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Advances in Understanding Ecosystem Structure and Function in the Gulf of Maine

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Abstract.—Here we summarize presentations given at the theme session "Structure and Function of the Gulf of Maine System" of the 2009 Gulf of Maine Symposium—Advancing Ecosystem Research for the Future of the Gulf, covering a broad spectrum of multidisciplinary research underway in one of the world's most intensively studied marine systems. Our objective was to attempt a synthesis of the current ecological and oceanographic understanding of the Gulf of Maine and, in particular, to document progress in these areas since the 1996 Gulf of Maine Ecosystem Dynamics Symposium more than a decade earlier. Presentations at the session covered issues ranging from habitat structure and function, biodiversity, population structure, trophic ecology, the intersection of the biological, chemical and physical oceanography of the region, and the dynamics of economically important species. Important strides in characterizing the broader dimensions of biodiversity in the region, the establishment of new sampling programs and the availability of new sensor arrays, and the renewed emphasis synthesis and integration to meet the emerging needs for ecosystem-based management in the gulf have all contributed to a deepened appreciation of its dynamical structure. The critical importance of the ecosystem goods and services provided by the gulf, and the factors affecting the sustainable delivery of these services, was clearly demonstrated in the course of the session. The papers presented at the session made it clear how far we have come and how far we need to go to ensure the sustainable delivery of these services into the future.

Introduction

An understanding of ecosystem structure and function requires identification and enumeration of the species comprising the system, as well as information on the interrelationships among these species. We further require documentation of patterns of energy flow and utilization, spatial characteristics and interchange among system components, and the role of external stressors, including climate and fishing in system dynamics. The theme session "Structure and Function of the Gulf of Maine System" at the 2009 Gulf of Maine Symposium—Advancing Ecosystem Research for the Future of the Gulf provided new and important insights into these issues. Here, ecosystem structure refers to fundamental organi-

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zational elements of the system, including the species present and their attributes (e.g., abundance, distribution, and ecological roles), and aspects of the physical environment (nutrients and their distribution/availability, environmental characteristics, etc.) that affect the biological components. Factors affecting ecosystem function include the interrelationships among species, related considerations of the transfer of energy among system components, nutrient cycling, and stabilizing mechanisms. The interwoven issues of biological diversity, interspecific interactions, and functional redundancy of species or species groups can hold important implications for the overall stability and functioning of the system and its likely response to natural and anthropogenic forcing factors. A recurrent theme of dramatic temporal and spatial change on a range of scales within the gulf emerged in presentations throughout the session. This theme was neatly foreshadowed in the keynote addresses by K. Frank (Fisheries and Oceans Canada, Bedford Institute of Oceanography) and J. Hare (National Marine Fisheries Service, Northeast Fisheries Science Center) that opened our session. As shown by Hare, the Gulf of Maine (GoM) has undergone dramatic alteration in fundamental structural aspects that can be tracked on multidecadal to centennial time scales (see also Hare and Kane 2012, this volume). Change on seasonal to interannual time scales is no less evident, and emerging issues, such as the possibility of important change in phenology, deserve urgent attention. The prospect of future climate change in the gulf highlights the need to understand its current status and past changes as related to anthropogenic and natural forcing factors. In complex systems, surprise is to be expected, and the possibility of rapid change to alternate stable states must be anticipated, as beautifully illustrated by Frank at the symposium.

This theme session covered a broad spectrum of topics, including advances in understanding of (1) patterns of biodiversity (largely focused on species richness); (2) nutrient dynamics, biogeochemical cycling, and biophysical coupling; (3) plankton community dynamics; and (4) upper trophic level and fishery resource dynamics. Our objective was to document progress in these areas since the 1996 Gulf of Maine Ecosystem Dynamics Symposium. Synthesizing recent research on the structure and function of the ecosystem has assumed greater importance, as the impetus to move toward ecosystem-based management (EBM) has gained momentum at both the national and international levels.

