

Chapter 3

Biodiversity Knowledge and its Application in the Gulf of Maine Area

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3.1 Introduction

The diversity of life at all levels, from ecosystems to genes, is part of our natural heritage, an inheritance molded by more than three billion years of evolutionary innovation, adaptation, and chance (Raup 1976; Knoll 2003; Falkowski *et al.* 2008). By comparison with Earth's long and complex history of biological, chemical, and geophysical change, modern humans are relative newcomers (Liu *et al.* 2006), albeit with enormous capacity to alter the environment, its species composition, and functioning (Millennium Ecosystem Assessment 2005). Despite our technological prowess, we depend on natural ecosystems for life support, economic activity, and pleasure. What will happen as human populations occupy, use, and transform ever-increasing portions of the environment (Rockström *et al.* 2009)? The question has practical, as well as ethical and aesthetic, dimensions. Managing human activities in ways that preserve the ability of ecosystems to provide goods, critical services, natural beauty, and wonder into the future is one of the great challenges we face as a society.

Many have advocated a comprehensive approach to the sustainable use of the marine environment, including the supporting role of the ecosystem in general, and the con-

servation of biodiversity specifically (Grumbine 1994; Pew Oceans Commission 2003; Ragnarsson *et al.* 2003; Sinclair & Valdimarsson 2003; US Commission on Ocean Policy 2004; McLeod *et al.* 2005; Rosenberg & McLeod 2005; Palumbi *et al.* 2009). Ecosystem-based management (EBM) is an integrated approach that considers the entire ecosystem, including humans, and circumscribes a broad set of objectives and principles designed to guide decision making whenever the environment might be impacted (Murawski 2007; McLeod & Leslie 2009). EBM is an evolving practice, and explicit incorporation of ecosystem considerations into management of human interactions has recently increased dramatically (McLeod & Leslie 2009; Rosenberg *et al.* 2009). Conserving biodiversity as a cornerstone of EBM, however, is challenging because most biodiversity is still unknown, most species are comparatively rare, and the "importance" (function) of many non-dominant species is difficult to quantify and impossible to predict. Even if it can be shown that a species plays no significant role today, its contribution to the future remains unknowable. This need not require evolutionary time scales for expression, because systems experiencing rapid change – whether by climate, major natural disturbance, or human disturbance – may suddenly favor a different set of genes or species (Yachi & Loreau 1999; Bellwood *et al.* 2006). Biodiversity is the reservoir of options that enables species (whose populations contain genetic diversity) and systems at all higher levels of organization to respond to changes over time, and

biodiversity is the encyclopedia of information about life itself. Thus, there are many reasons, practical and otherwise, to document, understand, and conserve it.

This chapter describes recent efforts by the Gulf of Maine Area (GoMA) project of the Census of Marine Life to improve our understanding of biodiversity in the Gulf of Maine Area (Fig. 3.1) and suggests ways this information can be used to support EBM in the marine environment. Most projects within the Census were focused on species discovery in remote and under-explored areas of the ocean (O'Dor & Gallardo 2005). Early on, however, the Census recognized the need for an integrative study of biodiversity on an ecosystem-wide scale, covering a range of trophic levels (from microbes to mammals) and habitats (from shallow intertidal to deep offshore). The Gulf of Maine was selected as the ecosystem project because it is a well-studied, comparatively data-rich body of water with a long history of commercial exploitation and associated management needs. Its moderate size and intermediate levels of biodiversity were other potential advantages in terms of tractability. Although there was a large body of knowledge about the region, there had not yet been any coordinated effort to summarize the Gulf's biodiversity in an accessible format (Foote 2003), or to consider how biodiversity information could be used to improve management of a system of this size.

3.2 Environmental and Biogeographic Setting and History of Human Use

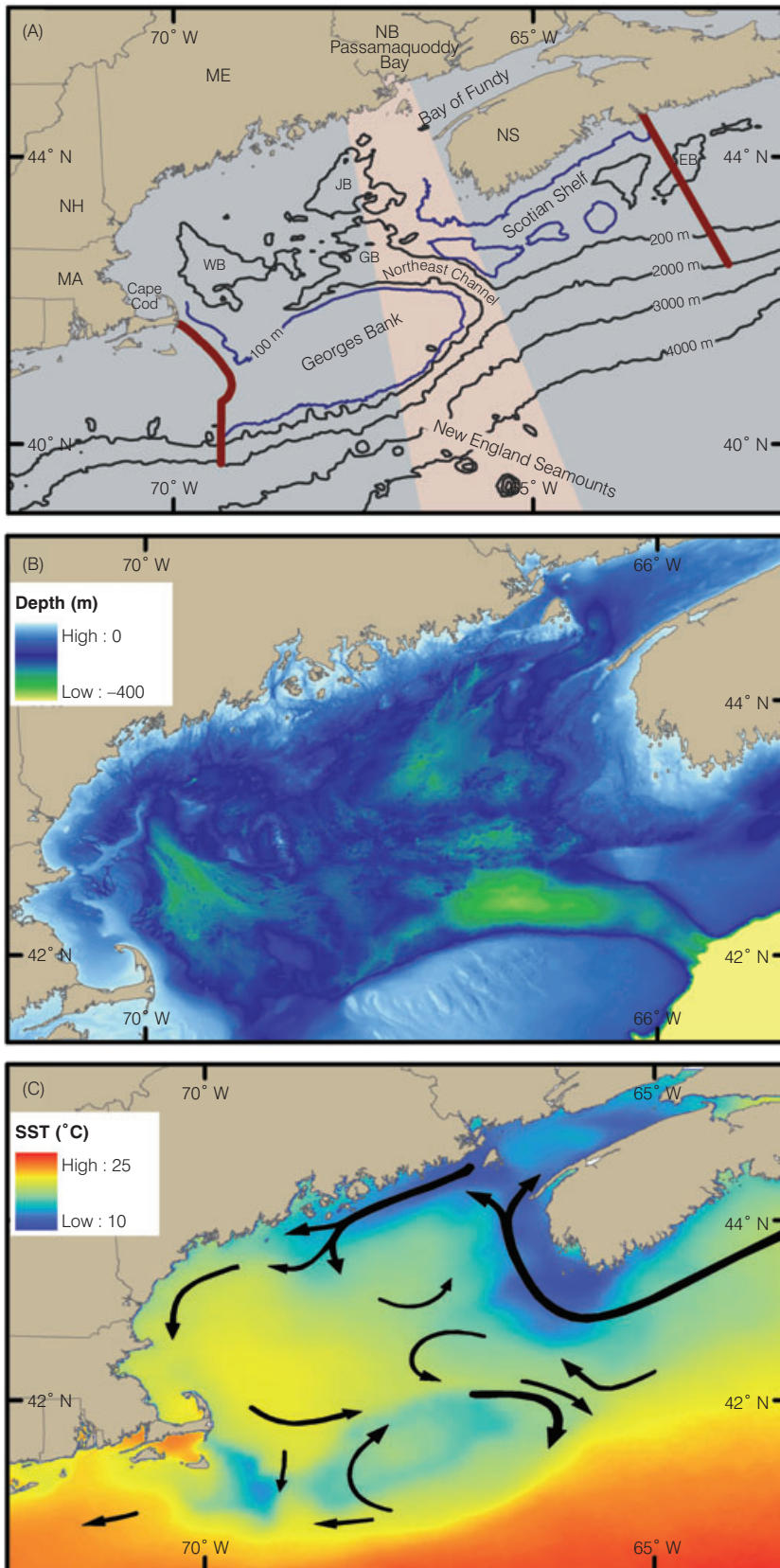
Biodiversity of the Gulf of Maine Area has been shaped over geologic time by geophysical and evolutionary processes, and, more recently, by anthropogenic pressures. During the Last Glacial Maximum (*ca.* 20,000 years before present (B.P.)), ice sheets extended onto the eastern North American continental shelf south of 41°N latitude, scouring the bedrock and depositing moraines that shape the present-day submarine topography of the Gulf of Maine and the Scotian Shelf (Knott & Hoskins 1968). Maximum present-day depths exceed 250 m in Georges and Emerald Basins (Figs. 3.1A and B), and the interior of the Gulf and the Scotian Shelf are generally deep except for a few large offshore banks and a narrow coastal fringe. The shoreline is diverse, consisting of extensive regions of tectonically deformed metamorphic rock, granites and other igneous intrusions, as well as sandy and gravelly shorelines of varying lengths. Salt marshes are mostly small and comparatively infrequent in rock-dominated sections of the coast, but are substantial in the aggregate and extensive along some sections of coast in the Bay of Fundy and in the southern Gulf (Gordon *et al.* 1985; Jacobson *et al.* 1987). Rocky sections are typically highly indented, with

numerous bays, peninsulas, and islands providing a wide variety of habitat types.

