ARTICLE IN PRESS

Progress in Oceanography xxx (2010) xxx–xxx

Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

Understanding climate impacts on recruitment and spatial dynamics of Atlantic cod in the Gulf of Maine: Integration of observations and modeling

Jeffrey A. Runge [a,*], Adrienne I. Kovach [b], James H. Churchill [c], Lisa A. Kerr [d], John R. Morrison [e], Robert C. Beardsley [f], David L. Berlinsky [g], Changsheng Chen [h], Steven X. Cadrin [i], Cabell S. Davis [j], Kathryn H. Ford [k], Jonathan H. Grabowski [o], W. Huntting Howell [l], Rubao Ji [m], Rebecca J. Jones [a], Andrew J. Pershing [a], Nicholas R. Record [a], Andrew C. Thomas [n], Graham D. Sherwood [o], Shelly M.L. Tallack [o], David W. Townsend [n]

[a] *School of Marine Sciences, University of Maine and Gulf of Maine Research Institute, 350 Commercial Street, Portland, ME 04101, USA*
[b] *Department of Natural Resources and the Environment, University of New Hampshire, 46 College Rd., Durham, NH 03824, USA*
[c] *Department of Physical Oceanography, Clark 304a, MS 21, Woods Hole Oceanographic Institution, Woods Hole, MA 02536, USA*
[d] *School for Marine Science & Technology, University of Massachusetts, Dartmouth, 200 Mill Road, Suite 325, Fairhaven, MA 02719, USA*
[e] *Northeastern Regional Association of Coastal Ocean Observing Systems (NERACOOS), Seacoast Science Center, 570 Ocean Blvd., Rye, NH 03870, USA*
[f] *Department of Physical Oceanography, Clark 343, MS 21, Woods Hole Oceanographic Institution, Woods Hole, MA 02536, USA*
[g] *Department of Biological Sciences, University of New Hampshire, 171 Spaulding Life Science Building, 38 College Rd., Durham, NH 03824, USA*
[h] *School for Marine Science & Technology, University of Massachusetts, Dartmouth, 706 South Rodney French Boulevard, New Bedford, MA 02744, USA*
[i] *NOAA/UMass Cooperative Marine Education and Research Program, 200 Mill Road, Suite 325 Fairhaven, MA 02719, USA*
[j] *Department of Biology, Redfield 2-20, MS 33, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA*
[k] *Massachusetts Division of Marine Fisheries, 1213 Purchase St. 3rd Floor, New Bedford, MA 02740, USA*
[l] *Department of Biological Sciences, University of New Hampshire, Spaulding Life Science Building, Durham, NH 03824, USA*
[m] *Department of Biology, Redfield 2-14, MS 33, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA*
[n] *School of Marine Sciences, University of Maine, Orono, ME 04469, USA*
[o] *Gulf of Maine Research Institute, 350 Commercial Street, Portland, ME 04101, USA*

ARTICLE INFO

Article history:
Available online xxxx

ABSTRACT

We put forward a combined observing and modeling strategy for evaluating effects of environmental forcing 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 within-decade 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 predator fields, usage of coastal habitat by juveniles and adult resident and migratory patterns, 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 in the United States (e.g., NOPP, 2006) 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

---

* Corresponding author. Tel.: +1 207 228 1652; fax: +1 207 772 6855.
E-mail addresses: jeffrey.runge@maine.edu (J.A. Runge), akovach@unh.edu (A.I. Kovach), jchurchill@whoi.edu (J.H. Churchill), lkerr@umassd.edu (L.A. Kerr), Ru.Morrison@neracoos.org (J.R. Morrison), rbeardsley@whoi.edu (R.C. Beardsley), david.berlinsky@unh.edu (D.L. Berlinsky), c1chen@umassd.edu (C. Chen), steven.cadrin@noaa.gov (S.X. Cadrin), cdavis@whoi.edu (C.S. Davis), kathryn.ford@state.ma.us (K.H. Ford), jgrabowski@gmri.org (J.H. Grabowski), whh@unh.edu (W.H. Howell), rji@whoi.edu (R. Ji), rjones@gmri.org (R.J. Jones), andrew.pershing@maine.edu (A.J. Pershing), nrecord@gmri.org (N.R. Record), thomas@maine.edu (A.C. Thomas), gsherwood@gmri.org (G.D. Sherwood), stallack@gmri.org (S.M.L. Tallack), davidt@maine.edu (D.W. Townsend).

0079-6611/$ - see front matter © 2010 Elsevier Ltd. All rights reserved.
doi:10.1016/j.pocean.2010.09.016

Please cite this article in press as: Runge, J.A., et al. Understanding climate impacts on recruitment and spatial dynamics of Atlantic cod in the Gulf of Maine: Integration of observations and modeling. Prog. Oceanogr. (2010), doi:10.1016/j.pocean.2010.09.016

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 (National Marine Fisheries Service, 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 (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 planktonic prey production with growth and survival of larvae. For example, 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 points to forcing by climatic variability acting on bottom-up processes. Change in