An important dimension to the progress since the last symposium, and very much evident in this theme session, is the development of enhanced sampling and analytical tools and the implementation of new research and monitoring programs in the GoM. Advances in genomics have made possible the identification of previously underrepresented microbial components. The now routine use of satellite observations for estimation of chlorophyll concentration on fine spatial and temporal scales has revolutionized our ability to document critical ecosystem processes related to bloom dynamics and overall levels of productivity. Advanced in situ sampling tools, ranging from gliders to coastal observatories, have provided important adjuncts to traditional sampling devices in the gulf. Isotopic signatures have been examined in investigations ranging from identification of GoM water mass characteristics to diet composition and trophodynamics. The establishment of new monitoring programs, such as the Gulf of Maine North Atlantic Time Series (1998–present), since the last symposium, has allowed fine-scale resolution of nutrients, hydrography, chlorophyll concentration, and primary production along a transect in the gulf. Finally, advances in high-end computing resources have opened important avenues for the development of coupled physical-biological models with data assimilation capabilities.

In the following, we summarize findings related to each of the four major theme areas identified above and place them in the context of recently published sources of information for this system. We then turn our attention to the implications for EBM in the region.

Patterns of Biodiversity

Since the last GoM symposium, our understanding of patterns of species richness, and its distribution in space and time, has increased substantially with the implementation of a major research program established under the auspices of the Census of Marine Life (CoML; Incze et al., in press). The Gulf of Maine is an extensively studied system with a long history of ecological research conducted by an impressive concentration of research facilities distributed along its coast. As a result, the species composition of mid- and upper-trophic levels, in particular, is well known, and the ecological roles of many of these species have been intensively studied. What is strikingly evident in the years since the last GoM symposium is the increase in knowledge of other components of the system. As noted by L. Incze (University of Southern Maine) and colleagues at the symposium, as a result of the CoML initiative, more than 50,000 new viral and bacterial operational taxonomic units have now been recognized (W. Li, Fisheries and Oceans Canada, Bedford Institute of Oceanography, unpublished data), which represents 20% of the maximum global estimate of bacterioplankton diversity. In addition, a Gulf of Maine Register of Marine Species (GoMRMS) has now been created by CoML, with a provisional total of more than 4,000 species represented. Important new insights have also been gleaned from studies conducted on a broad spectrum of spatial and temporal scales. These include a new CoML Discovery Corridor initiative, encompassing a broad swath from the intertidal through deep basins in the gulf to the edge of the Continental Shelf and beyond (Figure 1), as described at the symposium by P. Lawton (Fisheries and Oceans Canada) and colleagues.

Cobscook Bay, Maine (Figure 1) has long been recognized as a macroinvertebrate biodiversity hotspot (e.g., Larsen 2004). In our session, T. Trott (Suffolk University) confirmed that macroinvertebrate species richness at this site is indeed higher than any other sampled site in the GoM and is comparable to that of estimates for the highest biodiversity sites globally available for comparison from the Arctic to subtropical systems.

Increased sampling continues to augment the list of macroinvertebrates known to inhabit the GoM. A. Holmes and G. Pohle (Huntsman Marine Science Center) noted 38 species, previously unreported in the gulf, as part of the Discovery Corridor initiative, in samples collected in Jordan basin (Figure 1). S. Hale (Environmental Protection Agency) provided new insights into nearshore biogeographical patterns of macroinvertebrates in the gulf at the meeting (see Hale 2012, this volume). He reported faunal breaks within the Acadian province in relation to environmental factors, dominated by temperature patterns.

In an earlier study to examine changes in benthic biodiversity in the gulf, Link (2004) used fish stomachs as samplers of benthic communities for the northeast shelf to look at relative abundance and distribution of major benthic macrofauna, compared to surveys from earlier in the 1900s. Link found relatively stable levels of biodiversity of benthic fauna found in predator stomachs, but with declines evident in caprellids, cumaceans, and pagurids.

For zooplankton communities, sustained monitoring in the GoM, based on the Continuous Plankton Recorder (CPR) program by the National Marine Fisheries Service, has shown variation in decadal-scale species composition, as reported by Hare in his keynote address at the session. The CPR transect in the GoM runs from Boston, Massachusetts to Yarmouth, Nova Scotia (Figure 1). N. Record and A. Pershing (University of Maine) further described east–west gradients in plankton species diversity (with highest diversity in the west along the CPR Boston–Yarmouth transect: see Figure 1) and an increase in biodiversity, peaking in the 1990s.