The dominant circulation in the upper 100 m is southward over the Scotian Shelf and counterclockwise around the Gulf of Maine, with most water exiting around the northern end of Georges Bank (Xue *et al.* 2000; Smith *et al.* 2001; Townsend *et al.* 2006). The banks and shoals along the outer periphery of the Gulf of Maine restrict exchanges between the Gulf and the open Atlantic and lengthen the path and increase the residency time of water as it travels along the southern flank of Georges Bank, thus contributing to the temperature contrast between the interior of the Gulf and the more temperate region to the south (Fig. 3.1C). Deeper water enters the Gulf from the upper slope through the Northeast Channel (sill depth approximately 190 m) and may be of northern (Labrador Sea) or southern (Mid-Atlantic) origin (Greene & Pershing 2003). Sources of slope water influence the temperature, salinity, and nutrient ratios of water and are themselves under the influence of larger-scale climate forcing (Greene & Pershing 2003, 2007; Townsend *et al.* 2010).

Tidal ranges vary from less than 2 m along the Nova Scotia Atlantic coast and approximately 3 m in the southern Gulf of Maine to 16 m in the northeastern Bay of Fundy (Minas Basin), reputedly the largest tidal range in the world (Archer & Hubbard 2003; O'Reilly *et al.* 2005). Where the tidal range is large, the difference between neap and spring tides exceeds the entire tidal range of locations in the southern Gulf (Dohler 1970). In the northern Gulf and over the crest of many of the offshore banks and shoals, turbulence created by strong tidal bottom friction contributes to unstratified or only weakly stratified conditions even during warm months of the year (Garrett *et al.* 1978), whereas elsewhere there is strong seasonal stratification induced by salinity and temperature (Fig. 3.1C).

From a global perspective, the Gulf of Maine Area has relatively low diversity (Witman *et al.* 2004), and is generally less diverse than waters farther south along the US east coast (Fautin *et al.*, unpublished observations) and in the northeast Atlantic (Vermeij *et al.* 2008). The intertidal and subtidal zone of the Cobscook/Passamaquoddy Bay region (US–Canadian border) may prove to be an exception (Larsen 2004; Trott 2004; Buzeta & Singh 2008). Cape Cod, which partly defines the western boundary of our study area (Fig. 3.1A), is generally recognized as the transition between the southern Virginian and the northern Acadian biogeographic provinces (Engle & Summers 1999; Wares & Cunningham 2001; Wares 2002). Some argue that the transition may be focused slightly south of the Cape in association with changes in water mass properties (Wares 2002; Jennings *et al.* 2009), but many Virginian and Acadian species occur well north and south, respectively, of this transition (Fautin *et al.*, unpublished observations). The modern biogeographic provinces are aligned with a steep latitudinal gradient in surface water

**Fig. 3.1**

Gulf of Maine study area.

(A) Major physiographic features and names.

Isobaths in dark grey (200–4,000 m) show the continental slope, Northeast Channel, and major basins. EB, GB, JB, and WB are Emerald, Georges, Jordan, and Wilkinson basins, respectively. A portion of the 100 m isobath is shown in dark blue to illustrate the major banks and the inner Scotian Shelf (see next panel for details of inner Gulf).

Canadian provinces (Nova Scotia, New Brunswick) and US states (Maine, New Hampshire, and Massachusetts) are abbreviated (NS, NB, ME, NH, and MA, respectively). The highlighted sector across the northern Gulf is the “Discovery Corridor”, which roughly straddles the Canada–US border. The GoMA study area is bounded by the two red lines and the 2,000 m isobath (later extended to 3,500 m), plus Bear Seamount, the most western of the New England Seamount chain and located between 2,000 and 3,000 m.

(B) Bottom topography of the Gulf of Maine showing the complex structure and generally deep bathymetry of the interior, as well as the principal channels into the system (data from US Geological Survey). Complex structures pose extra challenges to assessing and describing benthic diversity patterns and ecological functioning.

(C) Climatological (1997–2008) satellite-derived (NOAA-AVHRR) sea surface temperatures (SST) for August, with schematic of the major surface circulation features. (SST data from Andrew Thomas, University of Maine, Orono, Maine, USA; circulation based on Beardsley *et al.* (1997)).

temperatures, with lower annual means and smaller annual ranges in the north. The transition has undergone large changes during the Holocene (a significant northward expansion and retraction of warm-water biota; Pielou 1991) and is likely to be affected by expected global warming (Hayhoe *et al.* 2007). The current regional warming trend of more than a decade is probably already affecting the distributions of some organisms (Fogarty *et al.* 2008), although the trajectory of future temperature changes may be affected by accelerated melting of Arctic ice (Häkkinen 2002; Smedsrud *et al.* 2008) and variations in ocean circulation (Greene & Pershing 2003, 2007; Fogarty *et al.* 2008; Townsend *et al.* 2010).

Humans have affected biodiversity of coastal systems around the world, and the Gulf of Maine is no exception (Jackson *et al.* 2001; Lotze *et al.* 2006). There is evidence of human habitation along coastal Gulf of Maine as early as 8,500 to 6,000 years B.P. (Bourque 2001; Bourque *et al.* 2008). Although some evidence suggests that prehistoric hunter-gatherers had negligible impacts on the coastal marine environment (Lotze & Milewski 2004), archaeological studies of faunal remains in middens have shown changes in the relative abundance of available prey species by 3,500 years B.P., indicating a decline in local cod (*Gadus morhua*) and changes in the food web (Bourque *et al.* 2008). Europeans started coming to the Gulf of Maine regularly in the mid-1500s to take advantage of rich natural resources, and colonized the area in the 1700s (Bourque *et al.* 2008). They rapidly transformed the coastal environment by multiple “top-down” (exploitation), “bottom-up” (nutrient loading), and “side-in” (habitat destruction, pollution) impacts, causing widespread changes in abundance and diversity at all trophic levels, from primary producers to top predators (Lotze & Milewski 2004). On the Scotian Shelf, regional cod stocks were severely reduced by 1859 (Rosenberg *et al.* 2005), and by 1900 most large vertebrates in the productive southwestern region of the Bay of Fundy were severely overexploited, leading to the extinction of three species of mammals and six bird species (Lotze & Milewski 2004).

In the early twentieth century, human pressures on the Gulf became more intense and far-reaching. Mechanized fishing technologies beginning in the 1920s led to a rapid decline in numbers and body size of many species, especially coastal cod in the Gulf of Maine (Steneck *et al.* 2004) and on Georges Bank (Sherman 1991). Starting in the middle of the twentieth century, commercial fish stocks experienced significant reductions (Cohen & Langton 1992; Sinclair 1996) and many important stocks remain at low levels. In 2007, cod landings in the entire Gulf of Maine were only 5–6% of those in 1861 (Alexander *et al.* 2009), and many historical fishing grounds along the coast from Massachusetts to Maine and Nova Scotia are no longer very productive (Ames 2004; Frank *et al.* 2005). The decline of large predatory fish has been used to explain cascading effects

at lower trophic levels involving various combinations of macroinvertebrates and their invertebrate and algal prey (Steneck *et al.* 2004; Frank *et al.* 2005). Fluctuating abundances of sea urchins (caused by trophic cascades, direct fishing on urchins, and disease) and kelp (caused by predation by urchins and other factors (see, for example, Schmidt & Scheibling 2006)) have attracted particular attention because of the structuring role of kelp in shallow subtidal communities (Scheibling *et al.* 2009). The naturally low diversity of the Gulf of Maine kelp ecosystem may have facilitated the rapidity of these changes (Steneck *et al.* 2004).

Today, fishing remains the anthropogenic activity with the greatest impact on the Gulf of Maine system through removals and trophic effects (Steneck *et al.* 2004; Frank *et al.* 2005; Lotze *et al.* 2006), impacts on bottom biota and habitats (Auster *et al.* 1996; Collie *et al.* 1997, 2000; Watling & Norse 1998; Norse & Watling 1999; Myers and Worm 2003; Simpson & Watling 2006), and possible genetic effects. Modern means of harvesting as well as expanding human development along shorelines can be significantly disruptive or destructive of habitat, and virtually all areas of the Gulf from the intertidal to deep basins have been affected to some extent by human activities. Over the past three decades such impacts have generated growing concern, and a long series of restrictions on participation, gear, season and areas fished have been implemented, with historical emphasis on “catch” management and an emerging consideration of habitats, species of special concern, and biodiversity (Auster & Shackell 2000; Murawski *et al.* 2000; Lindholm *et al.* 2004; Buzeta & Singh 2008; Gavaris 2009).

3.3 Objective, Approaches, and Progress

The Gulf of Maine is an international body of water shared by Canada and the United States. The GoMA Project involved scientists from both countries and the area of study was defined as the Gulf of Maine proper (waters between Cape Cod, Massachusetts, and Cape Sable in southeastern Nova Scotia, and inside Georges Bank), Georges Bank, the Great South Channel, the western Scotian Shelf, the neighboring continental slope down to 3,500 m, and Bear Seamount (Fig. 3.1A). It is difficult to know how to conceptualize biodiversity and its functioning in a physically and oceanographically complex ecosystem of this size, and when GoMA was initiated in 2003 there was little regional consensus on how to integrate biodiversity information into management decision making. More fundamentally, what is the biodiversity of the Gulf of Maine Area? At an early meeting organized by the Census in Woods Hole, Massachusetts, in 1999, one of the region’s taxonomic

experts asked a much simpler question: “How many *named* species are there in the Gulf of Maine?” No one knew.