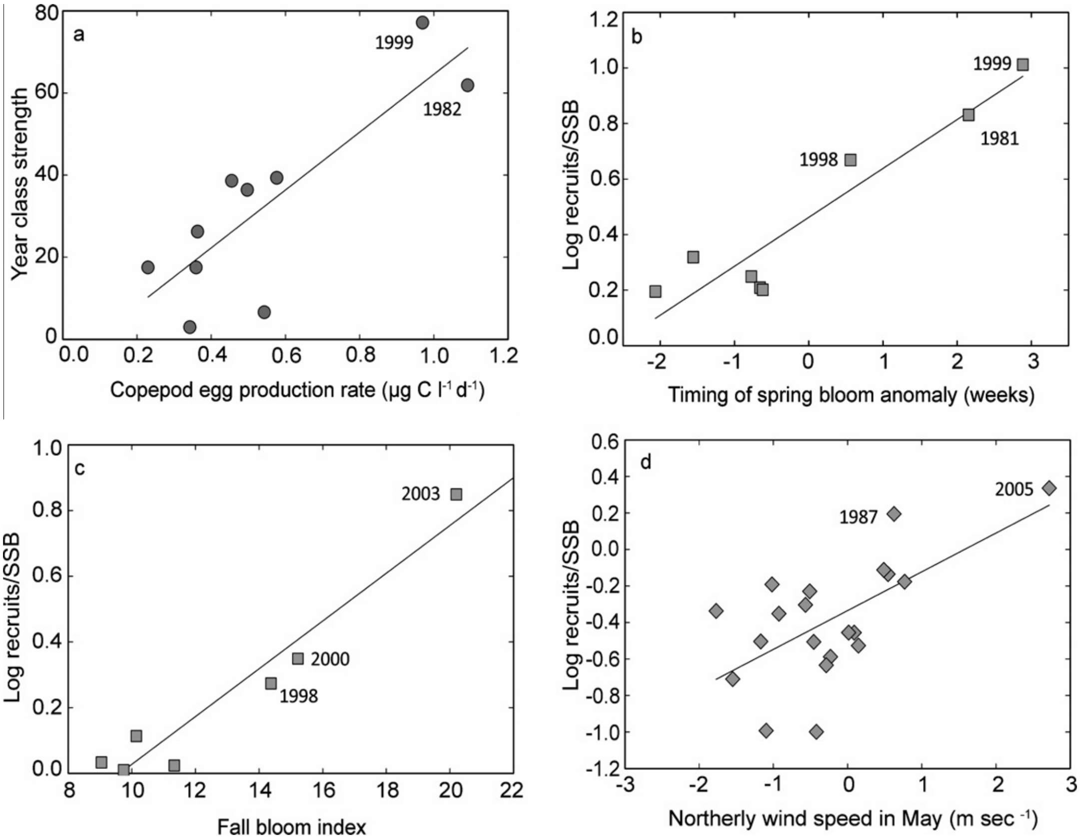

Fig. 1. Evidence for strong linkage between environmental conditions and fish recruitment in the coastal northwest Atlantic. (a) Mackerel recruitment (estimated from year class strength of corresponding 3-year olds, as percentage of total population) in the southern Gulf of St. Lawrence is related to 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 and 2005 (adapted from Churchill et al. (in press)). All regression lines are significant ($P \leqslant 0.003$).

Please cite this article in press as: Runge, J.A., et al. Understanding climate impacts on recruitment and spatial dynamics of Atlantic cod in the Gulf of Maine: Integration of observations and modeling. Prog. Oceanogr. (2010), doi:10.1016/j.pocean.2010.09.016

predation pressure during fish early life history, at the egg, larval or juvenile stage, may also influence recruitment success. This may result from changes to the abundance and diversity of predators at interannual or longer time scales or at seasonal scales related to changes in timing of spawning and hatch (e.g. Fortier and Quiñonez-Velazquez, 1998; Wieland et al., 2000; Lapolla and Buckley, 2005; Husebø et al., 2009). These changes may be related to variability in environmental forcing, but not necessarily.

In addition to biological factors influencing early life stage survival, recruitment success may be directly related to physical processes in the atmosphere and ocean (Hjort, 1914; Sinclair, 1988). 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 inter-decadal 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. (in press) 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.

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 (LCMs: Fig. 2). They review the status of, and challenges confronting, each coupled physical biological component.

Here we explore the feasibility of using coupled physical–biological models as an integrative tool for understanding climate forcing of Atlantic cod and other fish populations, using the Atlantic cod stock in the Gulf of Maine as an example. Drawing on results of the GLOBEC Georges Bank/Northwest Atlantic program and other research in the Gulf of Maine over the past decade, we review the present status of coupled physical–biological modeling as it applies to Atlantic cod in the western Gulf of Maine ecosystem. We examine existing observing data and explore the potential for the future regional observing system to supply data needed for model development, operation and validation. We develop a vision for integration of observing activities with coupled physical–biological modeling to provide forecasts of environmental conditions for recruitment in the context of 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 as part of the broader spatial dynamics of Gulf of Maine Atlantic cod, including population-specific juvenile habitat and connectivity among populations.

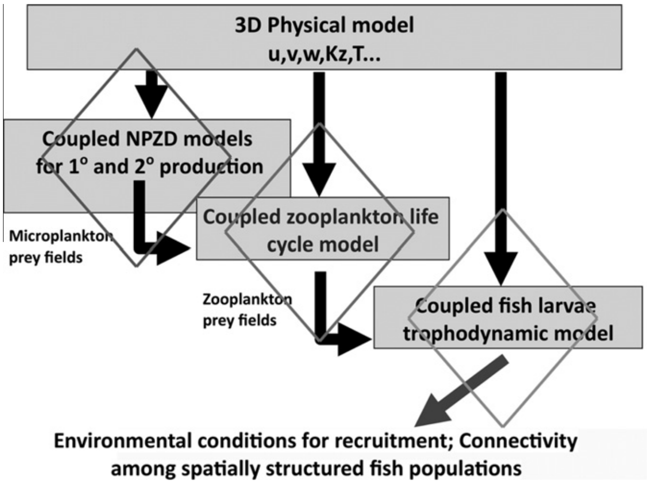

Fig. 2. Proposed structure for a system of linked, coupled physical–biological models to integrate data from observing systems, experimental studies and process oriented field studies. The rhomboids represent focus of each coupled model on one of three broad trophic levels, as discussed in de Young et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

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 and 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).

In the Gulf of Maine, Atlantic cod populations also appear to be structured on a fine scale, via the presence of spatially and temporally divergent spawning populations, some of which are genetically distinct (Wirgin et al., 2007; Kovach et al., 2010). Analysis of historical data by Ames (2004) suggests that there were once multiple sites of cod spawning along the Gulf of Maine coast. These spawning aggregations could be indicative of a number of subpopulations or one larger mixed population with multiple spawning sites. The number of active spawning sites has contracted considerably over the past few decades, however. Currently, known sites of consistently active spawning within U.S. waters (the Gulf of Maine, southern New England, and 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 et al., 2005; Fig. 3). 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 the Gulf of Maine stock can be explained by two major groupings: a northern spring coastal complex and a southern complex (Kovach et al., 2010; 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. Thus, these temporally divergent spawning groups overlap spatially: 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. A third population representing the Georges Bank stock spawns on the northeast peak of Georges Bank in the

Please cite this article in press as: Runge, J.A., et al. Understanding climate impacts on recruitment and spatial dynamics of Atlantic cod in the Gulf of Maine: Integration of observations and modeling. Prog. Oceanogr. (2010), doi:10.1016/j.pocean.2010.09.016