Changes in the diversity of fish species on decadal to centennial scales have been documented in the Gulf of Maine. It has been possible to examine evidence of temporal changes in biodiversity of fish through a careful comparison of samples collected in two research programs separated by a century, as described by J. Cournane and S. Claesson (University of New Hampshire) at the session. Higher levels of fish biodiversity were found in the most recent sampling period (using the National Marine Fisheries Service trawl survey database), relative to an earlier survey conducted by the U.S. Fish Commission (principally using beam trawls). However, the biodiversity in combined fish and invertebrate catches was higher in the earlier period (for further information, see Cournane 2010). The sampling efficiencies of the sampling gears for benthic and fish species differed markedly for the two periods, explaining a substantial part of the observed differences, although the effects of fishing and environmental change also appear to be important. Further work is required to disentangle these important sources of variation.

The History of Marine Animal Populations (HMAP) project of CoML has also provided cru-

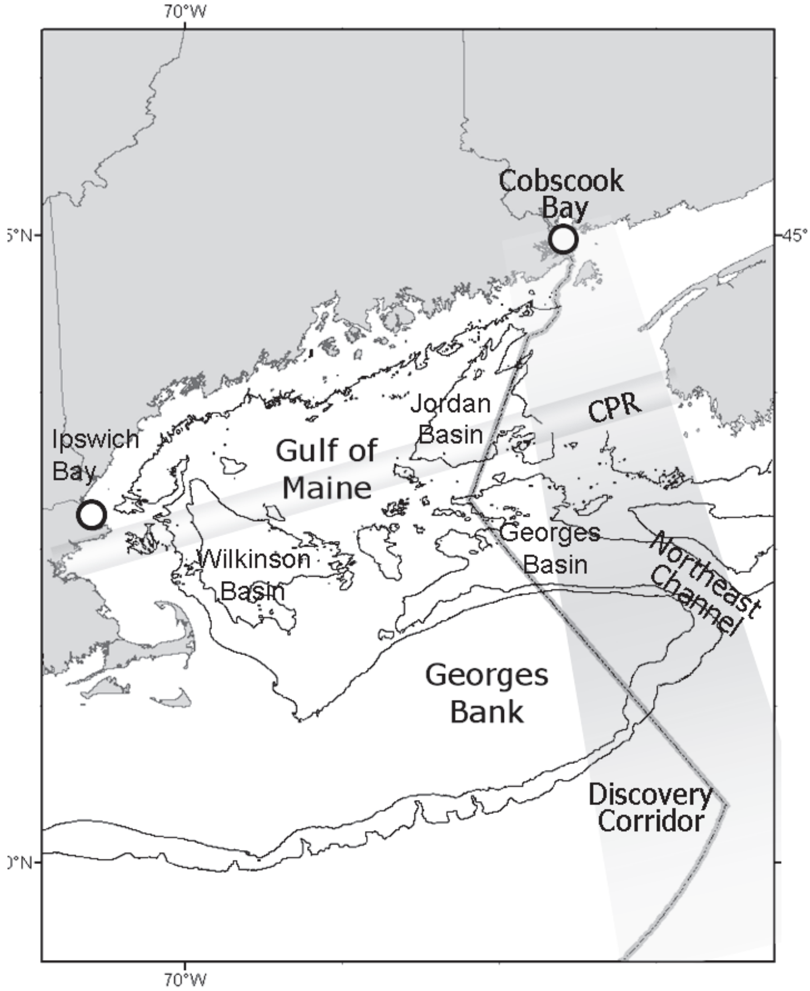

FIGURE 1. Map of the Gulf of Maine with major topographic features identified. The locations for the Continuous Plankton Recorder (CPR) transect (Boston, Massachusetts to Yarmouth, Nova Scotia) and the Census of Marine Life Discovery Corridor are indicated. Location of coastal areas (Ispwich Bay and Cobscook Bay) mentioned in the text are also shown.

cial insights into changes in system structure in the GoM on centennial time scales (e.g., Jackson et al. 2001; Bourque et al. 2008). This program has demonstrated an overall loss in complexity, biodiversity, and abundance of larger fish. In particular, coastal GoM systems, such as kelp forests (Jackson et al. 2001; Steneck et al. 2004; Bourque et al. 2008) and estuaries (Leavenworth 2008), have seen dramatic losses in species abundance and ecosystem complexity on centennial time scales. More recently (over the past four decades), however, a general increase in nekton species richness has been found for the GoM and Georges Bank (Link et al. 2002), reflecting, in part, a recent redistribution of more southerly species into the region as water temperatures have increased, particularly during the past decade