GoMA played a convening role in the region to consolidate and summarize existing data, identify gaps in knowledge, and stimulate new research. In addition, the project is developing a framework that can be shared by managers and scientists, of how knowledge of regional marine biodiversity could be used in management. The purpose is not to make recommendations on how to manage, but to encourage thinking about how biodiversity information could be used outside its purely scientific realm.

GoMA's objectives were the following:

- Synthesize current knowledge of biodiversity, including patterns of distribution, drivers of biodiversity patterns and change, and how biodiversity patterns affect function of the Gulf of Maine ecosystem.
- Assess the extent of unknown biodiversity.
- Lead and support development of information systems to increase access to data.
- Support selected field projects and emerging research technologies.
- Work with the scientific community and federal agencies in the US and Canada to help develop a framework for incorporating biodiversity information into EBM.
- Make recommendations for future research and monitoring.
- Educate the public on the role and importance of marine biodiversity.

In examining progress made toward these objectives during the first Census, we cover different aspects of how biodiversity is organized within the Gulf of Maine system, at diverse levels from the ecoregion to genes. We start with basic compositional features, proceed through considerations of how structure and function must be understood at multiple scales, and conclude with some perspectives on generating and using biodiversity knowledge.

3.3.1 The known regional biodiversity

One of our responses to the unanswered question of how many named species there are in our region was to assemble a Gulf of Maine Register of Marine Species (GoMRMS) based on species either known to exist here (using a variety of sources) or expected in the region based on a larger Northwest Atlantic register. The goal of GoMRMS (not yet complete) is to provide references and electronic links to taxonomic histories, descriptions, ecological and distributional information, museum holdings, and relevant databases, such as the Encyclopedia of Life (EOL; www.eol.org)

and the Ocean Biogeographic Information System (OBIS, see Chapter 17; www.iobis.org). In addition to being a resource for researchers interested in particular species, a well-developed and maintained list enables biogeographic comparisons (see, for example, Brunel *et al.* (1998) for the Gulf of St. Lawrence; the European Register of Marine Species for the North Sea), and can help answer the question “What kind of system is this?” The answer to this question helps to identify the extent to which systems may be similar and can be compared, which is one way of gaining insights into natural processes and responses to management actions (Murawski *et al.* 2010).

Currently, regional and global species registers are still works in progress that must be maintained with updated species entries, changing taxonomies, and documentation of sources, and they require a rigorous process of validation. As of November 2009, GoMRMS listed 3,141 species in the Gulf of Maine Area, with just under a third of the entries validated. To continue to build the register we have searched several databases to identify potential additions to the species already named in GoMRMS. Databases came from both countries and covered the shelf, interior basins, Northeast Channel, and the upper slope to 2,000 m. Data were from demersal trawl assessment surveys used for fisheries management, benthic surveys of infauna and epifauna, and planktonic collections from research and monitoring programs. In total, these data came from more than 11,000 trawls, 4,000 benthic samples, and 39,000 plankton samples collected since 1961. Most of the demersal trawl and benthic data were from depths shallower than 400 m, whereas plankton samples included the slope sea. Macrofaunal diversity of the slope and seamounts and microbial communities were evaluated by Expert Groups assembled for the purpose, and results are discussed later.

The database searches revealed location, date, and count data for 1,828 species: 1,403 from benthic/demersal samples (245 from near shore) and 559 from the net plankton (almost all metazoan, with some redundancies due to species with biphasic life histories). Of these, 821 were not listed in GoMRMS, bringing the provisional new total to 3,962 species. Significantly, nearly half of the species in GoMRMS now have spatial information, and the provisional additions provide guidance for prioritizing further work on the register. Other sources of information are being analyzed to assemble a better description of the system from work that has already been done, and new sampling programs for biodiversity studies are underway. In terms of species, large gains can be expected with increased effort directed at smaller organisms, and on all organisms in deep water environments. At all depths, however, closer looks reveal more species.

Recent subtidal sampling in Cobscook Bay, Maine, which has been studied for more than 160 years, produced 13 species not previously on the historical checklist (Trott 2004) of this well-studied bay (amphipods, polychaetes, a

mysid, a mollusk, and a cumacean; P.F. Larsen, unpublished observations). These are species that occur widely throughout the Gulf of Maine and were therefore not a surprise, but this example poses a challenge: when is a system adequately described, and what are pragmatic standards and approaches for doing this? In somewhat deeper (50–56 m) water and within 20 km of the coast in the south-western Gulf of Maine, a study of a small sample area found 70 genera of nematodes in 27 families from a total of 1,072 individuals (Abebe *et al.* 2004); eight of the genera had no previous representatives in GoMRMS. The nematode

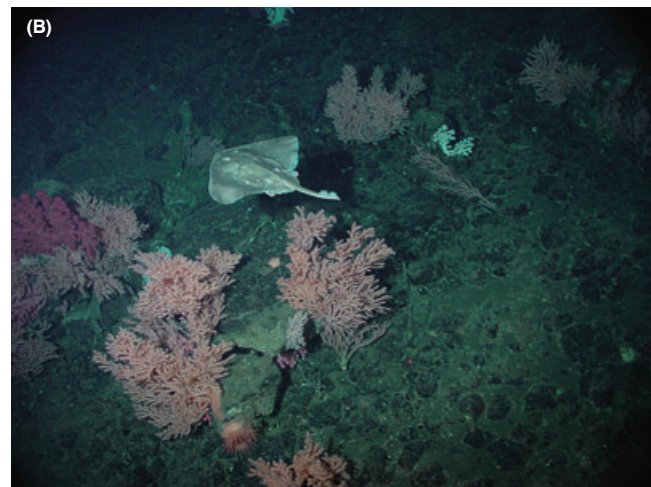
diversity was considered to be quite high (Abebe *et al.* 2004), and the number of local additions at the level of genus reflects the scant number of previous investigations of small infaunal organisms.

Farther from the coast, researchers from the Canadian Department of Fisheries and Oceans, Canadian Atlantic region universities, and the Centre for Marine Biodiversity have been documenting new species records within the offshore portion of the Gulf of Maine Discovery Corridor (Figs. 3.1A and 3.2A; see also Section 3.3.3). A current student thesis project (A.E. Holmes, unpublished

Fig. 3.2

Examples of Gulf of Maine fauna.

(A) Rich suspension-feeding community dominated by sponges and sea anemones, discovered on a deep (188 m) bedrock ridge (dubbed “The Rock Garden”) in Jordan Basin in 2005 by Canadian researchers working in the Discovery Corridor. Subsequent cruises in 2006 and 2009 have provided additional information on the overall extent of these hard substratum features within the otherwise sediment-dominated basin. Most species have not yet been identified below family and/or genus level owing to the predominant use of video- and still-imagery survey approaches (photograph: Department of Fisheries and Oceans, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada). **(B)** Winter skate (*Leucoraja ocellata*) cruising past deep-sea corals, *Primnoa resedaeformis* (sea corn) and *Paragorgia arborea* (bubble gum coral), in Northeast Channel (668 m) (photograph: ROPOS deep submergence vehicle, Canadian Scientific Submersible Facility, Sidney, British Columbia, Canada). **(C)** Humpback whale (*Megaptera novaeangliae*) feeding on a surface patch of krill (*Meganyctiphanes norvegica*) formed by interactions of krill with internal waves over a small offshore bank (photograph: H. McRae, New England Aquarium, Boston, Massachusetts, USA).



observations) sampled three soft sediment sites at 200–220 m depth in Jordan Basin during the first Discovery Corridor mission in 2005, with three 0.5 m² replicates per site sieved through 0.5 mm mesh screens. Thirty-two of the 183 species in the samples were not in GoMRMS, including several in minor phyla. Some represent northerly or southerly range extensions, but others may be new observations for the region.

During the 2005 mission, and again in 2006, dense stands of large, habitat-forming corals were surveyed within the Northeast Channel Coral Conservation Area, which lies within the corridor. Although the diversity of coral species may be higher elsewhere (Cogswell *et al.* 2009), this conservation area is the heart of the greatest known abundance of deep-sea corals in the region, particularly of *Primnoa resedaeformis* (sea corn) and *Paragorgia arborea* (bubble gum coral) (Fig. 3.2B). Abundance and colony height of these two corals were greater at depths more than 500 m than had been reported from previous surveys in shallower waters (Watanabe *et al.* 2009). Relationships between the size of a colony and the size of its attachment stone were typically stronger and less variable for *P. resedaeformis* than for *P. arborea*, suggesting that factors such as topographic relief may play an additional role in regulating distributions of *P. arborea* (Watanabe *et al.* 2009).

In deeper waters outside the Coral Conservation Area, but still within the corridor, two species of black corals, *Stauropathes arctica* and *Bathypathes patula*, were recorded for the first time in regional and Canadian waters, respectively (K. MacIsaac, unpublished observations). Using the remotely operated vehicle ROPOS, small samples were collected from coral colonies for genetic analyses to help future definition of coral populations and connectivity between corals in the corridor and elsewhere. Additional species that are potentially new to regional or Canadian waters include the amphipod crustaceans *Eusirus abyssi* and *Leucothoe*

spinicarpa, the holothurians *Psychropotes depressa* and *Benthoedites cf. sordida*, the carnivorous chiton *Placiphorella atlantica*, and the bone-devouring pogonophoran worm *Osedax* (K. MacIsaac, unpublished observations). More new species may emerge as samples continue to be processed.

