data and directing the observing system as to when and where to sample. Development of this interaction between the model and observing system will enable efficient acquisition of key data and improve model forecasting.

5.2 Data needs and developments in regional NERACOOS

The U.S. Integrated Ocean Observing System (IOOS) envisions a nationwide system of coastal ocean data collection and analysis organizations that can provide timely predictions of coastal ocean changes and their consequences for the public (U.S. IOOS, 2002; 2006). NERACOOS is part of the coastal component of IOOS representing the Gulf of Maine and southern New England Bight. Planning for NERACOOS started in 2005 with formal incorporation in 2008. As a regional association, NERACOOS has the capacity to institute observing time series covering a broad range of oceanographic and ecosystem variables. Current infrastructure, including buoys, has revealed spatial and temporal variability in key physical processes in the Gulf of Maine at unprecedented resolution. Observations contribute to modeling capability via assimilation of real-time information and hindcast assessment modeling skill, which can improve model forecasts. Sustained monitoring is essential for detecting, understanding, and ultimately predicting effects of climate change on ecosystems. Future enhancements of observing infrastructure, given sufficient funding, will enable sustained and improved monitoring of critical biological variables, including distribution and abundance of key species over time. The multidisciplinary modeling/observational synthesis discussed here will serve to maximize the observing system value to ecosystem-based fisheries management, particularly in responding to the impacts of climate change.

The current set of observations, however, only partially meet the needs of coupled physical and biological models, such as the modeling system proposed here for Atlantic cod. Four categories of model data needs have been recognized (Runge and Braasch 2005): (1) Key pieces of information about biological processes that are currently not well studied and therefore cannot be modeled accurately; (2) High resolution time-series of physical and biological data from the Gulf of Maine to inform and evaluate models; (3) Fixed time-series stations located strategically in coastal Gulf of Maine to observe seasonal as well as longer temporal change and to acquire data needed for model parameterization (operations at such stations should include repeat visits by research vessels for sampling of zooplankton and ichthyoplankton abundance and diversity as well as for routine sensor and system maintenance); (4) Key physical and biological observations in Canadian waters for information about the upstream boundary conditions.

In the near-term, capacity for modeling physical-biological processes in the Gulf of Maine may be enhanced by the addition of available and developing technology to the present observing system. In particular, the addition of *in situ* nutrient and chlorophyll sensors to the NERACOOS Gulf of Maine array would clearly benefit efforts to model nutrient fluxes and primary productivity in the Gulf. Development of these types of sensors for mooring systems is rapidly advancing through the efforts of academic and industry researchers, often working in partnership (Dickey et al. 2009). Modeling the transport of cod eggs and larvae would be enhanced by the expansion of the NERACOOS CODAR array to cover the entire coastal region of the Gulf of Maine. CODAR data would be particularly valuable in evaluating, and improving, a model's capability of capturing the interaction of wind-driven transport and the larger-scale Gulf of Maine circulation, an interaction that Churchill et al. (Woods Hole Oceanographic Institution, unpublished manuscript) found to be critical in controlling the extent to which larval cod spawned in the western Gulf of Maine are delivered to habitats suitable for early stage juvenile development (Fig. 7). The need to acquire high resolution data in certain areas in response to significant events, such as the appearance of a spawning fish aggregation, could be met by the addition of remotely controlled autonomous vehicles to the NERACOOS suit of instrument systems.

5.3. Modeling the spatial dynamics of Gulf of Maine cod populations

Predicting changes in the demography of a fish stock that has a complex life history, such as Atlantic cod, in response to changes in environmental conditions or fishing pressure requires a full life-cycle approach that encompasses growth, movement and mortality of fish beyond the settlement phase. Andrews et al. (2006) and Heath et al. (2008) recently developed spatially and physiologically explicit approaches to modeling the demography and distribution of Atlantic cod populations residing on the northern European continental shelf.

Given the current and future direction of research on Atlantic cod in this region, construction of a spatially and temporally explicit population model of western Gulf of Maine Atlantic cod that incorporates the ecological differences between winter and spring spawning populations across life stages is a feasible goal. This type of model can be used to examine the response of the spring- and winter-spawning cod stocks to varying conditions of climate, fishing intensity, and exchange of individuals across the stocks. The model could be informed by ongoing or planned research by collaborators on cod research in the region. For example, the movement, growth, and survival of eggs and larvae, up to the time of settlement, could be informed by the previously described coupled, IBM trophodynamic models. Field and laboratory studies could inform juvenile habitat preference and growth as a function of habitat type. Seafloor maps of the region created using multibeam and photographic surveying can then be used to define habitat available for settlement of juveniles. Life history parameters of each population at the adult stage can be estimated from measurements (length, weight, maturity, and age data) collected from adult sampling planned for winter and spring in the western Gulf of Maine, and supplemented with data collected by the NMFS bottom trawl survey. Distinguishing the spawning group of origin of adults is possible through genetic and otolith chemistry analysis. Adult habitat use can be specified from tagging data and otolith chemistry studies may provide further resolution regarding the spatial-scale of movement of winter- and spring-spawning fish. Connectivity among groups can be incorporated in the model as a straying rate, estimated from genetic differences (pairwise F_{ST} values) between the two spawning stocks. Once the basic model is constructed, it can be run under different scenarios extending over the time period of IBM simulations and include a range of climatic conditions.

The consequences of various life history differences between the two western Gulf of Maine cod populations, including differences in vital rates, larval dispersion and survival, fecundity, migration patterns, natural and fishing mortality, etc. can be evaluated in the framework of this model. This research effort would constitute a new, integrative approach to understanding spatial dynamics of Atlantic cod in the Gulf of Maine. The modeling approach would have applications for fisheries management and for assessing the possible impact of environmental perturbations (such as those caused by a changing climate) on a regional fish stock. Before such an approach can be applied with confidence a number of issues will need to be resolved, including further collection of data required to properly parameterize a model of this regional fish stock and testing the validity of model predictions. This approach could be adopted as part of a Gulf of Maine regional modeling/experimental environmental forecasting center.

6. Acknowledgements

We thank L. Fenderson for assistance with the preparation of Figure 3 and F. Maps for his comments. We gratefully acknowledge awards from the Northeast Consortium, the NOAA Fisheries and the Environment (FATE) program, the National Science Foundation under Grant Numbers OCE-0733910, OCE-0709518 and an NSF Coupled Natural and Human Systems award (0709527) in support of the preparation of this contribution to the Gulf of Maine Science Symposium.

Literature cited

Ames, E.P. 2004. Atlantic cod stock structure in the Gulf of Maine. Fisheries 29: 10-28.

Anderson, J.T. 1988. A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. J. Northwest Atl. Fish. Sci. 8:55-66.

Anderson, D., D. McGillicuddy, D. Townsend, and J. Turner. 2005. The ecology and oceanography of toxic Alexandrium blooms in the Gulf of Maine. Deep Sea Res. II 52**:** 2365-2368.

Andrews, J.M., W.S.C. Gurney, M.R. Heath, A. Gallego, C.M. O'Brien, C. Darby, and G. Tyldesley. 2006. Modelling the spatial demography of Atlantic cod (*Gadus morhua*) on the European continental shelf. Can. J. Fish. Aquat. Sci. 63: 1027-1048.