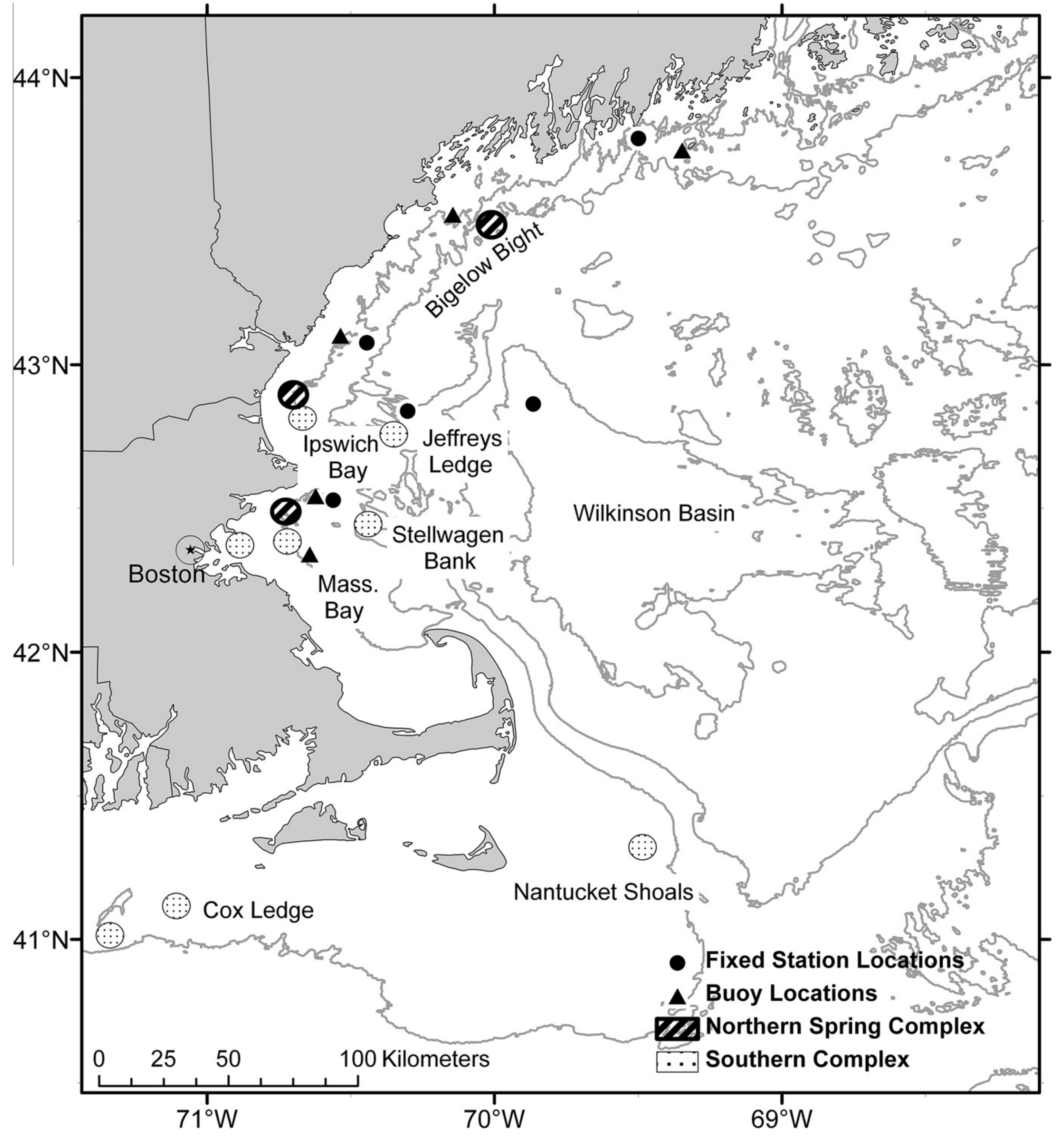

Fig. 3. The western Gulf of Maine (50, 100 and 200 m contours) showing locations of NERACOOS and NOAA buoys (triangles) and representative fixed sampling stations (sampled between 2003 and 2009 during the University of New Hampshire COOA and Northeast Consortium PULSE programs) proposed for long-term observing of zooplankton in coastal waters. The northeastern flank of Georges Bank is not shown. The genetic composition of spawning adults captured in the western Gulf and southern New England Bight is indicated. Large 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, 2007; Kerr et al., 2009) 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.

late winter. Fish within this spawning complex are differentiated from the southern Gulf of Maine complex, but only weakly differentiated or similar to fish of the northern spring complex. This genetic population structure is inconsistent with the current management model, which recognizes two stocks in US waters: a single Gulf of Maine stock and another stock consisting of cod from Georges Bank and adjacent areas to the south. Cod movement data from recent tagging studies also contradict the two-stock management model (Tallack, 2009), as did the results of earlier genetic studies (Lage et al., 2004; Wirgin et al., 2007).

The development of modeling tools to understand and predict bottom-up forcing of recruitment processes in Gulf of Maine

Please cite this article in press as: Runge, J.A., et al. Understanding climate impacts on recruitment and spatial dynamics of Atlantic cod in the Gulf of Maine: Integration of observations and modeling. Prog. Oceanogr. (2010), doi:10.1016/j.pocean.2010.09.016

Atlantic cod must take into account this 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. We address these issues in the following sections. In Section 3, we examine the present status of observing activities needed to provide data on present status and change of Gulf of Maine environmental conditions relevant to the Atlantic cod stock complex. In Section 4, we review the present status of physical–biological modeling relevant to the two Gulf of Maine populations. In Section 5, we discuss what needs to be done to integrate the observations and modeling into to assess and forecast environmental conditions for recruitment. In Section 6, we explore modeling of the spatial dynamics of Gulf of Maine Atlantic cod, in which environmental conditions for recruitment is part of the total life history of the cod populations.

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 system data that can provide understanding of the environmental contrasts influencing cod recruitment along the coastal Gulf of Maine. In addition to results from the GLOBEC Georges Bank/Northwest Atlantic program (e.g. Wiebe and Beardsley, 1996; Wiebe et al., 2001, 2002; Beardsley et al., 2003; Wiebe et al., 2006 and articles therein; Mountain et al., 2008), 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, from ship based collections by the University of New Hampshire Coastal Observing Center and Northeast Consortium supported projects (precursors to the present NERACOOS), and from moored and ship collected data in Massachusetts and Cape Cod Bays, funded by the Massachusetts Water Research Authority.

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 seven 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 larval transport in the Gulf of Maine 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, 2006; Townsend, 1991, 1998; Townsend and Ellis, 2010). Over the last four decades, the nutrient regime in the Gulf of Maine has been changing. Townsend et al. (2010) provide evidence that since the 1970s, the deeper waters in the interior Gulf of Maine (>100 m) have become fresher and cooler, with lower nitrate but higher silicate concentrations. They argue that these changes are related to accelerated ice 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 year to date) time series of nutrients has also been collected in Casco Bay by D. Townsend (http://www.grampus.umeoce.maine.edu/dave/homepage.htm). The Massachusetts Water Resources Authority (MWRA) time series, ongoing since 1992, includes measurement of nutrients, as well as salinity, temperature, chlorophyll concentration and other observations, at a suite of stations ranging in depth from 25 to 80 m in Massachusetts Bay (e.g. Libby et al., 2009).

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 US funded 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., 2008a,b). These chlorophyll time series show that the dominant events of primary

Please cite this article in press as: Runge, J.A., et al. Understanding climate impacts on recruitment and spatial dynamics of Atlantic cod in the Gulf of Maine: Integration of observations and modeling. Prog. Oceanogr. (2010), doi:10.1016/j.pocean.2010.09.016

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-derived 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 are being acquired by the US National Marine Fisheries Service using the Continuous Plankton Recorder (CPR) and seasonal bongo net surveys (ECOMON), and by the Canadian Department of Fisheries and Oceans under the Atlantic Zonal Monitoring Program (AZMP). These time series have shown 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).