These closer looks at the environment reveal not only new additions to knowledge of what lives in the Gulf of Maine, but also habitat features that previous ocean-sounding data had overlooked, and organism densities that were sometimes surprising. None of these were extensive efforts. Thus, the nature, extent, and patchiness of biological communities in the Gulf of Maine are all significantly under-characterized. Indeed, even within this comparatively well-studied environment, the question “What lives here?” remains only partly answered, and an understanding of abundance and patterns of distribution much less so. With such a large heterogeneous area to examine more closely, and interest not only in composition but also structure and function, a strategy is needed to make the discovery process efficient. More is said on this topic later.

The best example of a well-documented pattern of distribution and abundance at Gulf-wide scale is for the fishes (Fig. 3.3), which have been sampled by fishery-independent assessment surveys for more than 40 years. The average number of species per tow (sample diversity), averaged over all tows, is highest around the periphery of the Gulf and lowest in the deep basins, the Northeast Channel, and parts of the slope and Scotian Shelf. This is slightly affected by dominance patterns, as rarefaction curves show the highest *total* fish diversity on the upper slope and Georges Bank, followed by the coastal shelf between Cape Cod and Maine, and then other regions (L.S. Incze & N.H. Wolff, unpublished observations). The basins, Northeast Channel, and shelf regions south and east of Nova Scotia group together and have much lower total diversity. Fishes have habitat preferences such that certain species and communities can

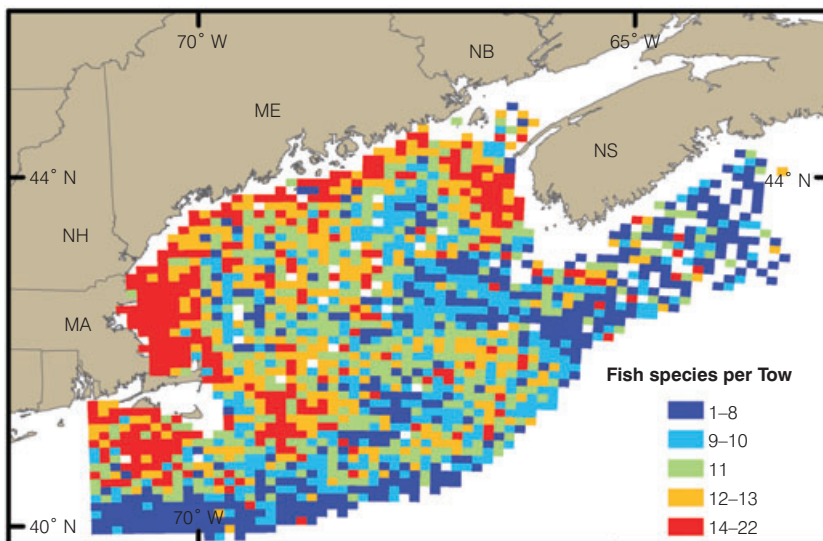


Fig. 3.3

Species diversity of fish in the Gulf of Maine (average number of species per tow per 10 km × 10 km cell), based on fall trawl surveys of the Northeast Fisheries Science Center (Woods Hole, Massachusetts), 1963–2008. Fall surveys took place between September and December (92% in October and November) and include 8,717 tows. Samples included 197 species of fish, with 15 elasmobranchs. Species richness groupings are quintiles of the frequency distribution of the samples. There is no correlation between species richness and the number of tows per cell.

serve as proxies for seafloor habitat distributions (Auster *et al.* 2001; Auster & Lindholm 2005). The extensive fish data then become an information resource that can be linked with other biological and physical data to help characterize diversity of the Gulf of Maine system at sub-regional scales. Watling & Skinder (2007) showed this with invertebrate assemblages. The above patterns resulted from analysis of abundance/tow data that are now available from OBIS, and Ricard *et al.* (2010) have shown that OBIS data provide a very similar view to that obtained by more detailed analysis using comprehensive source databases from the surveys.

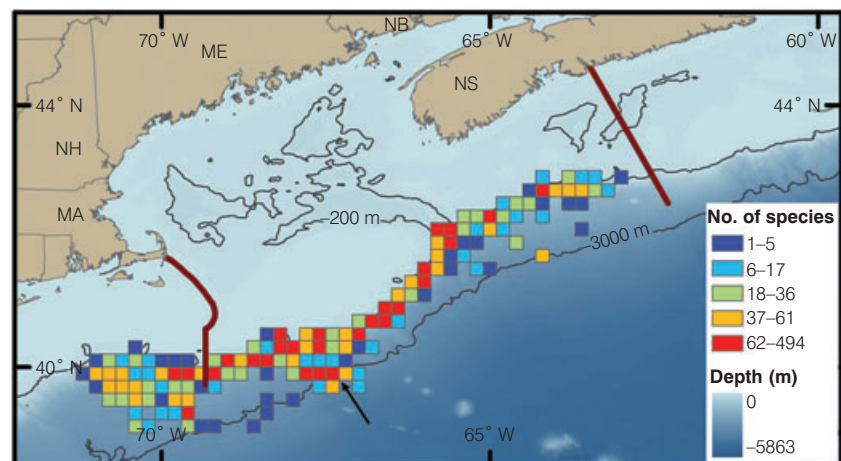
The continental slope and seamounts have not been studied as much or in the same way as the shelf, and so the status of biodiversity knowledge for this sub-region has been assessed separately by an ongoing Expert Group contributing to the Gulf of Maine Census (N.E. Kelly *et al.*, unpublished observations). Information has been assembled for benthic (infauna and epibenthic macro- and megafauna), demersal, mesopelagic, and bathypelagic taxa, comprising mostly adult stages, although a few larval fish were included. Sources of information include peer-reviewed literature, US and Canadian technical reports, OBIS, online museum collections and databases, and data provided by group members. Data extend west of GoMA, to 71.3°W, and from 150 to 3,500 m depth (Fig. 3.4). Although there have been studies on several of the western seamounts, only Bear Seamount was included in these analyses. So far, 899 species have been identified from the slope (mostly above 2,000 m) and 633 are associated with Bear Seamount; 240 were found in both locations. Bray-Curtis similarity (Clarke & Warwick 2001) between the slope and the GoMRMS species list is a little over 30%, and between Bear Seamount and GoMRMS is approximately 10%. A map of species numbers (Fig. 3.4) illustrates that many of the high values are associated with the seamount and major canyons. These values are

not corrected for effort or sampling method, so at this time they reflect the pattern of biodiversity knowledge, rather than intrinsic diversity patterns.

The smallest but most numerous and diverse organisms in the Gulf of Maine, as elsewhere, belong to a group of unicellular, prokaryotic, and eukaryotic organisms known collectively as marine microbes. The group includes viruses, bacteria, archaea, phytoplankton (for example diatoms), flagellates, ciliates, and other protists. We know most about the eukaryotic microalgae (“phytoplankton”: 696 names in 193 genera), and much less about the other groups. Heterotrophic and mixotrophic protists include some familiar groups (the Dinophyceae) as well as others that are rarely identified below the level of genus (amoeboid organisms and ciliates). For the bacteria and viruses, the basic unit of diversity, the species, is probably inadequate and several approaches have been considered to express diversity in these groups (see Cohan 2002; Pedrós-Alió 2006). A Microbial Expert Group assembled for GoMA (W.K.W. Li *et al.*, unpublished observations) estimated the diversity of prokaryotes and phytoplankton in operational taxonomic units (OTUs) for the purpose of placing GoMA in a global context. The calculation is based on scaling arguments using the total number of individuals in the community (for instance, the bacterioplankton) and the number of individuals comprising the most abundant members of the community (the corresponding group for GoMA is the SAR11 cluster *Candidatus* Pelagibacter; for methods see Curtis *et al.* (2002); Morris *et al.* (2002)). Population sizes were estimated from the depth-dependent average of cell densities from a time series on the Scotian Shelf and neighboring slope (an extension of work published earlier by Li and Harrison (2001)) times the volume at depth in GoMA derived from a hypsometric analysis (L.S. Incze & N.H. Wolff, unpublished observations). The calculations indicate, as a very rough approximation, that GoMA could have between 10^5 and 10^6 taxa of prokaryotes and between

Fig. 3.4

Species diversity knowledge for the slope, canyons, and Bear Seamount, depicted as number of species per 0.2 degree square. Red lines mark eastern and western ends of the GoMA study area to 2,000 m. Species counts are divided into quintiles and have not been corrected for effort or sampling method. Black arrow points to the grid over Bear Seamount where the highest species count (494) was recorded. Data compiled by N.E. Kelly, Centre for Marine Biodiversity, Dartmouth, Nova Scotia, Canada.



10^3 and 10^4 taxa of phytoplankton (because the assessment techniques used autofluorescence as a discriminator, the phytoplankton estimate includes the cyanobacteria). More specifically, the taxonomic richness of bacterioplankton in our study area is estimated to be 4×10^5 OTUs. This is 20% of the maximum global estimate of bacterioplankton diversity (2×10^6 OTUs; Curtis *et al.* 2002), which suggests a very diverse microbial community in Gulf of Maine Area.