Balch, W. M., D. T. Drapeau, B. C. Bowler, E. S. Booth, L. A. Windecker, and A. Ashe. 2008. Space-time variability of carbon standing stocks and fixation rates in the Gulf of Maine, along the GNATS transect between Portland, ME, USA, and Yarmouth, Nova Scotia, Canada. J. Plankton Res. 30: 119-139.

Bisagni, J. J., D. J. Gifford, and C. M. Ruhsam. 1996. The spatial and temporal distribution of the Maine Coastal Current during 1982. Cont. Shelf Res.16: 1-24.

Brown, W.S., A. Gangopadhyay, F.L. Bub, Z. Yu, and G. Strout, and A.R. Robinson, 2007a. An Operational Circulation Modeling System for the Gulf of Maine/Georges Bank Region, Part 1: The Basic Elements, IEEE J. Oceanic Eng. 32(4), doi: 10.1109/JOE.2007.895277.

Brown, W.S., A. Gangopadhyay, and Z. Yu, 2007b. An Operational Circulation Modeling System for the Gulf of Maine/Georges Bank Region, Part 2: Applications", IEEE J. Oceanic Eng., 32(4), doi: 10.1109/JOE.2007.895278.

Buckley, L.J. and E.G. Durbin. 2006. Seasonal and inter-annual trends in the zooplankton prey and growth rate of Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae on Georges Bank. Deep-Sea Res.II. 53: 2758-2770.

Castonguay, M., S. Plourde, D. Robert, J. A. Runge and L. Fortier. 2008. Copepod production drives recruitment in a marine fish. Can. J. Fish. Aquat. Sci. 65:: 1528-1531.

Chapman, R.D. and H.C. Graber. 1997. Validation of HF radar measurements. Oceanography 10: 76-79.

Chen, C., G. Cowles and R. C. Beardsley. 2006a. An unstructured grid, finite-volume coastal ocean model: FVCOM User Manual. Second edition, SMAST/UMASSD Technical Report-06-0602: 315.

Chen, C, R. C. Beardsley and G. Cowles. 2006b. An unstructured grid, finite-volume coastal ocean model (FVCOM) system. Special Issue entitled “Advance in Computational Oceanography”, Oceanography. 19(1): 78-89.

Chen, C., H. Huang, R. C. Beardsley, H. Liu, Q. Xu and G. Cowles, 2007. A finite-volume numerical approach for coastal ocean circulation studies: comparisons with finite difference models. J. Geophys. Res. 112: C03018, doi:10.1029/2006JC003485.

Churchill, J. H., N. R. Pettigrew and R. P. Signell. 2005. Structure and variability of the western Maine coastal current. Deep Sea Res. II 52: 2392-2410.

Cushing, D.H., 1982. Climate and Fisheries. Academic Press, London, 373 pp.

Cushing, D. H. 1990. Plankton production and year-class strength in fish populations - an update of the match Mismatch hypothesis. Adv. Mar. Biol. 26: 249-293.

Cushing, D. H., and J. W. Horwood. 1994. The growth and death of fish larvae. J. Plankton Res. 16: 291-300.

Cote, D., S. Moulton, D. A. Scruton, and R. S. McKinley. 2001. Microhabitat use of juvenile Atlantic cod in a coastal area of Bonavista bay, Newfoundland. Transactions of the American Fisheries Society 130:1217-1223.

de Young, B., F. Heath, F. E. Werner, B. Chai, B. A. Megrey, and P. Monfray. 2004. Challenges of modeling decadal variability in ocean basin ecosystems. Science 304: 1463 - 1466.

Dickey, T., N. Bates, R.H. Byrne, G. Chang, F P. Chavez, R.A. Feely, A.K. Hanson, D. M. Karl, D. Manov, C. Moore, C.L. Sabine and R. Wanninkhof. 2009. The NOPP O-SCOPE and MOSEAN Projects, Advanced Sensing for Ocean Observing Systems. Oceanography 22: 168-181.

Durbin, E., G., R.G. Campbell, M. C. Casas, M. D. Ohman, B. Niehoff, J. Runge and M. Wagner. 2003. Interannual variation in phytoplankton blooms and zooplankton productivity and abundance in the Gulf of Maine during winter. Mar. Ecol. Prog. Ser. 254: 81-100.

Fraser, S., V. Gotceitas, and J. A. Brown. 1996. Interactions between age-classes of Atlantic cod and their distribution among bottom substrates. Can. J. Fish. Aquat. Sci. 53.

Friedland, K.D., J.A. Hare, G.B. Wood, L.A. Col, L.J. Buckley, D.G. Mountain, J. Kane, J. Brodziak, R.G. Lough, and C.H. Pilskaln. 2008. Does the fall phytoplankton bloom control recruitment of Georges Bank haddock, Melanagrammus aeglefinus, through prenatal condition? Can. J. Fish. Aquat. Sci. 65: 1076-1086.

Gentleman, W. C., A. B. Neuheimer, and R. G. Campbell. 2008. Modelling copepod development: current limitations and a new realistic approach. ICES J. Mar. Sci. 63: 399-413.

GLOBEC, 1992. U. S. GLOBEC: Northwest Atlantic Implementation Plan, Report No. 6.

Gotceitas, V., and J. A. Brown. 1993. Substrate selection by juvenile Atlantic cod (*Gadus morhua*): efforts of predation risk. Oecologia 93:31-37.

Gotceitas, V., S. Fraser, and J. A. Brown. 1995. Habitat use by juvenile Atlantic cod (*Gadus morhua*) in the presence of an actively foraging and non-foraging predator. Mar. Biol. 123:421-430.

Greene, C.H. and A. J. Pershing. 2007. Climate drives sea change. Science. 315: 1084-1085.

Gregory, R. S., and J. T. Anderson. 1997. Substrate selection and use of protective cover by juvenile Atlantic cod *Gadus morhua* in inshore waters of Newfoundland. Mar. Ecol. Prog. Ser. 146:9-20.

Hauser, L. and G.R. Carvalho. 2008. Paradigm shifts in marine fisheries genetics: ugly hypotheses slain by beautiful facts. Fish and Fisheries 9: 333-362.

He, R., D. McGillicuddy., B. Keafer, D. Anderson, 2008. Gulf of Maine Circulation and Harmful Algal Bloom in Summer 2005: Part 2: Bio-physical Numerical Modeling. J. Geophys. Res.

Heath, M.R. and R.G. Lough. 2007. A synthesis of large-scale patterns in the planktonic prey of larval and juvenile cod (*Gadus morhua*). Fish. Oceanogr. 16: 169-185.

Heath, M.R., P.A. Kunzlik, A. Gallego, S.J. Holmes and P.J. Wright. 2008. A model of meta-population dynamics for North Sea and West of Scotland cod- the dynamic consequences of natal fidelity. Fish. Res. 93: 92-116.

Hermann, A.J., S. Hinckley, B. Megrey and J.M. Napp. 2001. Applied and theoretical considerations for constructing spatially-explicit individual-based models of marine fish early life history which includes multiple trophic levels. ICES J. Mar. Sci. 58: 1030-1041.