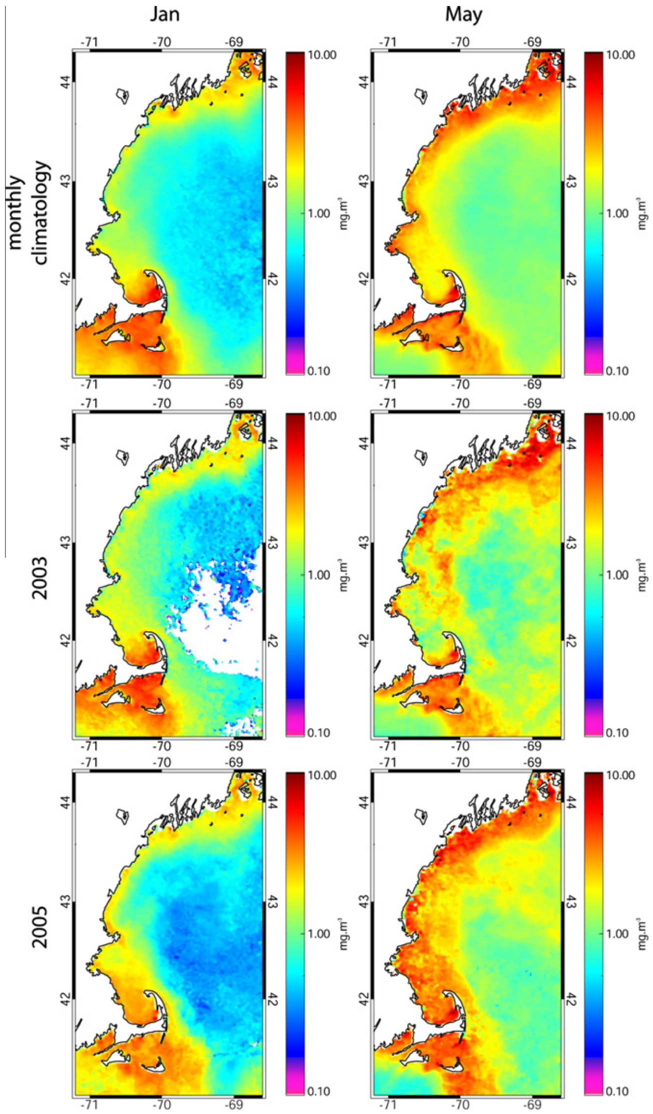

Fig. 4. Monthly composites of satellite-measured surface chlorophyll concentrations in the western Gulf of Maine in winter (January) and late spring (May). The top panels show the 11-year (1998–2008) mean climatological pattern, and the middle and bottom panels show the climatological patterns in 2003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

The present long-term zooplankton sampling series, however, do not necessarily represent zooplankton variability in the near coastal regions. Measurements of shorter duration (2–6 years) time series of zooplankton abundance and composition, employing sampling protocols similar to the AZMP time series, have been carried out between 2003 and 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 (e.g., Fig. 3). The time series includes data from 2004–2006, among the wettest years on record for the western Gulf of Maine. The results (Runge and Jones, in press) 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 frequency of sampling (2–3 times per month) allows for smoothing of variability at individual sample dates and allows depiction of seasonal variability in abundance and species diversity in the coastal plankton. 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 and 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 Atlantic Canada have confirmed that YOY cod associate with structured habitats such as sea grass beds and cobble/boulder habitat with high relief (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 and Anderson, 1997). Although juvenile cod may become more exposed to visual predators at shallow depths, many of the refuge habitats (i.e., seagrass beds, kelp) noted above that promote higher cod recruitment occur at these shallow depths. In general, predation risk is high during the early life-history stages of cod, which is reflected in their depth distribution and habitat use patterns.

Time series observations of juvenile cod are conducted by the National Marine Fisheries Service (NMFS), the Maine Department of Marine Resources and the Massachusetts Division of Marine Fisheries. 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

Please cite this article in press as: Runge, J.A., et al. Understanding climate impacts on recruitment and spatial dynamics of Atlantic cod in the Gulf of Maine: Integration of observations and modeling. Prog. Oceanogr. (2010), doi:10.1016/j.pocean.2010.09.016

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 an integral part of monitoring cod nursery habitat. The Commonwealth 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. Collection of spatial high resolution data every 5–10 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

Here we review present status of modeling to integrate observing system data for understanding bottom-up forcing of the western Gulf of Maine ecosystem and environmental conditions for cod recruitment, 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. The Marine Ecosystem Dynamics Modeling Laboratory at the University of Massachusetts, Dartmouth (http://www.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://www.rocky.umeoce.maine.edu/GoMPOM/). This 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 North Carolina State University (http://www.4.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). The Northeast Coastal and Ocean Data Partnership (www.necodp.org) has established a modeling committee to encourage discoverability, accessibility and interoperability of model output in the Gulf of Maine. It has recently launched the ‘‘Gulf of Maine Interoperability Pilot Project” (http://www.necodp.org/committees/modeling-committee/gulf-of-maine-model-interoperability-pilot-project) whose purpose is to promote easy and standardized access to the output from these various circulation models.

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 examine mechanistically the influence of local and external forcing on phytoplankton bloom dynamics and primary production (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,

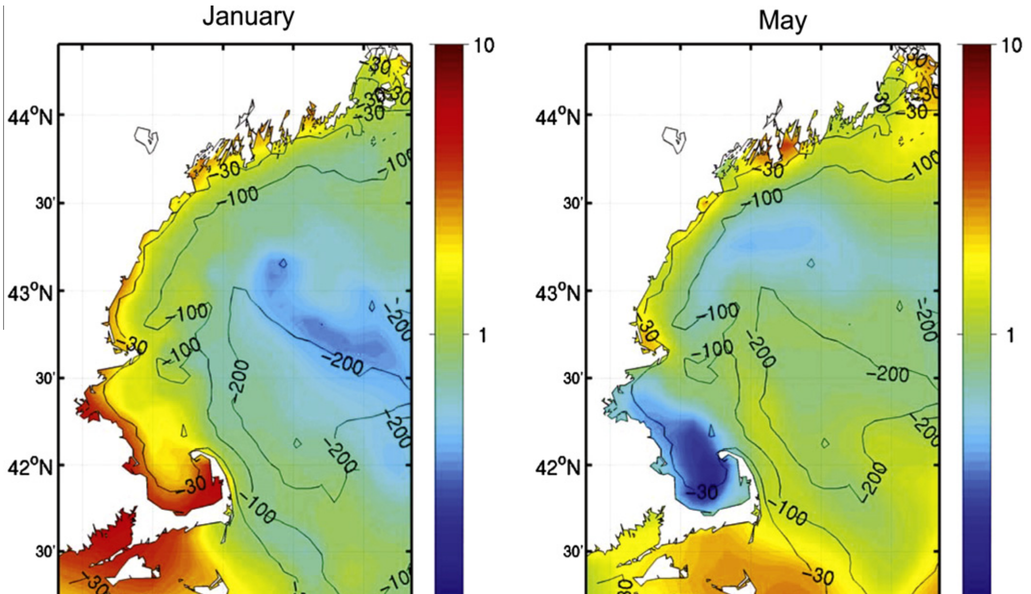

Fig. 5. Model-computed distribution of January (left panel) and May (right panel) monthly mean chlorophyll concentration (mg m^{-3}) in the western Gulf of Maine. The model was initiated using December climatology of nitrogen and chlorophyll concentration, and forced with surface and open boundary conditions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

Please cite this article in press as: Runge, J.A., et al. Understanding climate impacts on recruitment and spatial dynamics of Atlantic cod in the Gulf of Maine: Integration of observations and modeling. Prog. Oceanogr. (2010), doi:10.1016/j.pocean.2010.09.016

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) allow for the possibility of simulating the abundance and production of the dominant copepods in the Gulf of Maine. Ji and colleagues at the Woods Hole Oceanographic Institution and the U. Mass. 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). 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-derived 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. 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.