The taxonomic distribution of biodiversity knowledge in the Gulf of Maine Area is summarized in Table 3.1, alongside a recent estimate of the global known marine biodiversity (Bouchet 2006). The table includes GoMRMS and the provisional additions from the survey databases, but does not include the above slope and seamount assessment because it has not been completed. The estimated diversity (OTUs) of the bacteria calculated above cannot be compared with the species estimate given by Bouchet (2006). How do the general patterns of named diversity in the Gulf of Maine Area compare with the global pattern, aside from the huge differences in numbers of species? Relatively speciose groups in both lists include the cnidarians, annelids, crustaceans, mollusks, bryozoans, and echinoderms, reflecting relatively high species richness in these groups in general, as well as conspicuousness, human interest, and relative ease of sampling and description by methods that have been established for many years. Among other speciose groups globally, the named marine algae and fish comprise a higher proportion of named species in the Gulf of Maine Area compared with the global list, and for the Gulf the proportion is lower for urochordates, Porifera, platyhelminthes, and nematodes. For the Porifera, the diversity has not been elucidated but may be comparatively low, whereas for the nematodes, a lack of significant effort on the group must be a major factor. These are general reflections on the state of knowledge for the Gulf as a whole. Valuable comparisons of species occurrence, distribution, and abundance across the Atlantic and north and south along the North American coast can be made within well-studied groups to study past and ongoing ecological changes (Vermeij *et al.* 2008).

To convey how much is known and unknown about diversity in the Gulf of Maine Area, we used a length-based approach for all adult stages of biota from viruses to the largest whales (Fig. 3.5). This is a coarse and subjective approximation because animal size (length) can vary greatly within a phylum and it was not practical to try to perfect this estimate by assigning “best approximate sizes” to all the named species! The smoothed line indicating the known (named) taxa approximates species numbers for groups of organisms contained within size groupings of $10^x \pm 10^{0.5x}$ m, where x is a whole number from -8 to $+1$. OTUs are used for viruses, bacteria, and archaea because there is no agreement on what constitutes species for these organisms. Trends and relative numbers are the important features being depicted (Fig. 3.5). “Monitored” species are those for

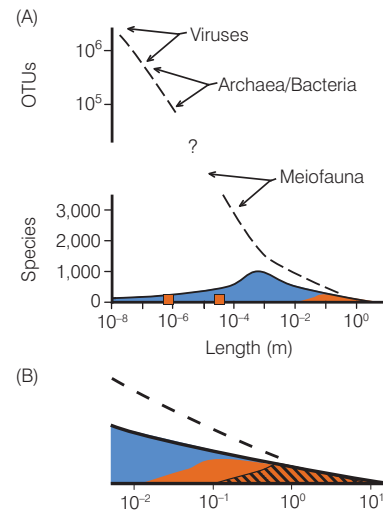


Fig. 3.5

Biodiversity size spectrum.

(A) Length-based schematic of Gulf of Maine biodiversity, showing the approximate size distribution of named species (solid line; blue shading is for emphasis), and a suggestion of the possible extent of the unknown biodiversity (broken line). For the prokarya and viruses, diversity is expressed as operational taxonomic units (OTUs), because there is no agreement on what makes a species in these groups. The shape of the curve of “unknowns” from meiofauna to viruses, and the maximum number of OTUs are unknown. The orange shape and orange squares are for monitored species, including harmful algae and coliform bacteria. Meiofauna is shown because it contains many unknown species, but there are other ecological and taxonomic groups that could be listed (see text). (B) Enlarged view of the lower right portion of the size-diversity curve, illustrating where most “monitored” (orange) and “managed” species (diagonal stripes) occur. Coliform bacteria, which are managed through effluent waste regulations, are not shown (see upper panel).

which we have some information on abundance over space and time (for example unmanaged species caught in fisheries assessment surveys, seabird abundances at long-term study sites); and “managed” species are those with management plans such as commercial fish, crustaceans and mollusks, cetaceans, and threatened or endangered species. At the far right end of the size spectrum, virtually all species are known, at least by name. “Unknowns” are dealt with in the next section. The schematic illustrates the point that the organisms of most concern to humans, whether for practical, aesthetic, ethical, or spiritual reasons, are a small fraction of the diversity in the system, and are supported by that diversity in ways that are only partly known.

3.3.2 Extent of unknown biodiversity

In general, we know less about the diversity of organisms as they get smaller, have softer bodies, inhabit more remote

Table 3.1

Comparison of the number of named species in the Gulf of Maine area with global estimates of marine species. Gulf of Maine totals are based on the Gulf of Maine Register of Marine Species and provisional additions from other sources (see section 3.3.1 for details on provisional additions to GoMRMS).

Taxon	GoMA species (this paper) ^a	Global species (Bouchet 2006)	Taxon	GoMA species (this paper) ^a	Global species (Bouchet 2006)
Bacteria	1 ^b	4,800	Acanthocephala	27	600
Cyanophyta/ Cyanobacteria	9	1,000	Entoprocta		165–170
Ciliophora	1	?	Gnathostomulida		97
Radiolaria		550	Priapulida		8
Foraminifera	2	10,000	Loricifera		18
Fungi		500	Cyclophora		1
Chlorophyta	98	2,500	Sipuncula	12	144
Bacillariophyta	224	5,000	Echiura	3	176
Phaeophyta	154	1,600	Annelida	489	12,000
Rhodophyta	148	6,200	Pogonophora		148
Dinomastigota	60	4,000	Tardigrada		212
Other protocista	3	750	Crustacea	762	44,950
Plantae			Chelicerata (non-arachnid)	21	2,267
Porifera	31	5,500	Mollusca	504	52,525
Placozoa			Phoronida	1	10
Cnidaria	186	9,795	Bryozoa/Ectoprocta	119	5,700
Ctenophora	5	166	Brachiopoda	1	550
Platyhelminthes	72	15,000	Echinodermata	110	7,000
Dicyemida/ Rhombzoa		82	Chaetognatha	12	121
Orthonectida		24	Hemichordata	5	106
Nemertea	35	1180–1230	Urochordata	44	4,900
Rotifera	4	50	Cephalochordata		32
Gastrotricha		390–400	Pisces	578	16,475
Kinorhyncha		130	Reptilia	2	— ^c
Nematoda	28	12,000	Aves	182	— ^c
Nematomorpha	2	5	Mammalia	27	110
			Total	3,962 ^a	229,175 ^d

^aTotal includes named species in GoMRMS plus provisional additions (see text).

^bA new estimate for bacterioplankton OTUs in the Gulf of Maine is 4×10^5 (W.K.W. Li *et al.*, unpublished observations), but this is not directly comparable with species (see text).

^cThese taxa are not included in Bouchet (2006).

^dFor taxa with a range of estimates, the average was used.

(deeper and offshore) places, and live within, rather than on, the bottom. Although the number of unknown species is impossible to estimate accurately, the more essential point is to illustrate where knowledge is most deficient. From this perspective, we can consider how these deficiencies affect our understanding of local communities and marine ecosystem processes, and what strategies might be used to understand better and conserve viable and functional populations of these poorly known and unknown parts of the ecosystem.

Recent studies have revealed a stunning level of diversity among marine prokaryotes (Sogin *et al.* 2006) and protists (Massana & Pedrós-Alió 2008), but many questions remain about how best to characterize it (Cohan 2002; Pedrós-Alió 2006; Not *et al.* 2009). The bacterial diversity was estimated in the section above with the “knowns” because there was a reasonable and interesting basis for making the calculation. We plot it as an “unknown” (Fig. 3.5), however, because OTUs do not necessarily correspond with phylogenetic relationships, and because the estimation is still very preliminary. The diversity of viruses was assumed to scale with abundance, and we have used a multiplier of ten (W.K.W. Li *et al.*, unpublished observations).

In the Gulf of Maine Area, we know that benthic and pelagic heterotrophic protists are seldom identified to species level despite the unquestioned importance of the “microbial loop” – the series of interactions among viruses, bacteria, archaea, and protists responsible for the large amount of cycling of organic matter and elements that occur in the water column (Sherr & Sherr 2000; Steele *et al.* 2007). A study by Savin *et al.* (2004) and subsequent work by the International Census of Marine Microbes comparing molecular methods with taxonomic assessments of microeukaryotic diversity in the Bay of Fundy show that the extent of diversity is not close to being understood. We know, too, that the soft-bottom infauna from all depths, and especially the meiofauna (Hicks 1985), are severely under-sampled and under-studied for their diversity, community composition, species–habitat relationships, and function. The nematodes provide an example within our area. One of the most diverse of marine animal phyla (*ca.* 12,000 named species estimated worldwide (Bouchet 2006)) and the most abundant of meiofaunal organisms (Chen *et al.* 1999), GoMRMS lists only 42 species. By contrast, the European Register of Marine Species (ERMS) lists over 1,800 (over a wider geographic and environmental range, but surely also incomplete). The addition of eight nematode genera to GoMRMS from a very small sample area (Abebe *et al.* 2004; Section 3.3.1) makes it reasonable to estimate that hundreds of nematode species, perhaps more than a thousand, have yet to be identified in the Gulf of Maine Area.