Hoffman, W.S., Salerno, D.J., Correia, S.J. and Pierce, D.E. 2006. Implementing the industry-based survey for Gulf of Maine cod pilot study. Final Report for Contract EA133F-03-CN-0010 to NOAA Northeast Cooperative Research Partners Program. NOAA Fisheries Service Northeast Regional Office, Gloucester MA. 37pp.

Hoffman, W.S., Correia, S.J. and Pierce, D.E. 2007. Implementing the industry-based survey for Gulf of Maine cod pilot study. Final Report for Contract EA133F-03-CN-0109 to NOAA Northeast Cooperative Research Partners Program. NOAA Fisheries Service Northeast Regional Office, Gloucester MA. 45pp.

Hu, Q., C. Davis, and C. Petrik. 2008. A simplified age-stage model for copepod population dynamics. Mar. Ecol. Prog. Ser. 360: 179–187.

Huret, M., J. Runge, C. Chen, G. Cowles, Q. Xu, and J. Pringle. 2007. Dispersal modeling of fish early life stages: Sensitivity with application to Atlantic cod in the western Gulf of Maine. Mar. Ecol. Prog. Ser. 347: 261-274.

Hutchinson, W.F., G.R. Carvalho, and S.I. Rogers. 2001. Marked genetic structuring in localised spawning populations of *Gadus morhua* in the North Sea and adjoining waters, as revealed by microsatellites. Mar. Ecol. Prog. Ser. 223: 251-260.

Ji, R., C. Davis, C. Chen, and R. Beardsley, 2008a. Influence of local and external processes on the annual nitrogen cycle and primary productivity on Georges Bank: A 3-D biological-physical modeling study. J. Mar. Systems, 73: 31-47.

Ji, R. C. Davis, C. Chen, D. Townsend, D. Mountain, R. Beardsley, 2008b. Modeling the influence of low-salinity water inflow on winter-spring phytoplankton dynamics in the Nova Scotian Shelf – Gulf of Maine region. J. Plankton Res. 30: 1399-1416

Ji, R., C. Davis, C. Chen, R. Beardsley, 2009. Life history traits and spatiotemporal distributional patterns of copepod populations in the Gulf of Maine-Georges Bank region. Mar. Ecol. Prog. Ser. 384: 187-205.

Johnson, C.L., A.W. Leising, J.A. Runge, E.J. S.Head, P.Pepin, S. Plourde and E.G. Durbin. 2008. Characteristics of Calanus finmarchicus dormancy patterns in the Northwest Atlantic. ICES J. Mar. Sci. 65: 339-350.

Jorde, P.E., H. Knutsen, S. H. Espeland, and N.C. Stenseth. 2007. Spatial scale of genetic structuring in coastal cod *Gadus morhua* and geographical extent of local populations. Mar. Ecol. Prog.Ser. 343: 229-237.

Kane, J. 2007. Zooplankton abundance trends on Georges Bank, 1977–2004. ICES J. Mar. Sci. 64: 909-919.

Keats, D. W., D. H. Steele, and G. R. South. 1987. The role of fleshy macroalgae in the ecology of juvenile cod (*Gadus morhua*L.) in inshore waters off eastern Newfoundland. Can. J. Fish. Aquat. Sci. 65:49-53.

Keafer, B. A., J. H. Churchill, D. J. McGillicuddy and D. M. Anderson. 2005. Bloom development and transport of toxic Alexandrium fundyense populations within a nearshore coastal plume in the Gulf of Maine. Deep Sea Res. II 52: 2674-2697.

Kerr, L.A., S.X. Cadrin and D.H. Secor. 2009. Consequences of spatial structure and connectivity to productivity and persistence of local and regional populations. ICES CM 2009/H:02. 26 pp

Kohut, J. T. and S. M. Glenn. 2003. Improving HF radar surface current measurements with measured antenna beam patterns. J. Atmos. Ocean. Tech. 20: 1303-1316.

Kristiansen, T., R. G. Lough, F. E. Werner, E. A. Broughton, and L. J. Buckley. 2009. Individual-based modeling of feeding ecology and prey selection of larval cod on Georges Bank. Mar. Ecol. Prog. Ser. 376: 227-243.

Lage, C., K. Kuhn, and I. Kornfield. 2004. Genetic differentiation among Atlantic cod (*Gadus morhua*) from Browns Bank, Georges Bank, and Nantucket Shoals. Fish. Bull. 102: 289-297.

Lindholm, J. B., P. J. Auster, and L. S. Kaufman. 1999. Habitat-mediated survivorship of juvenile (0-year) Atlantic cod *Gadhus morhua*. Mar. Ecol. Prog. Ser. 180:247-255.

Linehan, J. E., R. S. Gregory, and D. C. Schneider. 2001. Predation risk of age-0 cod (*Gadus*) relative to depth and substrate in coastal waters. J. Exp. Mar. Biol. Ecol. 263:25-44.

Lipa, B.J. and D.E. Barrick. 1983. Least-squares methods for the extraction of surface currents from CODAR cross-loop data: application at ARSLOE. IEEE J. Ocean. Engr OE-8: 226-253.

Liu, G., F. Chai, H. Xue, and A. Thomas. 2008. Spatial and temporal variation of phytoplankton biomass in the Gulf of Maine: observations and numerical investigations. AGU-ASLO Ocean Sciences Meeting. Orlando.

Lough, R. G., L. J. Buckley, F. E. Werner, J. A. Quinlan and K Pehrson Edwards. 2005. A general biophysical model of larval cod (*Gadus morhua*) growth applied to populations on Georges Bank. Fish. Oceanogr. 14:241-262.

Lynch, D.R., M.J. Holbrook and C.E. Naimie. 1997. The Maine coastal current: spring climatological circulation. Cont. Shelf Res. 17: 605–634.

Manning J.P, D.J. McGillicuddy, N.R. Pettigrew, J.H. Churchill and L.S. Incze. 2009. Drifter Observations of the Gulf of Maine Coastal Current. Cont. Shelf Res. 29:835-845.

Manning, J.P. and E. Pelletier. 2009. Environmental monitors on lobster traps (eMOLT): long-term observations of New England's bottom-water temperatures. J. Operational Oceanography 2: 25-33.

Mountain, D., J. Green, J. Sibunka, and D. Johnson. 2008. Growth and mortality of Atlantic cod *Gadus morhua*and haddock *Melanogrammus aeglefinus* eggs and larvae on Georges Bank, 1995 to 1999. Mar. Ecol. Prog. Ser. 353: 226-241.

Myers, R. A., and N.G. Cadigan. 1993. Is juvenile natural mortality in marine demersal fish variable? Can. J. Fish. Aquat. Sci. 50: 1591-1598.

Neuheimer, A. B., W. C. Gentleman, C. L. Galloway, and C. L. Johnson. 2009. Modeling larval *Calanus finmarchicus* on Georges Bank: time-varying mortality rates and a cannibalism hypothesis. Fish. Oceanogr. 18: 147-160.