Nutrient Dynamics, Biogeochemical Cycling, and Biophysical Coupling

Our understanding of the general oceanography of the GoM and Georges Bank, as well as the coastal and estuarine systems in the region, has without doubt greatly advanced since the last GoM workshop in 1996, particularly with respect to biophysical processes and sources, and cycling of carbon and nutrients. The general features of the system, including specific discussions of these issues, have been reviewed by Townsend et al. (2006). That review covers many of the advances made since 1996 as part of several major research programs, both on Georges Bank (the U.S. GLOBEC program) and in the greater GoM, in relation to red tides (National Oceanic and Atmospheric Organization's ECOHAB [Ecology and Oceanography of Harmful Algal Blooms] program). There is, however, an additional wealth of information available not included in that review. For example, the review does not include the Gulf of Maine Ocean Observing System (GoMOOS), which only became operational in the spring of 2001, as well as results of numerous other smaller research projects that have been completed and published. Special issues of the journals *Deep-Sea Research Part II* and *Journal of Geophysical Research* have been produced that detail much—but not all—of the research results from the U.S. GLOBEC Program (Wiebe et al. 2001, 2006; Beardsley et al. 2003), and the GoM ECOHAB research program (Anderson et al. 2005). Indeed, those volumes alone contain more than 1,700 pages of articles that have significantly advanced our level of understanding since 1996. Furthermore, the online availability of ocean mooring data, satellite imagery, and physical circulation models (GoMOOS and University of Maine) makes any synopsis of where we currently stand, with respect to our scientific advancement, a rapidly moving target.

While constituting a large and complex oceanographic system, the gulf operates almost in oceanographic isolation from the open northwest Atlantic Ocean, in that it is a semi-enclosed shelf sea. It has been known since Bigelow (1927) that at depths greater than 100 m, the exchange of waters between the gulf and the North Atlantic is limited, with much of exchange confined to the deep (>220 m) Northeast Channel (Figure 1) that separates Georges Bank from Browns Bank and the Scotian Shelf. However, more recent studies reported at this workshop are beginning to show that this exchange may be changing in overall character, driven by the indirect effects of global warming and increased melting in the Arctic (Townsend et al. 2010). It now appears that shelf waters from Nova Scotia, with origins in the Labrador Sea, are becoming more important to the GoM's water properties, including its dissolved inorganic nutrient loads, than the deep influxes through the Northeast Channel.

The gulf's physical characteristics, with its deep basins and limited deepwater exchanges with the open Atlantic, are coupled with other important features and processes that act together to control the general oceanography of the gulf, including nutrient fluxes and biological productivity. These features and processes include vertical mixing by tides; the seasonal cycle of heating and cooling, which leads to winter convection and vertical stratification in summer; pressure gradients from density contrasts set up by deepwater inflows and lower salinity waters; and influxes of the cold, but fresher waters associated with Scotian Shelf water. The tides in the GoM are among the highest in the world and consequently generate swift tidal currents. Tidal ranges decrease from northeast to southwest, and the resulting differences in intensity of tidal mixing exert a strong influence on the spatial pattern of hydrographic structure in the gulf, nutrient delivery to the euphotic zone, benthic–pelagic coupling, and, ultimately, the total biological productivity.

The mean circulation in the GoM–Georges Bank region is generally cyclonic, driven by density contrasts between slope waters residing in the three offshore basins and fresher waters along the coast that are fed principally by discharges from the St. John, Penobscot, Kennebec/Androscoggin, and Merrimac rivers. However, river discharges account for only about half of the freshwater budget for the GoM; the remaining half enters the gulf as a surface flow of relatively cold, low salinity Scotian Shelf waters. The resulting surface circulation in the gulf is thus dominated by a buoyancy-driven coastal current system that flows counterclockwise around its edges. This system has been argued to be important to the overall nutrient budget and biological oceanography of the GoM. J. Churchill (Woods Hole Oceanographic Institution) and colleagues demonstrated the importance of wind-driven processes on recruitment of cod originating in Ipswich Bay in the western gulf. Downwelling, in particular, was associated with high recruitment success.