Small infaunal crustaceans (mostly harpacticoid copepods) and polychaetes are also abundant and diverse members of infaunal communities (Li *et al.* 1997;

Vanaverbeke *et al.* 1997). The polychaetes are better represented in the provisional list for the GoMA (411 of the 455 annelid species are polychaetes), but may be locally as diverse as the nematodes (De Bovée *et al.* 1996; Gobin & Warwick 2006). By comparison, only nine harpacticoid species are currently identified among the Crustacea listed in Table 3.1, and the diversity of this group in coastal, shelf, and slope waters from elsewhere (Baguley *et al.* 2006) suggests that a significant number of species living in the area have yet to be confirmed. It is likely that platyhelminth worms, another highly diverse marine phylum with only 73 named species in GoMRMS, are also significantly undercounted among the GoMA animal phyla. Recent field work demonstrated that it is still easy to add to the list of named species in our region (see earlier discussion), hinting at the size of the gap to be filled. With few exceptions, GoMRMS and the above discussion refer only to free-living forms (see discussion of symbionts by Bouchet (2006)).

Collectively, we estimate that the list of invertebrates yet to be identified must number in the thousands and extend from nearshore to the outer limits of our study area. Although these numbers are dominated by smaller organisms, the larger macrofauna and megafauna of the slope, canyons, and seamounts, including some fishes and cephalopods, are also incompletely known owing to their less accessible nature and the lack of widespread sampling across these regions so far. Research cruises conducted during the past decade have identified species new to science as well as additional specimens thought to be new species (Moore *et al.* 2003, 2004; Cairns 2007; Watling 2007; Hartel *et al.* 2008). Genetic studies will almost certainly add to the assessment of species composition. In addition to confirming suspected species splits (based on subtle characteristics, such as behavior, reproduction, habitat, morphotype, or physiology), genetics can also reveal cryptic species where single species were once thought to exist. The potential for cryptic species among “familiar” organisms is well illustrated by algae, which have simple morphologies, high rates of convergence, and phenotypic variation in varying environmental conditions, and for which there is often a lack of authoritative understanding of the complete life history (Saunders 2008). Increasingly, molecular tools are being used to resolve cryptic algal species (Saunders 2005, 2008; Kucera & Saunders 2008). Far from being mere taxonomic “splitting”, such revelations are important to our understanding of the biological and ecological processes operating in the Gulf of Maine Area ecosystem.

3.3.3 Resolving structure and function

In the preceding sections we focused on which species are present in the Gulf of Maine Area. However, organisms

exist in a context; they interact with each other and with their chemical and physical environment, and the resulting patterns of species distributions, abundances, vital rates, and behaviors affect the properties and functioning of an ecosystem. An over-arching series of questions, then, is (1) how are species distributed (including patterns of abundance and community composition), (2) what determines these patterns (including their temporal variations), and (3) how do the patterns affect the ecosystem? At small scales (meters to tens of meters) and in shallow water, patterns of biodiversity can be observed directly and intensively, but at larger scales (hundreds of meters to hundreds of kilometers) and in deeper water, observations are more difficult to make and there usually are trade-offs between intensive and extensive data collection. To understand biodiversity at the level of an ecosystem, new strategies and technologies are needed to obtain, analyze, and interpret data at multiple scales. We examine research at a few size scales in our area that bear on achieving ecosystem-level understanding.

Microbes – viruses, bacteria, archaea, and unicellular eukaryotic autotrophs, mixotrophs, and heterotrophs – are the most numerous and diverse organisms in the sea, and they constitute the largest reservoir of biomass (Kirchman 2008). Even among microbial groups with extensive morphology to support traditional methods of classification, molecular techniques have indicated far greater species diversity than previously thought (Savin *et al.* 2004). Because microbes play fundamental roles in primary fixation of carbon, recycling of elements, and gene transfer (some leading to disease), their dynamics are unquestionably relevant to the ecology of multicellular organisms and the Gulf of Maine ecosystem. However, ecosystem processes are usually considered at a high level of biological organization, often in the context of the major players, with a much reduced emphasis on diversity at the lower levels where speciation processes are more important. Thus a question arises about microbial diversity: to what extent is it linked to patterns and processes evident at the ecosystem level? At this early stage of discovery, microbial lessons may not be easily transferred to an understanding of diversity in multicellular organisms and the multifarious trophic dependencies. Nonetheless, the Gulf of Maine Area has a rich history of research on marine microbes, and it is impossible to predict what insights to local processes might come from continuing work. Given modern techniques for high throughput analysis (Stepanauskas & Sieracki 2007), one foreseeable application is that microbial diversity might prove to be a sensitive, integrative signal of environmental change, owing to the great dispersive capacity of microbial populations.

Biological activity is patchily distributed in space and time and is often driven by hydrodynamic effects on the distribution of small particles. These effects are often tied to interactions between water movement and bottom depth, thus, banks, ridges, and other areas of steep topographic

change are frequently biological “hot spots” that attract attention and study because of the concentration of biomass and interactions, and the putative importance of these centers of activity to biological production over a larger area (Yen *et al.* 2004; Cotté & Simard 2005; Stevick *et al.* 2008). Small and isolated features offer other advantages for study because the signals of interest can be distinguished from the surrounding background, one can examine the whole system and not just part of it, and the feature may be less frequently disturbed by humans than areas closer to the coast (although distance does not offer the protection it once did). In the Gulf of Maine Area, many such features have been implicated as hot spots, often because they are frequented by upper trophic level predators such as seabirds (Huettmann & Diamond 2006) and cetaceans (Kenney & Winn 1986). One challenge when examining structure and processes and calculating the ecological functioning of these features is to distinguish unique aspects from those that can be generalized. Studies of Cashes Ledge in the central Gulf of Maine illustrate this point: the top of the ledge system is shallow enough that it protrudes into the internal wave field, causing large fluctuations in energy and temperature, and mixing nutrients into the surface layer (Witman *et al.* 1993). Although the degree of mixing is unusual, the biological community includes mature kelp beds and large predatory fish reminiscent of what coastal hard substrate communities probably looked like many decades ago (Steneck *et al.* 2004). The vertical zonation, although made somewhat unique by the shallow top and unusually steep sides, provides a mesocosm for studying communities from a range of depths within a relatively small area. Studies at another site, a small offshore bank named Platts Bank in the southwestern Gulf, show that the depth of the bank interacts with the internal wave field to cause surface patches of krill and sometimes other plankton, attracting whales and birds to a small crest region where they feed intensively while the krill and other small prey are abundant (Stevick *et al.* 2008; Fig. 3.2C). A multi-year investigation of the bank shows that it is often inactive, however, the difference perhaps being in the vertical movements and abundance of krill in this portion of the Gulf of Maine. It appears that the bank is nonetheless frequently visited by whales, especially humpback whales (*Megaptera novaeangliae*) which may be moving among a network of potential feeding sites and switching between krill and fish as their primary prey. We do not know what this network looks like, which makes it difficult to speculate on the ecosystem dynamics supporting the summer population of this species. Significantly, little else on Platts Bank has been studied, although there is commercial and recreational fishing on it.

The Stellwagen Bank National Marine Sanctuary in the southwest corner of the Gulf of Maine is a little over 2,100 km² (6% the size of Georges Bank) and presents a very heterogeneous environment with well-mapped mud, sand, gravel, and boulder habitats in a bank and basin

topography from 19 to more than 60 m depth. The sanctuary is heavily used by sea life and by people, and has been an important fishing area for more than 400 years (Claesson & Rosenberg 2009). It does not have a high level of protection by sanctuary standards, but its status as a sanctuary has attracted considerable research on fishes (Auster *et al.* 2001, 2006; Auster 2002), benthic communities (Blake *et al.* 1993; Cahoon *et al.* 1993), plankton and hydrography (Clark *et al.* 2006), seabirds (Pittmann & Huettmann 2006), and marine mammals (Pittmann *et al.* 2006). A sliver of the bank and a large section of the seafloor northeast of the sanctuary have been protected from bottom fishing gear for several years, and the combined areas offer opportunities for study of altered and, in some areas and to some extent, recovering communities. To do this requires expanded, non-intrusive sampling techniques that operate with high resolution and high location accuracy over significant sampling tracks. Although several vehicles have been under development, a towed habitat camera system (HabCam) developed at the Woods Hole Oceanographic Institution resolves over significant distances the patterns of organism-organism relationships (abundance, species, and distance), organism-substrate relationships, and other oceanographic parameters, and affords population assessments for resolved species (Fig. 3.6A; York 2009). A significant development is that much of the data processing is automated, including a growing proportion of the acquired images. These types of systems will make quantitative assessments of the bottom and epibenthic communities possible, a large step forward in sampling, understanding, and monitoring the seafloor. Analysis of demersal fish assemblages on Stellwagen Bank as sampled by the trawl surveys has shown surprisingly good concordance between predicted ecological associations for certain fish with the bottom type, and the mapped benthic substrates. The surprise is that the patterns would be resolved by trawl assessments within the mixture of habitats on Stellwagen Bank, and the promise is that we can start to draw the two types of datasets together.