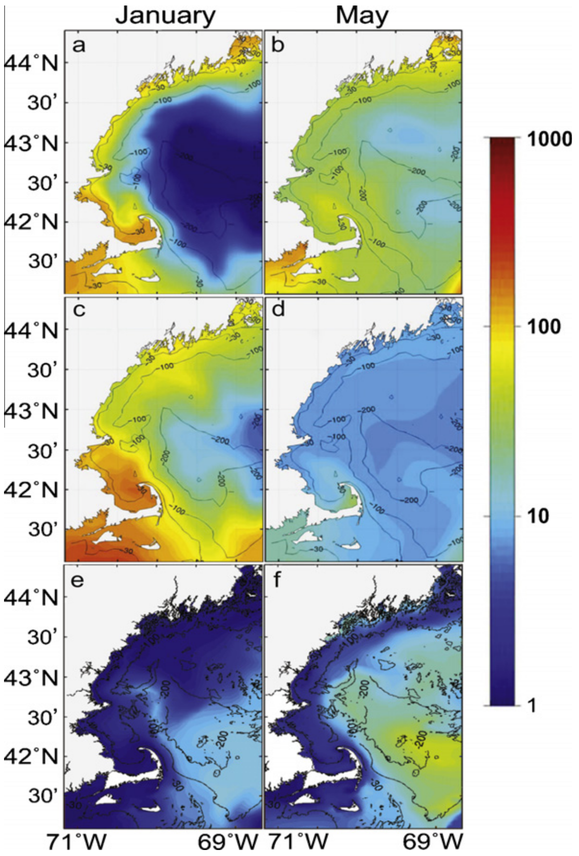

Fig. 6. Model-computed adult planktonic copepod distributions in the western Gulf of Maine for the months of January (left panels) and May (right panels) 1999. Panels a and b illustrate monthly mean *Pseudocalanus* spp. abundance (No. m^{-3}), and panels c and d illustrate monthly mean *Centropages typicus* 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, unpubl.).

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, growth and mortality 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., 2006a,b). The initial study (Huret et al., 2007) was confined to the 1995 spawning period. More recently Churchill et al. (in press) 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).

Several IBMs of cod feeding and growth have been developed by Lough et al. (2005), Vikebø et al. (2007), Kristiansen et al. (2009a,b) and Petrik et al. (2009). 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. Kristiansen et al. (2009a) concluded that larval cod prey selection on Georges Bank is dependent on light, ease of capture and relative abundance of its prey. Kristiansen et al. (2009b) further showed the dependence of larval cod growth on daylength and temperature in addition to prey abundance. Larval mortality may be estimated as composed of size-dependent invertebrate predation and predation from visual piscivores that changes with light intensity. These models may be supplied with forecasts of the copepod prey fields and estimates of predator fields to indicate environmental conditions for growth and survival of the early cod life-history stages.

5. Integration of modeling and data: 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 environmental influences on population-rich species such as Atlantic cod on time scales of months to several years. 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,

Please cite this article in press as: Runge, J.A., et al. Understanding climate impacts on recruitment and spatial dynamics of Atlantic cod in the Gulf of Maine: Integration of observations and modeling. Prog. Oceanogr. (2010), doi:10.1016/j.pocean.2010.09.016

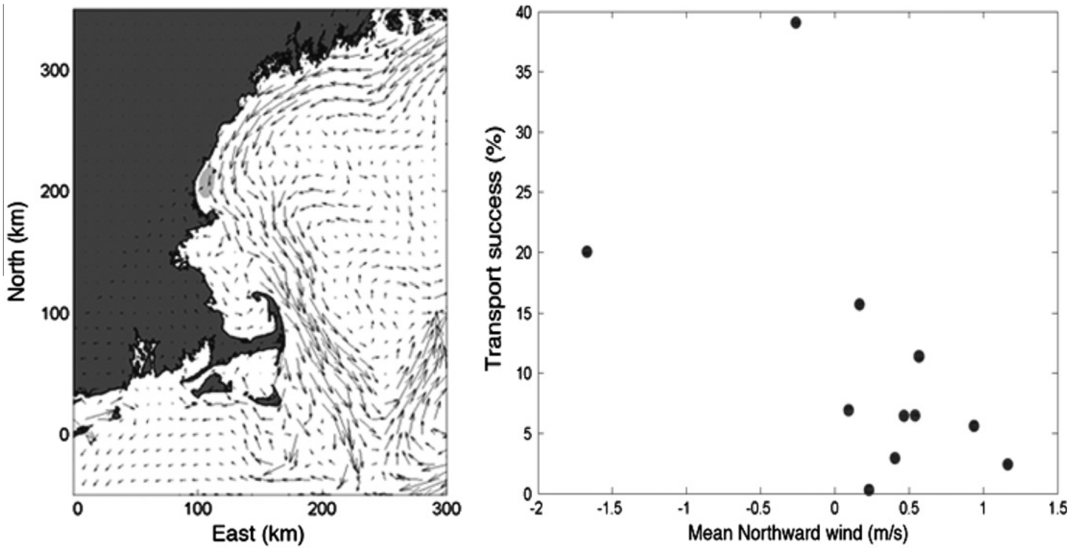

Fig. 7. Left panel: Mean surface currents generated by the first-generation FVCOM in the western Gulf of Maine during May 1995. This representation approximates mean flows not driven by the local wind stress, as the mean wind in May, 1995 was negligible. The area shaded represents the modeled region of May egg release from the Ipswich Bay spawning area. Right panel: interannual variability in simulated larval transport success to Ipswich Bay and Massachusetts Bay nursery areas between 1995 and 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. (in press)).

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; Daewel et al., 2008; 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. The skill of the coupled models and LCM system can be evaluated in hindcast mode and refined over time with the addition of the new observational data collected each year. The models then can be used to project environmental conditions for recruitment over the medium term (i.e. within a decade) using regional forecasts of ocean and climate conditions from larger-scale ocean and climate models. This approach to understanding spatial dynamics of recruitment variability in 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.

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). Highlighted was a critical need for regional infrastructure that would: (1) facilitate regional model evaluation, including skill assessment, evaluation of uncertainty, and model ensemble approaches to predictions; (2) serve to link data analyses, modeling and prediction capabilities to specific regional management needs; (3) facilitate coordination among government agencies, research institutions, and universities; and (4) develop and demonstrate environmental analysis and forecast products that could be implemented operationally. Recommendations included establishment of a Regional Modeling Center, which may involve a coordinating entity (NERACOOS) and distributed output of observations and modeling to desktop computers of researchers and resource managers via standards-based tools, and/or a Gulf of Maine Experimental Environment Forecast Center, whose primary objective would be to develop, test and refine forecast models that could then be adapted for delivery to decision-makers after tailoring of output to end-user needs. The word “experimental” refers to forecast models that are not operational, but rather can be seen as precursors for the development of operational models, in that the experimental forecast predictions may be expected to fail. Experimental environmental forecasting encourages a critical feedback process, in which model forecasts can be readily compared with new data, which in turn can lead to refinements in both models and the observing system which result in improved predictive capabilities in future model iterations.