Levels of primary production in the GoM's offshore waters, the least productive areas in the GoM, are reported to average about 270 gC/m^2/year, based on ^{14}C bottle incubations (O'Reilly and Busch 1984; O'Reilly et al. 1987). More recent estimates are available based on satellite-derived sources. Estimates in phytoplankton species composition, based on CPR samples (Hare, personal communication), document a shift in dominance from diatoms to dinoflagellates, notably in the past decade. In light of apparent changes in the nutrient dynamics reported by D. Townsend (University of Maine), and the fundamental dependence on bloom productivity of particle fluxes to deep waters and the benthos, as reported at this symposium by C. Pilskaln (University of Massachusetts-Dartmouth), primary production processes deserve careful reconsideration for the gulf. Satellite-measured variability in the timing and intensity of the spring phytoplankton bloom, as reported at the symposium by A. Thomas (University of Maine) and colleagues, would also benefit from more detailed studies of phytoplankton productivity in relation to remotely sensed chlorophyll biomass estimates. Total phytoplankton productivity is currently being measured along commercial ferry transects across the offshore gulf, as reported by B. Balch (Bigelow Institute for Ocean Sciences) in this symposium. Those data, as well as yet to be proposed or initiated inshore productivity measurements, will be especially important to modeling efforts to assess growing concerns of artificial nutrient enrichment and eutrophication, as well as dynamics of red tides in the gulf (Anderson et al. 2008) and on Georges Bank, as reported at this meeting by D. Anderson (Woods Hole Oceanographic Institution) and colleagues.

Biological-physical modeling efforts have advanced rapidly in the years following the 1996 workshop, stimulated by the large research programs just mentioned and facilitated by dramatic increases in computing capabilities. Online circulation models are available at the University of Maine (http://rocky.umeoce.maine.edu/Gulf-of-Maine/GoM.htm), Dartmouth College (www-nml.dartmouth.edu/circmods/GoM.html), and the University of Massachusetts, Dartmouth (http://fvcom.smast.umassd.edu/research_projects/GB/index.html). These models have been coupled with biological models of plankton dynamics at the University of Maine (http://rocky.umeoce.maine.edu/Gulf-of-Maine/GoM.htm) and Woods Hole Oceanographic Institution (www.whoi.edu/hpb/viewPage.do?id = 1200). Models have also been applied to many specific research questions, such as the actions of internal waves on phytoplankton productivity, as presented at this symposium by Z. Lai (University of Massachusetts-Dartmouth) and colleagues, and the variability in timing and intensity of the spring phytoplankton bloom by R. Ji (Woods Hole Oceanographic Institution).

Plankton Community Dynamics

Research on plankton communities in the GoM has a long and storied history, beginning with the pioneering work of Henry Bigelow in the early decades of the past century. Bigelow's (1926) seminal study of the GoM provided an important impetus to the establishment of the long-term monitoring programs noted above. His identification of the copepod *Calanus finmarchicus* as a keystone species at the nexus of the food web in the gulf remains a vital research area. At the symposium, R. Jones and J. Runge (University of Maine) described a 5-year monitoring program, with high temporal resolution, that documented seasonal patterns in zooplankton and ichthyoplankton communities in the western GoM. This program highlighted the dominant role of *C. finmarchicus* in the system and changes in the abundance of this species. F. Maps (University of Maine) and colleagues described an individual-based model of *C. finmarchicus* in the GoM that has been used to explore the interplay of environmental factors and food reserves in determining the timing of diapause. This species is at the southern extent of its range in the GoM, and if temperatures increase under climate change, particularly in the deepwater layer where diapause occurs, the overwintering success of this species could be adversely affected. The loss or decline of a keystone species can have important direct and indirect effects on ecosystem structure by affecting energy pathways.

Our understanding of the role and relative importance of gelatinous zooplankton in the GoM is still in an early stage of development. Large-scale increases in these taxa have been noted in many parts of the world oceans. These increases have been associated with anthropogenic effects related to overfishing and climate change. Link and Ford (2006) found a major increase in gelatinous ctenophores in spiny dogfish *Squalus acanthias* stomachs across the GoM from 1981 to 2000. They suggested possible consequences, including increased competition with and predation on other species, decreased fish recruitment, and increases in ctenophore predators. Altered food webs, as a result of changes in abundance of gelatinous zooplankton, have been noted in other areas of the world ocean (Mills 2001).