Detailed sampling, which HabCam and similar developments make possible, must be nested within a larger geography of habitat space determined by oceanography and other broad-scale biological datasets (see, for example, Watling *et al.* 1978; Watling & Skinder 2007). One question is the degree to which factors such as location in the Gulf (for example, distance from the Northeast Channel and Scotian Shelf inflows), water mass and hydrographic characteristics, chlorophyll production, temperature properties, depth, substrate, and substrate spatial heterogeneity affect benthic community types and processes. As one of the synthesis projects of the Census, Canadian and US scientists are working with Australian researchers to apply a Random Forests statistical analysis (a bootstrapped randomized tree statistical method: Breiman (2001); see Peters *et al.* (2007) and Knudby *et al.* (2010) for recent application examples) to shelf-scale biological and physical datasets from the temperate Gulf of Maine and two tropical/subtropical

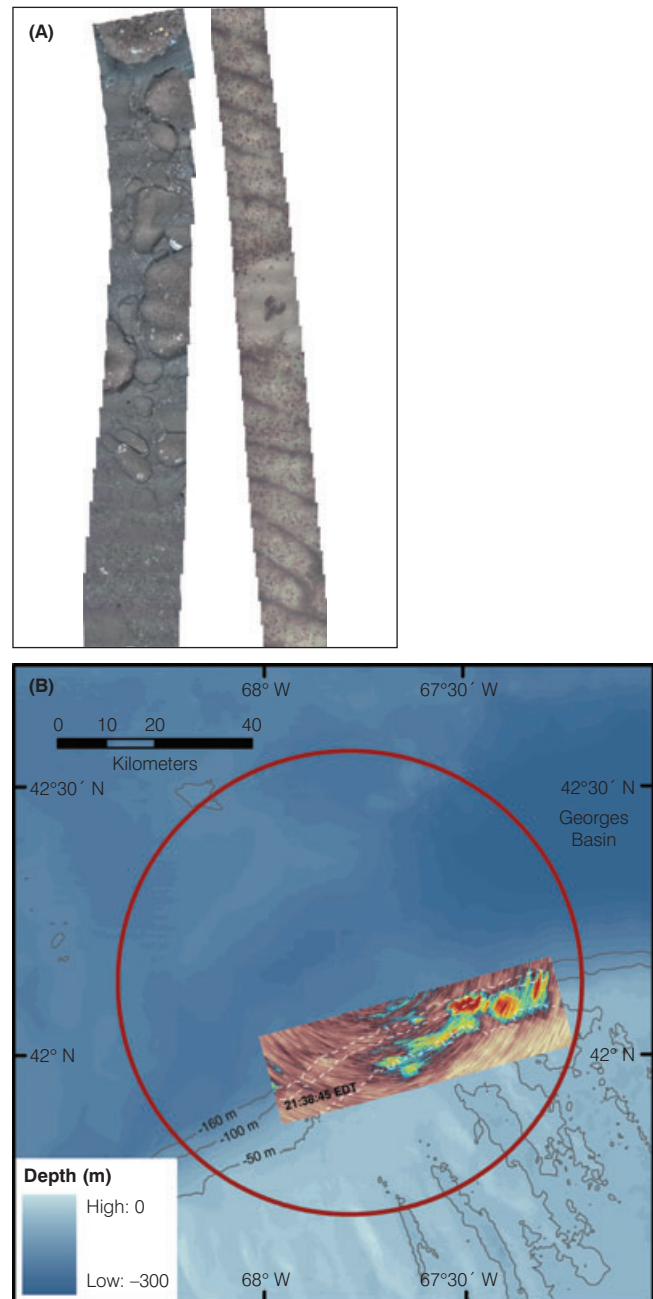


Fig. 3.6

Automated imaging of biological patterns, from sub-meter to tens of kilometers. **(A)** Mosaic imagery of benthic habitat from two towed transects taken by HabCam (towed habitat camera system) on Stellwagen Bank. Serrations mark the corners of individual 1 m² images that have been automatically adjusted for light, color, and elevation and then stitched together (photographs courtesy of S. Gallager, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, USA, and The HabCam Group®). **(B)** Synoptic view of schooling herring (*Clupea harengus*) on the northern edge of Georges Bank, sampled during a 75 s scan (full sweep of red circle) by OAWRS (Ocean Acoustic Waveguide Remote Sensing), 3.4 h after sunset on September 29, 2006. School densities are -45 (blue) to -33 dB (red) (data from N.C. Makris, Massachusetts Institute of Technology, Cambridge, Massachusetts, USA). This is one of a sequence of images showing the formation and movement of herring toward the bank (Makris *et al.* 2009).

systems, the Gulf of Mexico and the Great Barrier Reef. The statistical analysis involves a modification to Random Forests that collates numerous split values and change in deviance information for each physical variable and species (Pitcher *et al.* unpublished observations). The results are presented as cumulative distributions of splits, weighted by deviance, averaged over multiple species within selected levels of aggregation. Species come from the spatial datasets on fishes and benthic invertebrates that we presented in the section on the “known biodiversity”. The results represent patterns of biological change along gradients for each physical variable. The outputs also summarize the overall prediction performance of physical surrogates and identify the physical variables that contribute most to the prediction. The statistical techniques being developed in this work will contribute to understanding the importance of physical drivers in the marine environment and should allow a first-order prediction of macrofaunal benthic and demersal fish biodiversity and community patterns based on seabed and environmental characterizations. This would provide an intermediate level of spatial resolution that could facilitate design of the next higher-resolution stage of sampling and evaluation, and eventual monitoring.

Although much of the above information has focused on resolving benthic and demersal community structure at sub-meter to 100-m scales, another technological development has provided unprecedented views of pelagic fish (Makris *et al.* 2006, 2009). In this case, low-frequency, long-range acoustic sampling was used to provide a synoptic assessment of the behavior, density distribution, and scale of herring schools as they emerge from depth off the northern flank of Georges Bank (Fig. 3.6B), and move onto the bank for spawning. The large-scale view (tens of kilometers) afforded by this technique was coupled to traditional transect acoustic sampling and biological (net) sampling to supply biological detail, but the large, synoptic dataset described, as no other method could, the magnitude, coordinated nature, and timing of the event. Further development and testing could make these approaches applicable to geophysically more complicated environments, opening up opportunities for researchers to measure and understand behavior of some sound-scattering pelagic organisms in other settings.

A recent Canadian research initiative aims to contribute to our understanding of intermediate scales of biodiversity structure within the northern Gulf of Maine by creating a focus area for long-term research. In 2004, the Canadian Department of Fisheries and Oceans, with several Canadian academic institutions, launched the Discovery Corridor Initiative. This “corridor” in the sea begins in the intertidal zone at the US–Canadian border (Passamaquoddy Bay) and extends across the banks and basins of the northern Gulf of Maine to the base of the continental slope (Fig. 3.1A). There have been three offshore research missions so far that have used surface-deployed video,

digital photography, and benthic grab-sampling tools, as well as a deep-submergence vehicle to sample benthic habitats in water depths from 60 to 2,500 m (Figs. 3.2A and B). The corridor concept has recently been embraced by a new national marine biodiversity research program (the Canadian Healthy Oceans Network) that will establish similar corridors in the Arctic and Pacific oceans, based in part on the model developed in the Gulf of Maine. Passamaquoddy Bay and the adjacent Cobscook Bay are also the site of joint US–Canadian studies for Natural Geography in Shore Areas (NaGISA) and History of the Near Shore (HNS). The corridor concept is strategically useful – it is large enough to enable a complementary range of spatially resolved sampling and experimental designs to be undertaken, taking advantage of both commercial fisheries management questions and conservation planning needs (for example, the North East Channel Coral Conservation Area), to inform EBM approaches. A corridor from the shore to the deep sea also captures public imagination and becomes a vehicle for education.

In this brief review of some of the ongoing research into the structure of biological communities in the Gulf of Maine Area, we should point out that some important ecological functions in our current ecosystem state are performed by species whose distributions we know quite well. Examples include the copepod *Calanus finmarchicus* as a food source for some planktivorous fish and whales; the important role that certain planktivorous fish, such as herring (*Clupea harengus*) and sand lance (*Ammodytes americanus*), play in the food web of large predators such as tunas and whales; the importance of mud-flat amphipods (*Corophium volutator*) to the diet of benthic fish (McCurdy *et al.* 2005) and migrating seabirds (Hamilton *et al.* 2006); and the effect of kelp in structuring nearshore benthic communities (Steneck *et al.* 2004). Although their distributions and ecological roles are generally well known, there are few ecosystem-level assessments of their impacts. There are other “well-known” and important species that we know have large trophic roles, but we understand relatively little about them in terms of population patterns. These include organisms such as krill (especially the abundant *Meganycitiphanes norvegica*), gelatinous zooplankton, and squids. These are difficult to sample, but as important consumers and prey, their distribution, abundance, behavior, and dynamics are also an important part of understanding regional biodiversity. Finally, interesting and important perspectives can be gained by examining historical data and considering shifting baselines in the Gulf (Lotze & Milewski 2004; Steneck *et al.* 2004; Rosenberg *et al.* 2005; Bourque *et al.* 2008; Alexander *et al.* 2009; Claesson & Rosenberg 2009). These provide insights into previous states of the system, the magnitude and nature of previous impacts, and factors determining the current state of the system. These can be a basis for discussing trade-offs and setting goals for the future.