Pampoulie, C., D.E. Ruzzante, V. Chosson, T.D. Jörundsdóttir, L. Taylor, V. Thorsteinsson, A.K. Daneílsdóttir, and G. Marteinsdóttir. 2006. The genetic structure of Atlantic cod (*Gadus morhua*) around Iceland: insight from microsatellites, the Pan I locus, and tagging experiments. Can. J. Fish. Aquat. Sci. 63: 2660-2674.

Pershing, A. J., Greene, C. H.,Jossi, J.,O'Brien, L., Brodziak, J. K. T. and Bailey, B. A. 2005. Interdecadal variability in the Gulf of Maine zooplankton community, with potential impacts on fish recruitment. Ices J. Mar. Sci. 62: 1511-1523.

Petrik C. M., T. Kristiansen, R. G. Lough, C. S. Davis. 2009. Prey selection of larval haddock and cod on copepods with species-specific behavior: a model-based analysis. Mar. Ecol. Prog. Ser., doi: 10.3354/meps08268.

Pettigrew, N.R., D.W Townsend, H. Xue, J.P. Wallinga, P.J. Brickley and R.D. Hetland. 1998. Observations of the Eastern Maine Coastal Current and its offshore extensions in 1994. J. Geophys. Res. 103: 30,623–30,639.

Pettigrew, N. R., J. H. Churchill, C. D. Janzen, L. J. Mangum, R. P. Signell, A. C. Thomas, D. W. Townsend, J. P. Wallinga, and H. Xue, 2005. The kinematic and hydrographic structure of the Gulf of Maine Coastal Current. Deep Sea Res. II 52: 2369-2391.

Pettigrew, N.R., H. Xue, J.D. Irish, W. Perrie, C.S. Roesler, A.C. Thomas and D.W. Townsend. 2008. The Gulf of Maine Ocean Observing System: generic lessons learned in the first seven years of operation (2001-2008). MTS Journal 42: 91-102.

Platt, T., C. Fuentes-Yaco, and K.T. Frank. 2003. Spring algal bloom and larval fish survival. Nature 423: 398-399.

Ramp, S.R., R.J. Schlitz and W.R. Wright. 1985. The deep flows through the Northeast Channel, Gulf of Maine. J. Phys. Oceanogr. 15: 1790-1808.

Record, N. R. and A.J. Pershing. 2008. Modeling zooplankton development using the monotonic upstream scheme for conservation laws. Limnol. Oceanogr. Methods. 6: 364-373.

Runge, J.A. 1988. Should we expect a relationship between primary production and fisheries? The role of copepod dynamics as a filter of trophic variability. Hydrobiologia 167/168: 61-71.

Runge, J.A., P.J.S. Franks, W.C. Gentleman, B.A. Megrey, K. A. Rose, F.E.Werner and B. Zakardjian. 2005. Diagnosis and prediction of variability in secondary production and fish recruitment processes: developments in physical-biological modelling. Pages 413-474 *in* A.R. Robinson and K. Brink, editors. The Sea. Vol. 13: The Global Coastal Ocean: Multi-Scale Interdisciplinary Processes. Harvard Univ. Press. Cambridge, Massachusetts.

Runge, J.A. and Braasch, E. 2005. Modeling needs related to the regional observing system in the Gulf of Maine. RARGOM Report 05-01. (www.rargom.org). 79 pp.

Schlitz, R.J. and E.B. Cohen. 1984. A nitrogen budget for the Gulf of Maine and Georges Bank. Biol. Oceanogr. 3: 203-222.

Sinclair, M. 1988. Marine populations: an essay on population regulation and speciation. Washington Sea Grant Press, Seattle.

Swain, D. P. 1993. Age- and density dependent bathymetric patterns of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. Canadian Journal of Fisheries and Aquatic Sciences 50:1255-1264.

Tallack, S.M.L. 2009. Proceedings from a workshop to identify future research priorities for cod tagging in the Gulf of Maine, 12 February, 2009. Northeast Fisheries Science Center Reference Document: 09-09. 76 pp.

Thomas, A. C., D. W. Townsend, and R. Weatherbee. 2003. Satellite-measured phytoplankton variability in the Gulf of Maine. Cont. Shelf Res. 23: 971-989.

Townsend, D.W., J.P. Christensen, D.K. Stevenson, J.J. Graham and S.B. Chenoweth. 1987. The importance of a plume of tidally-mixed water to the biological oceanography of the Gulf of Maine. J. Mar. Res. 45: 699-728.

Townsend, D.W. 1991. Influences of oceanographic processes on the biological productivity of the Gulf of Maine. Reviews in Aquatic Sciences 5: 211-230.

Townsend, D.W. 1998. Sources and cycling of nitrogen in the Gulf of Maine. J. Mar. Systems 16 (3/4): 283-295.

Townsend, D.W.,A.C. Thomas, L.M. Mayer, M. Thomas and J. Quinlan. 2006. Oceanography of the Northwest Atlantic Continental Shelf. Pages 119-168. *in* A.R. Robinson and K.H. Brink, editors. The Sea, Volume 14, Harvard University Press, Cambridge, Massachusetts.

Townsend, D.W. and W.G. Ellis. 2009. Primary production and nutrient cycling on the Northwest Atlantic continental shelf. i*n* K.K. Liu, L. Atkinson, R. Quinones, and L. Talaue-McManus, editors. Carbon and Nutrient Fluxes in Continental Margins: A Global Synthesis. Springer-Verlag, New York. (In Press)

Tupper, M., and R. G. Boutilier. 1995. Effects of habitat on settlement, growth, and postsettlement survival of Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 52:1834-1841.

Vikebø, F. B., S. Sundby, Bjørn Adlandsvik and O. H. Otterå. 2007. Impacts of a reduced thermohaline circulation on transport and growth of larvae and pelagic juveniles of Arcto-Norwegian cod (*Gadus morhua*). Fish. Oceangr. 16:216-228.

Wiebe, P. H. and R.C. Beardsley (eds.). 1996. Physical-biological interactions on Georges Bank and its environs. Deep Sea Res. II 43: 1437-2005.

Wiebe, P. H., R.C. Beardsley, A.C. Bucklin and D. G. Mountain (eds.). 2001. Coupled biological and physical studies of plankton populations: Georges Bank and related North Atlantic regions. Deep Sea Res. II 48: 1- 684.

Wiebe P., R. Beardsley, D. Mountain, and A. Bucklin. 2002. U.S. GLOBEC Northwest Atlantic/Georges Bank program. Oceanography 15:13–29.

Wiebe, P. H., R.C. Beardsley, D. Mountain and R.G. Lough (eds.). 2006. Dynamics of plankton and larval fish populations on Georges Bank, the North Atlantic U.S. GLOBEC Study Site. Deep Sea Res. II 23-24: 2455-2832.

Wirgin I., Kovach, A., Maceda, L., Roy, N.K., Waldman, J., and Berlinsky, D.L. 2007. Stock identification of Atlantic cod in U.S. waters using microsatellite and single nucleotide polymorphism (SNP) DNA analysis. Trans. Amer. Fish. Soc. 136: 375-391.