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., 2010). 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 3-D coupled model can then interact with the observing

Please cite this article in press as: Runge, J.A., et al. Understanding climate impacts on recruitment and spatial dynamics of Atlantic cod in the Gulf of Maine: Integration of observations and modeling. Prog. Oceanogr. (2010), doi:10.1016/j.pocean.2010.09.016

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 US 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 (US 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 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 of 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 meets 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 the coastal Gulf of Maine (e.g., Fig. 3) 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 can be enhanced by the addition of available and developing technology to the present observing system, as well as establishment of several strategically located coastal fixed stations. 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. (in press) 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 on potential larval cod predators (e.g. euphausids and herring) in certain areas in response to significant events, such as the appearance of a spawning fish aggregation, could be met by surveys with broadband acoustic systems operating at the upper range of resonance frequencies (e.g. Stanton et al., 2010) in combination with the addition of acoustic systems installed on remotely controlled autonomous vehicles to the part of the NERACOOS suite of instrument systems. A small number of fixed stations visited semimonthly (following the Canadian AZMP protocol) would contribute time series of physical, chemical and biological variables not presently amenable to acquisition by available technology. These include regular salinity, temperature and pH profiles, particulate carbon and chlorophyll a by conventional methods (for ground truthing of satellite sensors and data processing methods), and assessment of zooplankton abundance and diversity, for life cycle analysis and documentation of changes in biodiversity and phenology (e.g., Ji et al., 2010).

6. 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 addresses habitat, growth, movement and mortality of fish beyond the planktonic larval 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 (e.g., Kerr et al., 2010). 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,

Please cite this article in press as: Runge, J.A., et al. Understanding climate impacts on recruitment and spatial dynamics of Atlantic cod in the Gulf of Maine: Integration of observations and modeling. Prog. Oceanogr. (2010), doi:10.1016/j.pocean.2010.09.016

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.

7. Concluding remarks

Our conclusion is that it is feasible to develop forecasts of environmental conditions for recruitment into Gulf of Maine Atlantic cod populations by integrating observations acquired from a regional observing system with linked coupled physical–biological models that provide mechanistic understanding of key Gulf of Maine ecosystem properties and species dynamics. This combination of observations and modeling provides a mechanistic characterization of many processes not directly represented in stock assessment models and therefore represents a complimentary view of cod early life history that could aid in the interpretation of the stock assessment results.

The linked coupled model system addresses time scales of months to a decade in terms of outlook for recruitment success. The accuracy of forecasts will depend on the abilities of basin-scale ocean climate models or statistical analysis of trends based on climate indicators to provide reasonable climate scenarios over these time scale, which can then be downscaled to project conditions in the northwest Atlantic. While this remains a challenging frontier of climate science, recent research indicates substantial improvements in predictive skill over the medium term (Smith et al., 2007; Keenlyside et al., 2008). Additional sources of error include the ability of the model system to capture interannual and longer term changes in mortality of cod eggs and larvae due to predators, although this source of error can be constrained by inclusion of observed trends in abundance of dominant predators (e.g. herring and euphausids) and timing of spawning in forecast scenarios. The combination of forecasting of environmental conditions for recruitment with an age structured cod life history model that includes population specific dynamics, behavior and connectivity among populations would have value for spatial management of Atlantic cod and protection of individual populations from overexploitation (Reich and DeAlteris, 2009; Kerr et al., 2010).

In order to implement this integration of observations and modeling in the Gulf of Maine, changes would be needed to the regional research infrastructure. Development of increasingly sophisticated multidisciplinary models with forecasting capability integrated with an observing system and the complex process of transitioning these research models to management applications are beyond the scope of regional academic research activities, although these play an important role. Ways forward, discussed at a number of regional workshops (Runge and Braasch, 2005), involve establishment of organizational infrastructure as discussed in Section 5.1. This new infrastructure may be possible through collaboration of relevant US government agencies, in particular the National Oceanic and Atmospheric Administration (NOAA), with NERACOOS, the regional observing association, and CINAR (Cooperative Institute for the North Atlantic Region), a NOAA cooperative institute of academic institutions.

While the time scale envisioned here is medium term, the analysis by Rothschild (2007) also suggests a role for an integrated model-observing system in the Gulf of Maine/Northwest Atlantic to understand environmental and plankton changes on the interdecadal scale as well. Coherent, decadal-scale increases and declines in spawning stock biomass in populations of cod across the Northwest Atlantic occurred during periods of relatively low fishing mortality and the major declines occurring between 1985 and 1992 were associated with reduced growth rates, implying a strong negative environmental signal, perhaps due to dynamics of the plankton. Looking forward, testing of decadal-scale environmental hypotheses involving plankton to explain major fluctuations in cod population abundance becomes possible with adequate observing of changes in the plankton combined with coupled physical–biological models continuously refined to account for changes in dominant planktonic species. The observing–modeling system we have outlined here would contribute to tests of this environmental hypothesis for the Gulf of Maine and Georges Bank; conceivably a similar system could also be developed in other regions, for example the Scotian Shelf. In general, by providing a mechanistic characterization of the impact of physical conditions on cod, the observing–modeling system could be used to detect and understand periodic regime-shifts observed in these populations. Driven by global scale general circulation and climate projections, the models have the potential to provide estimates of population responses to long-term climate change. These long-term projections are beyond the scope of empirical stock assessment models.

Finally, we have focused here on Atlantic cod populations in the Gulf of Maine as an example application of integrated observations and modeling. A similar approach could be adopted to address environmental conditions for recruitment and spatial population dynamics of other key species in the regional ecosystem, e.g. Atlantic herring. The physical, ecosystem and zooplankton life cycle models as well as the data requirements supporting them are basically the same; the models depicting larval trophic dynamics, transport, and spatial population dynamics (e.g. Kerr et al., 2010) would be particular to the species in question.

Acknowledgements

This paper represents a contribution to the final workshop of the ICES Cod and Climate Change program, held at the 3rd GLOBEC Open Science Meeting. We thank F. Maps, A. Doubleday and L. Fenderson for assistance, and Ian Perry and two anonymous reviewers for thoughtful comments. Awards from the NOAA Center for Sponsored Coastal Ocean Research, Northeast Consortium, NOAA Fisheries and the Environment (FATE) program, National Science Foundation under Grant Numbers OCE-0814413, 0815051 and 0815336, and the NSF Coupled Natural and Human Systems program (0709518) are gratefully acknowledged. This is contribution number 677 to the US GLOBEC program.

References

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.

Andrews, J.M., Gurney, W.S.C., Heath, M.R., Gallego, A., O'Brien, C.M., Darby, C., Tyldesley, G., 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., Drapeau, D.T., Bowler, B.C., Booth, E.S., Windecker, L.A., Ashe, A., 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.

Beardsley, R.C., Smith, P.C., Lee, C.M., 2003. Introduction to special section: US GLOBEC: physical processes on Georges Bank (GLOBEC). J. Geophys. Res. 108 (C11), 8000. doi:10.1029/2003JC002165, 2003.