Connections between plankton communities and climate and physical processes have now been established. The GoM, and the greater northeast shelf ecosystem, is heavily affected by remote environmental forcing (Greene and Pershing 2007). In terms of plankton dynamics, increases in the North Atlantic oscillation and northward movement of the Gulf Stream and decreases in Labrador Slope water and salinity may result in decadal scale alterations in zooplankton community composition (Ecosystem Assessment Program 2009). Greene and Pershing (2007) indicated that decreases in salinity in the 1990s enhanced water column stratification, which led to increases in productivity and phytoplankton biomass. In addition, a reorganization of zooplankton communities, with an increase in smaller species, were also noted during this time (Frank et al. 2005; Greene and Pershing 2007).

Further alterations in lower trophic levels may have been due to top-down effects. For example, although increased abundance of the juvenile stages of *C. finmarchicus* have been observed in CPR samples over the past decade, the adult stages decreased. As reported by J. Stockwell (Gulf of Maine Research Institute) and colleagues and W. Golet (University of New Hampshire) and colleagues at the meeting, this may be due to size-selective predation by herring populations, which were also on the rise in the 1990s (see, also, Greene and Pershing 2007). Frank et al. (2005) noted possible trophic cascades as a result of changes in groundfish, benthic crustacean, and plankton populations on the nearly Scotian Shelf. These authors attributed these changes to predator release resulting from overfishing of cod and allowing an increase in planktivorous fish (Frank et al. 2005). However, the impacts of this cascade on lower trophic level dynamics are uncertain. Greene and Pershing (2007) propose that this shift may also have been attributable to changes in oceanographic conditions related to the influence of the Labrador Current.

Upper Trophic Level and Fishery Resource Species

Presentations at the workshop, dealing with upper trophic level species, covered a range of species and taxonomic groups. A common theme throughout was the critical role of trophodynamics in the distribution and abundance of these species. No overview of the GoM ecosystem, however, could be complete without special consideration of two iconic species, Atlantic cod *Gadus morhua* and American lobster *Homarus americanus*, and both species received considerable attention at the session. Fisheries for these species have strongly shaped the history of the region and determined the character of local fishing communities. Evidence presented by K. Wilson and T. Willis (University of Southern Maine) at the session suggests that once numerous, local, nearshore populations of cod have been decimated through overfishing in the gulf by the turn of the last century (see also Ames 2004). This decline was possibly exacerbated by declines in river herring populations, a principal prey resource. There is some evidence of a recent resurgence of cod over the past decade in these areas, and studies have been undertaken to examine the possible role of recovery of river herring in some Maine rivers. An examination of cod feeding inside and outside the western Gulf of Maine fishery closed area has revealed higher levels in prey availability and growth rates within the closed area, but also in modes of feeding (higher levels of benthic feeding within the closure), as shown by G. Sherwood and J. Grabowski (Gulf of Maine Research Institute) at the session. Closed areas as a tactical management tool, therefore, seem to have implications for trophodynamics, as well as abundance and demography.

As cod populations in the gulf underwent long-term declines over the past century or more, lobster fishing gradually replaced groundfisheries in these coastal environments as a dominant resource species. Lobster populations and catches have increased markedly over the past several decades, as shown by D. Cowan (The Lobster Conservancy) at the meeting. A reduction in predation on lobsters by fish predators is among the hypotheses under consideration for the increase. Since 1993, the establishment of a long-term intertidal monitoring program has both documented the increase in juvenile lobsters and explored mechanisms for increased utilization of hard substrate habitats through shelter-sharing. These observations have enhanced our understanding of patterns of shelter use and overall carrying capacity of the system. The observed increase of lobster abundance may reflect broader patterns of habitat use overall under reduced risk of predation. It has been proposed that energy subsidies provided through herring bait in lobster traps may also have played a role in the increase (Grabowski et al. 2010).

Information on other fish species, including forage species such as Atlantic herring *Clupea harengus* and apex predators such as bluefin tuna *Thunnus thynnus*, was also highlighted during the symposium. Detailed studies of ontogentic shifts in diet composition for herring by Stockwell and colleagues at the session demonstrated a propensity of larger herring to feed selectively on copepods. These high-energy-content prey have potentially strong effects on herring bioenergetics. In related observations, Golet and colleagues documented declines in condition factors in tuna, an extremely valuable commercial and recreational species, apparently as a result of lower energy content of herring, an important prey item for tuna. In turn, this change was linked to a decline in availability of adult *C. finmarchicus*, with a resulting decline in herring condition factors.