Xue, H., L. Incze, D. Xu, N. Wolff, and N. Pettigrew, 2008. Connectivity of lobster populations in the coastal Gulf of Maine. Part I: Circulation and larval transport potential. Ecol. Modelling. 210: 193-211.

Figure captions

Figure 1. Evidence for strong linkage between environmental conditions and fish recruitment in the coastal northwest Atlantic. (a) Mackerel recruitment (estimated from year class strength of corresponding 3-yr olds, as percentage of total population) in the southern Gulf of St. Lawrence is related to total copepod egg production rate during the larval feeding period. The data include two exceptional year classes of 1982 and 1999 (adapted from Castonguay et al. 2008). (b) Recruits per spawner index (log transformed) of Scotian Shelf haddock (including exceptional year classes in 1981 and 1999) is correlated with the timing of the spring bloom, estimated from analysis of satellite images of sea surface color (adapted from Platt et al. 2003). (c) Recruits per spawner index (log transformed) of Georges Bank haddock (including the exceptional year class in 2003) is related to the magnitude of the fall phytoplankton bloom prior to spawning (adapted from Friedland et al. 2008). (d) Recruits per spawner index (log-transformed) of western Gulf of Maine Atlantic cod (including strong year class in 2005) is related to downwelling winds in May between 1985-2005 (adapted from Churchill et al., Woods Hole Oceanographic Institution, unpublished manuscript). All regression lines are significant ($P \leq 0.003$).

Figure 2. Proposed structure for a system of linked, coupled physical-biological models to integrate data from observing systems, experimental studies and process oriented field studies. The rhomboids represent focus of each coupled model on one of three broad trophic levels, as discussed in de Young et al. (2004) and Runge et al. (2005).

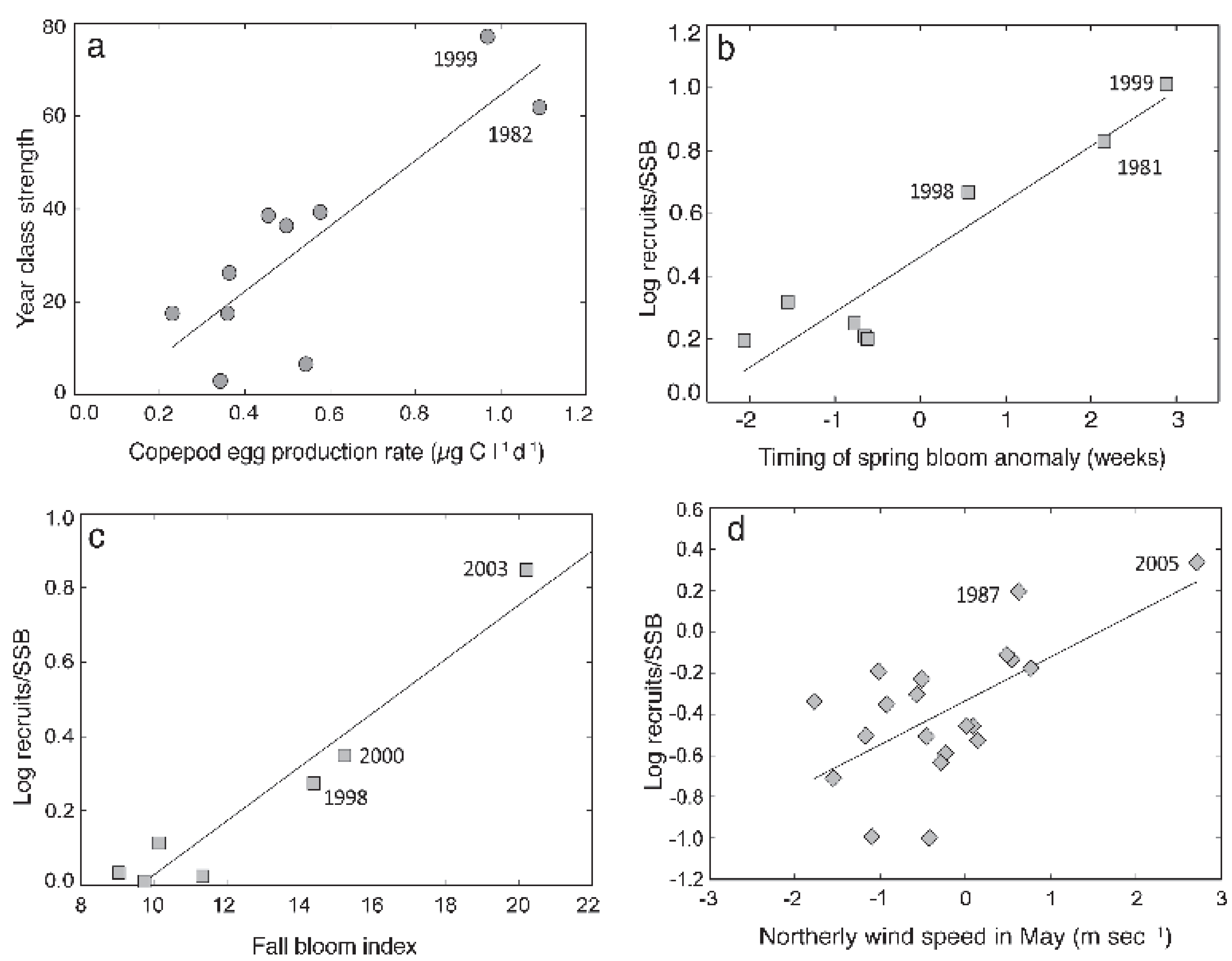
Figure 3. The western Gulf of Maine (50, 100 and 200 m contours) showing locations of NERACOOS and NOAA buoys (triangles) and fixed sampling stations (sampled between 2003-2009 during the University of New Hampshire COOA and Northeast Consortium PULSE programs; filled black circles), including the high frequency time series station “S” on Jeffreys Ledge. The genetic composition of spawning adults captured in the western Gulf and southern New England bight is indicated (purple circles: northern spring complex; red circles: southern complex). Circles represent presence of one or both populations, but do not show spatial extent of spawning areas or relative spawning biomass at each location. Present understanding (Huret et al. 2007; Hoffman et al., 2006; Hoffman et al. 2007; Kerr et al. 2009; Churchill et al., Woods Hole Oceanographic Institution, unpublished manuscript) indicates that the main spawning area supporting most of the northern spring (May-June) spawning biomass is located in Ipswich Bay, and that the main spawning area for the fall-winter spawning components of the southern complex is located in Massachusetts Bay.