Brown, W.S., Gangopadhyay, A., Bub, F.L., Yu, Z., Strout, G., Robinson, A.R., 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., Gangopadhyay, A., Yu, Z., 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.

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

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

Chen, C., Cowles, G., Beardsley, R.C., 2006a. An Unstructured Grid, Finite-Volume Coastal Ocean Model: FVCOM User Manual, second ed. SMAST/UMASSD Technical Report-06-0602, p. 315.

Chen, C., Beardsley, R.C., Cowles, G., 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., Huang, H., Beardsley, R.C., Liu, H., Xu, Q., Cowles, G., 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., Pettigrew, N.R., Signell, R.P., 2005. Structure and variability of the western Maine coastal current. Deep-Sea Res. II 52, 2392–2410.

Churchill, J., Runge, J., Chen, C., in press. Processes controlling retention of spring-spawned Atlantic cod (*Gadus morhua*) in the western Gulf of Maine and their relationship to an index of recruitment success. Fish. Oceanogr.

Cote, D., Moulton, S., Scruton, D.A., McKinley, R.S., 2001. Microhabitat use of juvenile Atlantic cod in a coastal area of Bonavista bay, Newfoundland. Trans. Amer. Fish. Soc. 130, 1217–1223.

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

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., Horwood, J.W., 1994. The growth and death of fish larvae. J. Plankton Res. 16, 291–300.

Daewel, U., Peck, M., Kühn, W., St. John, M.A., Alekseeva, I., Schrum, C., 2008. Coupling ecosystem and individual-based models to stimulate the influence of environmental variability on potential growth and survival of larval sprat (*Sprattus sprattus* L.) in the North Sea. Fish. Oceanogr. 17, 333–351.

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

Dickey, T., Bates, N., Byrne, R.H., Chang, G., Chavez, F.P., Feely, R.A., Hanson, A.K., Karl, D.M., Manov, D., Moore, C., Sabine, C.L., Wanninkhof, R., 2009. The NOPP O-SCOPE and MOSEAN projects, advanced sensing for ocean observing systems. Oceanography 22, 168–181.

Durbin, E.G., Campbell, R.G., Casas, M.C., Ohman, M.D., Niehoff, B., Runge, J., Wagner, M., 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.

Fortier, L., Quiñonez-Velazquez, C., 1998. Dependence of survival on growth in larval pollock Pollachius virens and haddock Melanogrammus aeglefinus: a field study based on individual hatchdates. Mar. Ecol. Prog. Ser. 174, 1–12.

Friedland, K.D., Hare, J.A., Wood, G.B., Col, L.A., Buckley, L.J., Mountain, D.G., Kane, J., Brodziak, J., Lough, R.G., Pilskaln, C.H., 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., Neuheimer, A.B., Campbell, R.G., 2008. Modelling copepod development: current limitations and a new realistic approach. ICES J. Mar. Sci. 63, 399–413.

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

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

Gotceitas, V., Fraser, S., Brown, J.A., 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., Pershing, A.J., 2007. Climate drives sea change. Science 315, 1084–1085.

Gregory, R.S., Anderson, J.T., 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., Carvalho, G.R., 2008. Paradigm shifts in marine fisheries genetics: ugly hypotheses slain by beautiful facts. Fish Fish. 9, 333–362.

He, R., McGillicuddy, D., Keafer, B., Anderson, D., 2008. Gulf of Maine Circulation and Harmful Algal Bloom in Summer 2005: Part 2: Bio-physical Numerical Modeling. J. Geophys. Res. 113, C07040, doi:10.1029/2007JC004602.

Heath, M.R., Lough, R.G., 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., Kunzlik, P.A., Gallego, A., Holmes, S.J., Wright, P.J., 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., Hinckley, S., Megrey, B., Napp, J.M., 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.

Hjort, J., 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-V. Réun. Cons. Int. Explor. Mer. 20, 1–228.

Hoffman, W.S., Salerno, D.J., Correia, S.J., 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, p. 37.

Hoffman, W.S., Correia, S.J., 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, p. 45.

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

Huret, M., Runge, J., Chen, C., Cowles, G., Xu, Q., Pringle, J., 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.

Husebø, Å., Stenevik, E., Slotte, A., Fossum, P., Salthaug, A., Vikebø, F., Aanes, S., Folkvord, A., 2009. Effects of hatching time on year-class strength in Norwegian spring-spawning herring (*Clupea harengus*). ICES J. Mar. Sci. 66, 1710–1717.

Hutchinson, W.F., Carvalho, G.R., Rogers, S.I., 2001. Marked genetic structuring in localized 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., Davis, C., Chen, C., Beardsley, R., 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. Syst. 73, 31–47.

Ji, R., Davis, C., Chen, C., Townsend, D., Mountain, D., Beardsley, R., 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., Davis, C., Chen, C., Beardsley, R., 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.

Ji, R., Edwards, M., Mackas, D., Runge, J., Thomas, A., 2010. Marine plankton phenology and life history in a changing climate: Current research and future directions. J. Plankton Res. 32 (10), 1355–1368.

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

Jorde, P.E., Knutsen, H., Espeland, S.H., Stenseth, N.C., 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.

Keafer, B.A., Churchill, J.H., McGillicuddy, D.J., Anderson, D.M., 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.

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

Keenlyside, N.S., Latif, M., Jungclaus, J., Kornblueh, L., Roeckner, E., 2008. Advancing decadal-scale climate prediction in the North Atlantic sector. Nature 453, 84–88.

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

Kerr, L.A., Cadrin, S.X., Secor, D.H., 2010. Simulation modelling as a tool for examining the consequences of spatial structure and connectivity to local and regional population dynamics. ICES J. Mar. Sci. 67, 1631–1639.

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

Kovach, A.I., Breton, T.S., Berlinsky, D.L., Maceda, L., Wirgin, I., 2010. Fine-scale and temporal genetic structure of cod off the Atlantic coast of the USA. Mar. Ecol. Prog. Ser. 410, 177–195.

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

Kristiansen, T., Vikebo, F., Sundby, S., Huse, G., Fiksen, O., 2009b. Modeling growth of larval cod (gadus morhua) in large-scale seasonal and latitudinal gradients. Deep-Sea Res. 59, 2001–2011.

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

Lapolla, A., Buckley, L.J., 2005. Hatch date distributions of young-of-year haddock *Melanogrammus aeglefinus* in the Gulf of Maine/Georges Bank region: implications for recruitment. Mar. Ecol. Prog. Ser. 290, 239–249.

Libby, P.S., Anderson, D.M., Borkman, D.G., Geyer, W.R., Keller, A.A., Oviatt, C.A., Turner, J.T., 2009. 2008 Water Column Monitoring Results. Boston. Massachusetts Water Resources Authority. Report 2009-12. 31 p. plus appendices. <http://www.mwra.state.ma.us/harbor/enquad/trlist.html>.

Lin, P., Ji, R., Davis, C., McGillicuddy, D., 2010. Optimizing plankton survey strategies using observing system simulation experiments. J. Mar. Syst. 82, 187–194.