For another historically important species, Atlantic salmon *Salmo salar*, K. Friedland et al. (2012, this volume) described the interplay of environmental conditions and predator distribution patterns as a predation gauntlet for salmon smolts as they exit river systems and enter the marine environment.

Historical records document sharp declines of many GoM stocks, including Atlantic halibut *Hippoglossus hippoglossus* (Grasso 2008) and Atlantic cod *Gadus morhua* (Rosenberg et al. 2005), as well as whales, seabirds, sturgeons *Acipenser* spp., and anadromous fish such as alewives *Alosa pseudoharengus* and Atlantic salmon *Salmo salar* (Bolster 2008; Leavenworth 2008). Depleted local stocks resulted in fishing restrictions as early as 1688 (Bolster 2008; Leavenworth 2008). The HMAP Gulf of Maine Cod Project has shown dramatic declines in mean trophic level, species richness, abundance, and habitat quality in the area now covered by the Stellwagen Bank National Marine Sanctuary and the GoM proper (Claesson and Rosenberg 2009).

Embedded within each of the issues described above is the overarching theme of trophodynamics and energy flow. This topic has been extensively studied in the gulf, and several generations of network models have been developed over the past three decades. These models depend heavily on information on feeding interactions at upper trophic levels. It was demonstrated by A. Bundy (Fisheries and Oceans Canada, Bedford Institute of Oceanography) at the session that long-term diet composition studies conducted by both Fisheries and Oceans Canada and the National Marine Fisheries Service can be effectively combined to provide broad spatial coverage and long-term trajectories of change in consumption patterns (see Link and Bundy 2012, this volume).

Implications for Ecosystem-Based Management

It is now widely appreciated that a more holistic approach to management is needed that accounts for the full spectrum of human impacts in the marine environment and the implications for ecosystem services that these systems provide (USCOP 2004). The EBM embodies several key attributes: (1) it is place-based and entails the development of integrated management plans for defined ecological regions, (2) it considers humans as integral components of the ecosystem, and (3) it requires an understanding of the interrelationships among the components of the system and the environment. Adoption of EBM strategies for the GoM will require the implementation of new regulatory and legislative frameworks. These include confronting trade-offs among and within different ocean-use sectors. It will further require the development of appropriate governance structures and close cooperation between the United States and Canada.

An ecosystem overview report for the GoM has been developed by Fisheries and Oceans Canada and the National Marine Fisheries Service to provide an overview of our current understanding of the GoM (broadly defined to include the Bay of Fundy and Georges Bank; East Coast Aquatics 2011). This document is intended to provide an overall context for critical issues associated with EBM for the region.

To move forward with EBM in this region, it will be necessary not only to define spatial management units, but to determine the fishery production potential for these units, to specify sustainable exploitation rates for the units as a whole, and to grapple to allocation strategies among different stakeholder groups. Research strategies to lay the groundwork for this approach have been developed at the Northeast Fisheries Science Center and presented to the New England Fishery Management Council for their consideration (see www.nefsc.noaa.gov/ecosys/EBFMbrochure.pdf). The council is responsible for fishery management within the U.S. exclusive economic zone of the GoM.

In all of this, it must be remembered that the GoM was subject to important alteration long before detailed scientific studies were undertaken. These include the dramatic reduction of whale populations, the decimation of anadromous fish stocks due to obstruction of rivers, habitat loss and overfishing, and overfishing of once dominant species such as halibut. We must be aware of the implications of these factors for overall system productivity in any consideration of what might be possible.

With this backdrop, it is clear that the rich history of research in the GoM provides a strong foundation for moving toward EBM in this region. The gulf is a semi-enclosed continental shelf sea with distinctive physical characteristics relative to adjacent regions such as Georges Bank and the Scotian Shelf. Reasonable arguments can accordingly be made for the GoM proper as a spatial unit for EBM. Indeed, an analysis of spatial patterns of physiography, hydrography/oceanography, and lower trophic level dynamics (chlorophyll and primary production) point to features in the western and central GoM that distinguish this area relative to Georges Bank and the eastern GoM/Scotian Shelf (Fogarty et al. 2012, this volume). The nearshore GoM emerges as a distinct subregion of the gulf. Primary production is relatively low in the central gulf, particularly over the deep basin areas relative to adjacent regions, coloring our expectations for potential yield in the deeper regions, which stand in sharp contrast to the more highly productive coastal regions.