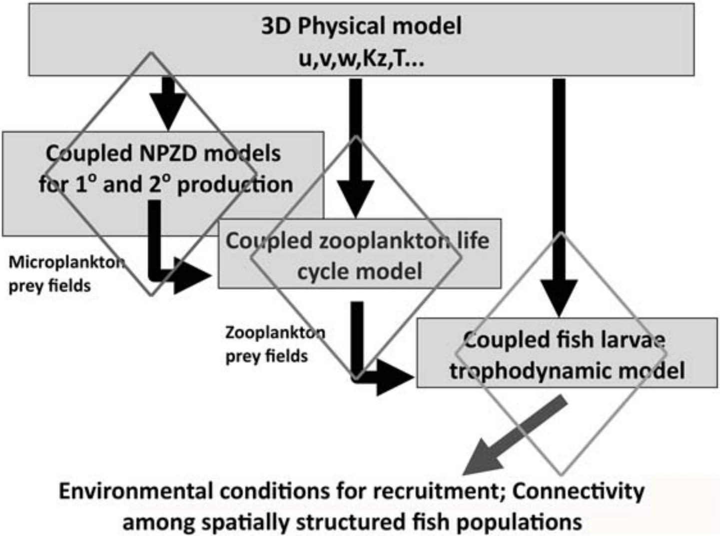
Figure 4. Monthly composites of satellite-measured surface chlorophyll concentrations in the western Gulf of Maine in winter (January) and late spring (May). The top panels show the 11-year (1998 – 2008) mean climatological pattern, and the middle and bottom panels show the climatological patterns in 2003 and 2005,respectively.

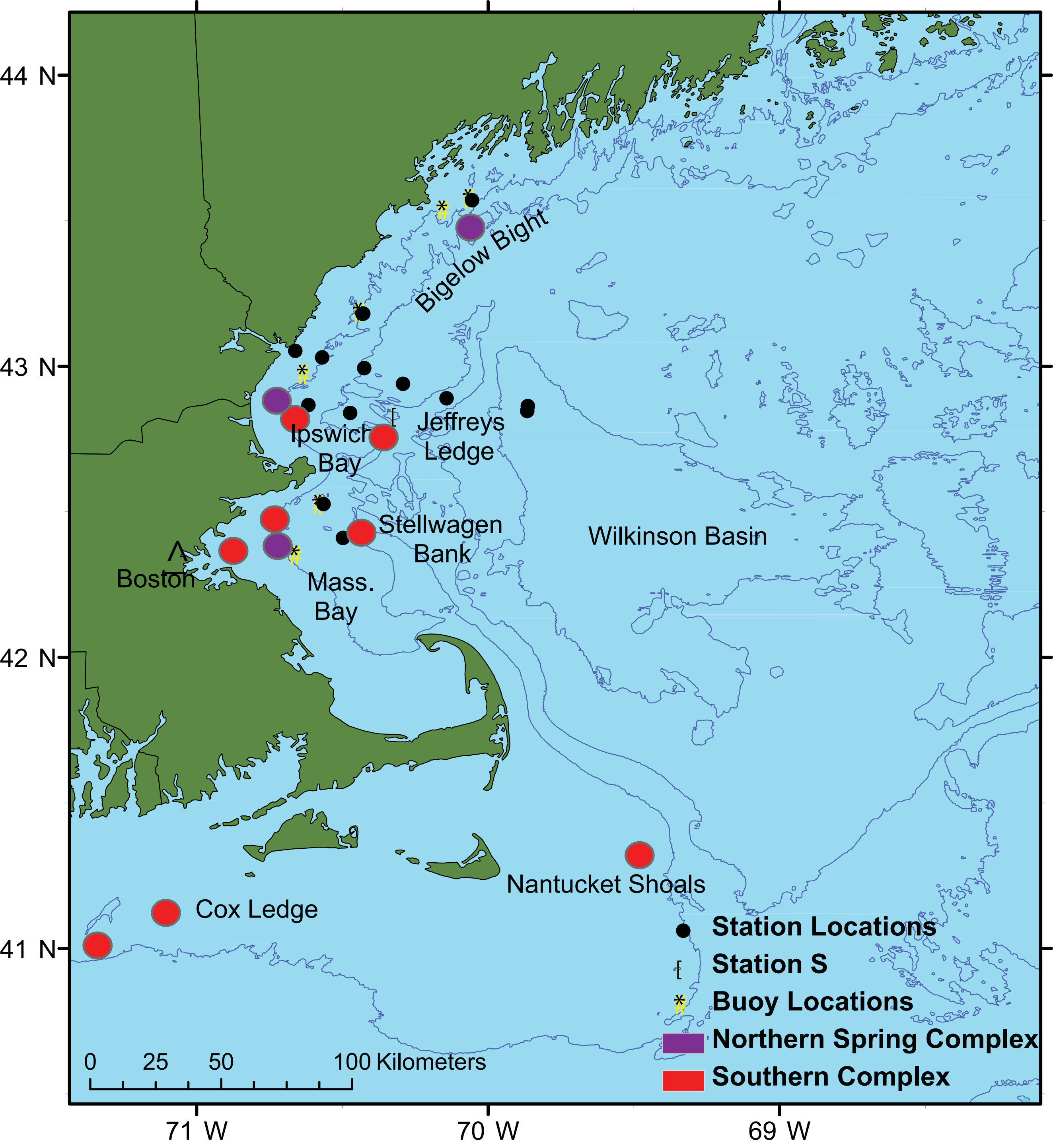
Figure 5. Model-computed distribution of January (left panel) and May (right panel) monthly mean chlorophyll concentration (mg m^{-3}) in the western Gulf of Maine. The model was initiated using December climatology of nitrogen and chlorophyll concentration, and forced with surface and open boundary conditions for year 1999.

Figure 6. Model-computed adult planktonic copepod distributions in the western Gulf of Maine for the months of January (left panels) and May (right panels) 1999. Panels a-b illustrate monthly mean *Pseudocalanus* spp. abundance (no. m^{-3}), and panels c-d illustrate monthly mean *Centropages typicus* abundance (no. m^{-3}). In both cases, the model was initiated using December climatology of species abundance and forced with 1999 surface and open boundary conditions (adapted from Ji et al. 2009). Panels e-f represent climatological modeled abundance and distribution of adult female *Calanus finmarchicus* (no. m^{-3}) based on a stage-resolved copepod model (Pershing et al. 2009). The climatology couples 2D climatological flow fields with satellite imagery and a biological model, and includes the years 1998-2006. In these images, near coastal *Calanus* distribution is not resolved; work is in progress to more accurately simulate coastal *Calanus* abundance using year-specific, high-resolution FVCOM flow fields plus data assimilation (Record et al. University of Maine, unpublished manuscript).