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

Linehan, J.E., Gregory, R.S., Schneider, D.C., 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., Barrick, D.E., 1983. Least-squares methods for the extraction of surface currents from CODAR cross-loop data: application at ARSLOE. IEEE J. Ocean. Eng. OE-8, pp. 226–253.

Liu, G., Chai, F., Xue, H., Thomas, A., 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., Buckley, L.J., Werner, F.E., Quinlan, J.A., Edwards, K.P., 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., Holbrook, M.J., Naimie, C.E., 1997. The Maine coastal current: spring climatological circulation. Cont. Shelf Res. 17, 605–634.

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

Manning, J.P., McGillicuddy, D.J., Pettigrew, N.R., Churchill, J.H., Incze, L.S., 2009. Drifter observations of the Gulf of Maine coastal current. Cont. Shelf Res. 29, 835–845.

Mountain, D., Green, J., Sibunka, J., Johnson, D., 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., Cadigan, N.G., 1993. Is juvenile natural mortality in marine demersal fish variable? Can. J. Fish. Aquat. Sci. 50, 1591–1598.

National Marine Fisheries Service, 2009. Report to Congress: The State of Science to Support an Ecosystem Approach to Regional Fishery Management. US Dep. Commerce, NOAA Tech. Memo. NMFS-F/SPO-96, 24 p.

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

NOPP (National Oceanographic Partnership Program), 2006. The first US Integrated Ocean Observing System (IOOS) development plan. National Office for Integrated and Sustained Observations, Ocean. US Publication 9, 86 p.

Pampoulie, C., Ruzzante, D.E., Chosson, V., Jörundsdóttir, T.D., Taylor, L., Thorsteinsson, V., Daneílsdóttir, A.K., Marteinsdóttir, G., 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., 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.

Pershing, A.J., Record, N.R., Monger, B.C., Pendleton, D.E., Woodard, L.A., 2009. Model-based estimates of *Calanus finmarchicus* abundance in the Gulf of Maine. Mar. Ecol. Prog. Ser. 378, 227–243.

Petrik, C.M., Kristiansen, T., Lough, R.G., Davis, C.S., 2009. Prey selection of larval haddock and cod on copepods with species-specific behavior: a model-based analysis. Mar. Ecol. Prog. Ser. 396, 123–143.

Pettigrew, N.R., Townsend, D.W., Xue, H., Wallinga, J.P., Brickley, P.J., Hetland, R.D., 1998. Observations of the Eastern Maine Coastal Current and its offshore extensions in 1994. J. Geophys. Res. 103, 30623–30639.

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

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

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

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

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

Reich, D.A., DeAlteris, J.T., 2009. A simulation study of the effects of spatially complex population structure for Gulf of Maine Atlantic cod. N. Am. J. Fish. Manage. 29, 116–126.

Rothschild, B.J., 2007. Coherence of Atlantic cod stock dynamics in the northwest Atlantic Ocean. Trans. Am. Fish. Soc. 136, 858–874.

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. Hydrobiology 167–168, 61–71.

Runge, J.A., Braasch, E., 2005. Modeling Needs Related to the Regional Observing System in the Gulf of Maine. RARGOM Report 05-01, pp. 1–79. <http://www.rargom.org>.

Runge, J.A., Jones, R.J., in press. Results of a collaborative project to observe coastal zooplankton and ichthyoplankton abundance and diversity in the western Gulf of Maine: 2003–2008. In: Watson, J., Stephenson, R., Annala, J., Hall-Arber, M. (Eds.), Advancing Ecosystem Research for the Gulf of Maine. American Fisheries Society.

Runge, J.A., Franks, P.J.S., Gentleman, W.C., Megrey, B.A., Rose, K.A., Werner, F.E., Zakardjian, B., 2005. Diagnosis and prediction of variability in secondary production and fish recruitment processes: developments in physical–biological modeling. In: Robinson, A.R., Brink, K. (Eds.), The Sea, vol. 13. Harvard University Press, Cambridge, Massachusetts, pp. 413–474.

Schlitz, R.J., Cohen, E.B., 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.

Smith, D.M., Cusack, S., Colman, A.W., Folland, C.K., Harris, G.R., Murphy, J.M., 2007. Improved surface temperature prediction for the coming decade from a global climate model. Science 317, 796–799.

Stanton, T.K., Chu, D., Jech, J.M., Irish, J.D., 2010. New broadband methods for resonance classification and high-resolution imagery of fish with swimbladders using a modified commercial broadband echosounder. ICES J. Mar. Sci 67, 365–378.

Swain, D.P., 1993. Age- and density dependent bathymetric patterns of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. 50, 1255–1264.

Tallack, S.M., 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, pp. 1–76.

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

Townsend, D.W., 1991. Influences of oceanographic processes on the biological productivity of the Gulf of Maine. Rev. Aquat. Sci. 5, 211–230.

Townsend, D.W., 1998. Sources and cycling of nitrogen in the Gulf of Maine. J. Mar. Syst. 16, 283–295.

Townsend, D.W., Ellis, W.G., 2010. Primary production and nutrient cycling on the Northwest Atlantic continental shelf. In: Liu, K.-K., Atkinson, L., Quiñones, R., Talaue-McManus, L. (Eds.), Carbon and Nutrient Fluxes in Continental Margins: A Global Synthesis, IGBP Book Series. Springer, Berlin, pp. 234–248. 744 p + XXVIII.

Townsend, D.W., Christensen, J.P., Stevenson, D.K., Graham, J.J., Chenoweth, S.B., 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., Thomas, A.C., Mayer, L.M., Thomas, M., Quinlan, J., 2006. Oceanography of the Northwest Atlantic Continental Shelf. In: Robinson, A.R., Brink, K.H. (Eds.), The Sea, vol. 14. Harvard University Press, Cambridge, Massachusetts, pp. 119–168.

Townsend, D.W., Rebuck, N.D., Thomas, M.A., Karp-Boss, L., Gettings, R.M., 2010. A changing nutrient regime in the Gulf of Maine. Cont. Shelf Res. 30, 820–832.

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

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

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

Wiebe, P.H., Beardsley, R.C., Bucklin, A.C., Mountain, D.G., 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., Beardsley, R., Mountain, D.G., Bucklin, A.C., 2002. US GLOBEC Northwest Atlantic/Georges Bank program. Oceanography 15, 13–29.

Wiebe, P.H., Beardsley, R.C., Mountain, D.G., Lough, R.G., 2006. Dynamics of plankton and larval fish populations on Georges Bank, the North Atlantic US GLOBEC study site. Deep-Sea Res. II 23–24, 2455–2832.

Wieland, K., Jarre-Teichmann, A., Horbowa, K., 2000. Changes in the timing of spawning of Baltic cod: possible causes and implications for recruitment. ICES J. Mar. Sci. 57, 452–464.

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

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

Please cite this article in press as: Runge, J.A., et al. Understanding climate impacts on recruitment and spatial dynamics of Atlantic cod in the Gulf of Maine: Integration of observations and modeling. Prog. Oceanogr. (2010), doi:10.1016/j.pocean.2010.09.016