Results from this session provide further insight into questions related to the appropriate spatial scales for management. Based on these investigations, it is clear that distinctive variations in physical and ecological characteristics exist in the eastern and western GoM. It is further evident that, for a number of reasons, the nearshore GoM may require special attention that goes beyond the physical and lower trophic level considerations noted above in defining subregions. The diversity of human activities on the coast, and in the immediate coastal zone, requires consideration of cumulative impacts of fishing, pollution, and habitat alteration/destruction. The nearshore region is also substantially affected by watershed influences that affect productivity patterns and other characteristics. Collectively, these and other concerns suggest that it is possible that nested spatial structures for management could be recognized within the gulf to account for these differences.

With respect to understanding interrelationships among parts of the system and with the environment, again it is clear that we have much to build on. There is important evidence of bottom-up control in the system with effects throughout the food web. A critical issue that remains is understanding potential changes in nutrient regimes and possible changes in the role of the microbial food web in energy transfer in this system. The impressive gains in identifying microbial components of the system during the symposium must be continued and the role of this component in system productivity fully explored.

Evidence of changing stratification patterns in the gulf, reviewed at the session, holds important implications for the relative balance of productivity in the pelagic and benthic components of the system. Our understanding of benthic communities in the gulf has also greatly benefited from renewed attention, as amply demonstrated at the symposium. This effort must be expanded to permit a fuller understanding of issues such the role of benthic–pelagic coupling in overall system structure under changing environmental conditions—increased stratification can impede energy flow among benthic and pelagic subsystems. The immensely complex physiographic structure of the gulf substantially increases the sampling difficulties involved, but the task is essential.

Results presented at the session show that the system has undergone regime shifts related to climate and physical forcing affecting nutrient dynamics, with attendant consequences for primary production, zooplankton community composition, and fish community structure. The effects of far-field forcing on oceanographic properties and productivity of the GoM and, in particular, changes attributable to the influence of the Labrador Current under changing climate conditions (Greene and Pershing 2007), will require a dynamic view of system productivity patterns and sustainable exploitation rates. These considerations will necessarily play an important role in devising management strategies in an ecosystem context. Basic biology of ecologically and economically important species and aspects of community structure of nektonic, planktonic, and benthic assemblages were all highlighted. In particular, for EBM, understanding shifts in productivity states will be essential in adjusting sustainable exploitation strategies at the ecosystem level to account for variation in environmental states.

Continued emphasis on synthesis of the rich body of research in the gulf, and the development of models for integration of this information, and predicting the effects of changing environmental conditions and the implications of alternative management actions are essential. Important strides have been made, particularly in development of coupled biophysical models. Linkage of numerical hydrodynamic models to a broader array of ecological models will be necessary to place the modeling efforts in service to management. For example, we must further develop approaches that link our hydrodynamic models to general circulation models to evaluate the potential impacts of climate change on the gulf.

Our session highlighted the rich information base available for the ecology of secondary producers and of higher trophic levels in the gulf. This information can be integrated into coupled physical-biological models and in other multispecies or ecosystem models. Ecosystem models have, in fact, been developed for the GoM to explore the implications of alternative fishery management options. These include static energy flow models (Link et al. 2007, 2008), dynamic ecosystem models (Overholtz and Link 2009), and multispecies production models (Fogarty et al., in press). In addition, single-species models for key resource species of the gulf, such as herring, have been evaluated in an ecosystem context (Overholtz et al. 2008). These, and other models now in development, provide the foundation to evaluate approaches to EBM for this system.

Finally, it must be recognized that we are still in the very early stages of understanding how best to integrate the human dimension into EBM in the gulf. We need to understand the role of humans as part of the ecosystem and how changes in the GoM affect human communities dependent on the gulf for work, recreation, transport, and other activities. Important work is now underway to understand human use patterns in space and time in the GoM, and ways to define fishing communities (Olson 2005; St. Martin 2006; St. Martin and Hall-Arber 2008). Climate-related changes in the gulf are likely to result in changes in the distribution patterns of resource species and their abundance. The factors will have direct implications for fishing patterns and will certainly contribute to the long history of change in the gulf. We need both to be able to anticipate shifting patterns of ecosystem structure and function and to implement adaptive management strategies to deal with both expected and unexpected change in system dynamics.

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