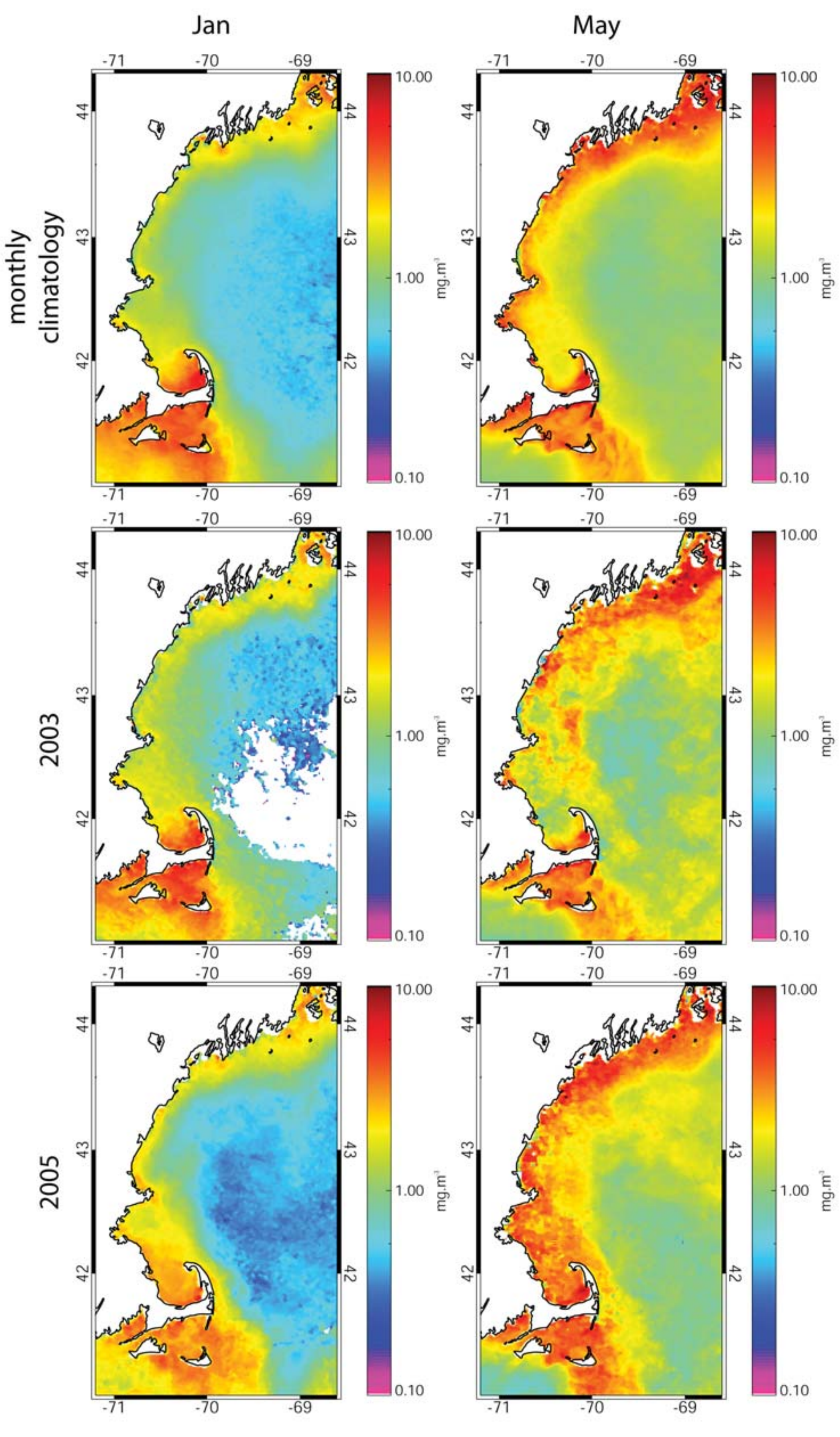
Figure 7. Left panel: Mean surface currents generated by the first-generation FVCOM in the western Gulf of Maine during May 1995. This representation approximates mean flows not driven by the local wind stress, as the mean wind in May, 1995 was negligible. The area shaded represents the modeled region of May egg release from the Ipswich Bay spawning area.
Right panel: interannual variability in simulated larval transport success to Ipswich Bay and Massachusetts Baynursery areas between 1995-2005, in relation to estimated mean northward wind velocity measured in the month of May at NOAA buoy 44013 off Boston Harbor (adapted from Churchill et al. Woods Hole Oceanographic Institution, unpublished manuscript).


a
Year class strength
Copepod egg production rate (μg C l⁻¹ d⁻¹)
1999
1982
b
Log recruits/SSB
Timing of spring bloom anomaly (weeks)
1999
1998
1981
c
Log recruits/SSB
Fall bloom index
2003
2000
1998
d
Log recruits/SSB
Northerly wind speed in May (m sec⁻¹)
2005
1987

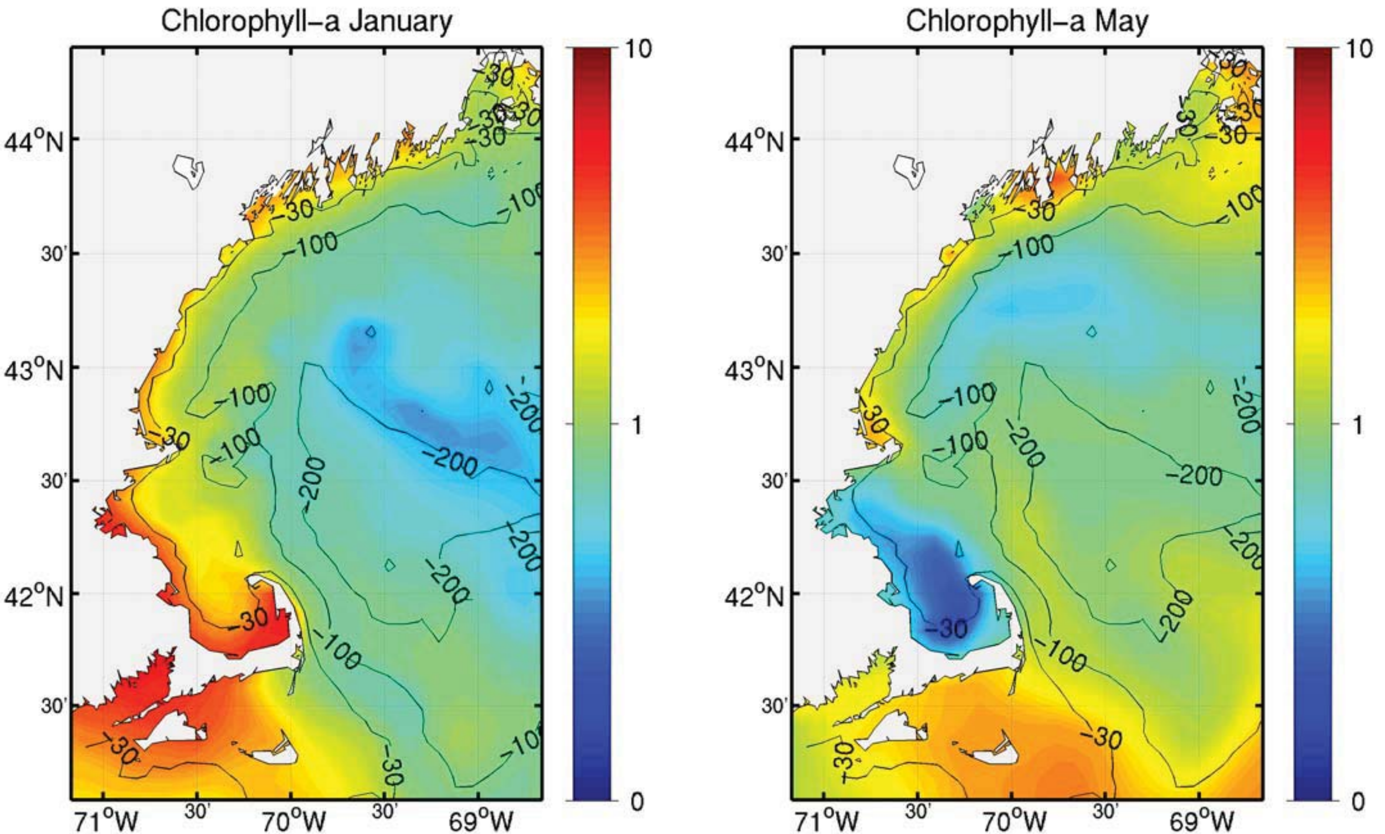

3D Physical model
u,v,w,Kz,T...
Coupled NPZD models
for 1° and 2° production
Microplankton
prey fields
Coupled zooplankton life
cycle model
Zooplankton
prey fields
Coupled fish larvae
trophodynamic model
Environmental conditions for recruitment; Connectivity
among spatially structured fish populations



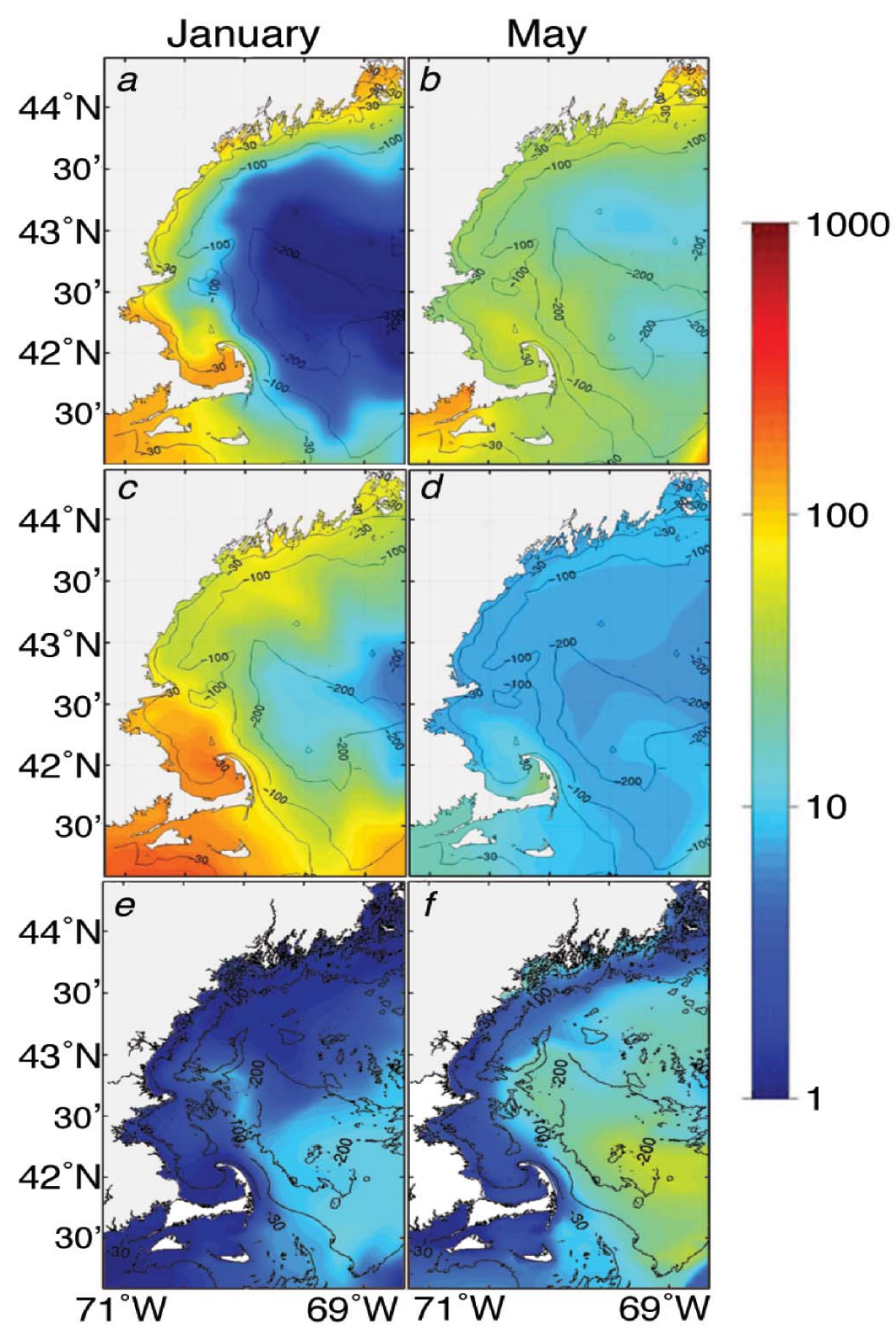
44 N
43 N
42 N
41 N
71 W
70 W
69 W
Bigelow Bight
Ipswich Bay
Jeffreys Ledge
Stellwagen Bank
Wilkinson Basin
Boston
Mass. Bay
Nantucket Shoals
Cox Ledge
0 25 50 100 Kilometers
Station Locations
Station S
Buoy Locations
Northern Spring Complex
Southern Complex



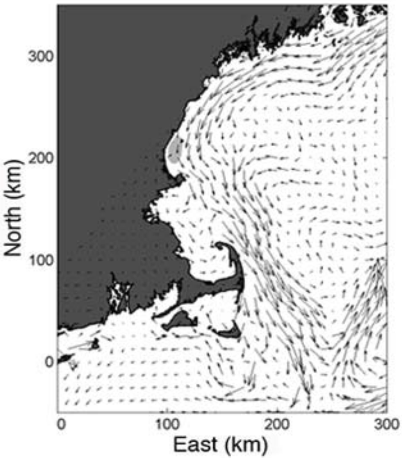
Jan
May
monthly climatology
2003
2005
-71
-70
-69
44
43
42
10.00
1.00
0.10
mg.m⁻³



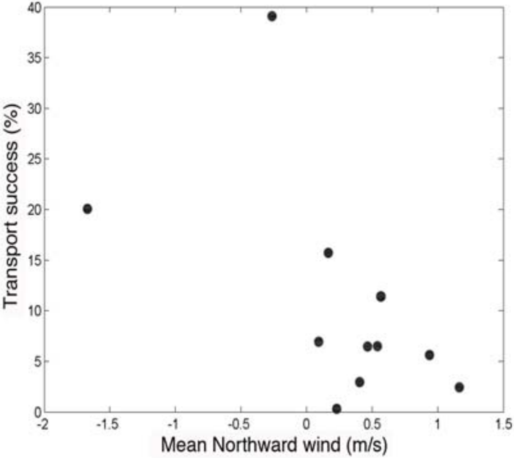
Chlorophyll-a January
Chlorophyll-a May
44°N
30'
43°N
30'
42°N
30'
71°W
30'
70°W
30'
69°W
10
1
0



January
May
a
b
c
d
e
f
44°N
30'
43°N
30'
42°N
30'
71°W
69°W
71°W
69°W
1000
100
10
1



North (km)
East (km)
0
100
200
300



Transport success (%)
Mean Northward wind (m/s)
0
5
10
15
20
25
30
35
40
-2
-1.5
-1
-0.5
0
0.5
1
1.5