3.3.4 A framework for representing biodiversity in EBM applications

In the preceding overview of sources of scientific information that contribute to our present-day knowledge of regional biodiversity, we presented examples that span a range of spatial and temporal scales, and also a wide array of species and environments. This reflects the bewildering complex of details and uncertainties that need to be incorporated into an understanding of biodiversity patterns and processes at a large (GoMA) scale, and incorporated into decision making on human usage of the oceans. To ensure development of a realistic and useful concept of how biodiversity knowledge can be used in public policy and management, GoMA has worked with other groups and projects that emphasized stakeholder involvement, planning and implementation. These included US and Canadian fisheries agencies, which are working on implementing ecosystem approaches to fisheries management (Ecosystem Assessment Program 2009; Gavaris 2009) or integrated management approaches (O'Boyle & Jamieson 2006; O'Boyle & Worcester 2009), as well as academic, industry, non-federal management, and conservation groups.

In the search for ways to capture the complexity of biodiversity organization within an ecoregion, and in relation to the development of indicators and monitoring programs to assess status and trends of regional biodiversity, various hierarchical frameworks have been proposed. One approach stems from an adaptation of earlier conceptual frameworks on ecosystem structure and function put forward by Noss (1990) and articulated around then-available techniques for monitoring terrestrial biodiversity. Recently, Cogan and Noji (2007) refined Noss's schema for application toward marine biodiversity research and monitoring. Cogan *et al.* (2009) also found use in this approach in helping to codify how marine habitat mapping could be logically connected to EBM principles and implementation.

As Noss (1990) did for terrestrial applications, these later marine frameworks (Cogan and Noji 2007; Cogan *et al.* 2009) deconstructed biodiversity organization into three principal elements, each of which is further represented through a hierarchical (nominally spatially referenced) structure ranging from the ecoregion to genetic levels.

Compositional diversity elements represent the identity and variety of biodiversity at different levels within the system from biogeographic provinces and ecoregions to genes. Commonly used biodiversity metrics for species composition are inventory diversities (alpha, gamma, epsilon; Whittaker 1977; Stoms & Estes 1993).

Structural diversity elements are concerned with the physical organization or pattern within the system, from ecoregion- to habitat-scales, including both biotic and abiotic variables that modulate patterns. Common biodiversity

metrics that help define structure are differentiation diversities (beta, delta) that characterize the amount of change in species composition between different structural features in the environment (Whittaker 1977; Stoms & Estes 1993). At the ecoregion level, structural diversity may be thought of in relation to the arrangement of physiographic regions and landscapes that contribute to the internal makeup of the ecoregion. At finer scales, we must grapple with ways to understand and represent the dynamics of graininess of biotic and abiotic processes.

In these monitoring frameworks, *functional* diversity *elements* are those abiotic and biotic factors (or processes) that are influential in either maintaining characteristic biodiversity features within the system, or which contribute to changes. These range from genetic processes to regional natural and anthropogenic forcing variables that operate at various spatial, ecological and evolutionary scales. It is important to distinguish here that the term functional diversity *elements* relates to *processes* and is thus different from functional diversity as a *property* within a system, such as the depth of membership or number of feeding guilds, or an aggregate set of functions and services.

We have found this hierarchical view, organized around compositional, structural, and functional diversity elements (which we term a CSF template), to be useful in deriving overviews of the status of biodiversity knowledge, but alone it does not fully encompass features of biodiversity organization that need to be taken into account in developing a comprehensive view of the regional biodiversity science/management framework. As shown in Section 3.3.2 (Fig. 3.5), only a very minor component of the regional biodiversity is routinely monitored, and much of it is completely unknown. Indeed, organism size and the number of known and potentially unknown species (or OTUs) fundamentally influence how the science community approaches research on different ecosystem "compartments". Much of the existing work on the microbial system, for example, emphasizes functional diversity as a way of characterizing composition, especially at the prokaryote level.

Cogan *et al.* (2009) considered the CSF template to be a good fit into marine habitat mapping applications articulated within adaptive EBM approaches. We agree with this assertion, but advocate that an additional overarching conceptual model that integrates the complexity and spatial extent of different structural features in the system may help clarify the connections and transfer of knowledge between research and management applications. The system can be considered as a nested set of spatial domains that range from fine-scale micro-habitat features influencing occupancy, to seascapes, and at the broad-scale the ecoregion itself. Oceanographically modulated processes, such as benthopelagic coupling, and transport and mixing, promote connectivity across these spatial domains and represent an important consideration for spatial management under EBM. Layered on top of this spatial matrix

of habitats, organisms, and linkages is temporal variability, including year-to-year variations (natural and human) and secular change (climate and community trajectories). Conceptually, it can be argued that although discovery-based research is interested in investigation across the full range of these spatial domains, monitoring and spatial planning largely remain focused on periodic assessments and decision making above a certain minimum domain size and at lower levels of complexity.

Marine conservation has traditionally focused on individual species or populations. More recently, there has been a shift of emphasis toward managing specific marine habitat spaces, species assemblages, and hot spots of biodiversity (Buzeta & Singh 2008). Marine protected areas, long-term ecological research sites, and other types of natural heritage sites have been established as a means for conserving biodiversity, and they can serve as important experimental and control areas for long-term studies (Lubchenco *et al.* 2003; Satie *et al.* 2003; Cook & Auster 2006, 2007; Palumbi *et al.* 2009) and as a means to educate the public. Within the Gulf of Maine there are more than 200 coastal and marine protected areas, comprising parks, sanctuaries, research reserves, critical habitat areas, and restricted fishing areas (Baumann *et al.* 1998; Recchia *et al.* 2001). These have been created for numerous purposes, by many types of organizations. Most allow considerable usage. Significantly, from the perspective of EBM, most of these were not developed with consideration as to how they provide for conservation of biodiversity and function at the higher level of the ecosystem.

3.4 Perspectives on Generating and Using Biodiversity Information

Large ecosystems consist of mixtures of habitats and communities that exist at various sizes and patterns of distribution. Organisms within these communities exhibit great differences in size, abundance, mobility, life expectancy, and recruitment patterns, and they participate in a wide variety of ecological interactions. A single species may act differently in different environments or over time. These variations tend to focus scientific investigations in specific ways, perhaps emphasizing structure, or composition, or function of a particular community or habitat. Often, and for pragmatic reasons, a study must focus on a small subset of species, conditions, and time. In science, many questions are of potential interest, but there will always be compartments of knowledge that are hard to connect to one another, or to connect directly to management needs. A challenge to establishing a regional scale of understanding and management is to

integrate across the types of knowledge that tend to be generated for different groups of organisms and spatial and temporal scales of processes. It is difficult to do this well after the fact, suggesting that a conceptual framework is needed to help identify needs and opportunities. But beware: a framework should stimulate rather than dictate.

The challenge of understanding so much information at multiple scales in a spatially and temporally heterogeneous environment is daunting. The three principal components of the framework that we have discussed (CSF template) provide a means by which to gauge and communicate the relative completeness of our inventory and understanding of biodiversity organization within a regional ecosystem. Our references to knowledge along the size spectrum of organisms and to spatial hierarchies and function are meant to illustrate gaps in knowledge as well as ways that we might connect biodiversity information and processes to EBM at the scale of a regional ecosystem. A framework, discussed and improved over time, can help draw the long connections between scientific investigations, which typically focus on details, and EBM, which must operate at longer, larger, average, and less certain scales. In assembling the first list of species already known to exist in the Gulf of Maine, it became clear that even that basic information was not very accessible, and so much more is needed to advance research and support application. To make progress in this coupled research–application framework, biodiversity informatics must be developed as a component of ocean observing and analysis (O’Dor *et al.* 2010; Ricard *et al.* 2010).

3.5 Future Directions

Exploration of the oceans is essential to our understanding and conservation of biodiversity, but such an undertaking will take many years and is expensive. How do we conduct investigations and monitoring so that scientific and societal objectives can both be met, and the efforts and benefits sustained? The ecological questions are multi-scaled, multi-layered, and complex. The past focus on dominant organisms must somehow accommodate the larger and growing list of rarer species; the individual and collective role of rarer species must be incorporated into the immediate and longer-term perspective on ecosystem function and adaptation; community-wide patterns and dynamics need to be understood; and the relation between biodiversity, ecosystem functioning, and societal benefits must be elucidated.

Strategies might include a program to evaluate rigorously multi-scale relationships between community types, organism abundances, habitat types, and broader patterns of distribution. For example, how do patterns vary within and between basins around the Scotian Shelf and Gulf of Maine? In what ways are they the same or different, and

how interdependent are the basins in terms of population dynamics? What methods would be needed to answer these questions? What about the same questions applied to banks, ridges, and outcroppings? What are the relationships between shallower and deeper parts of the region; among the coastal sections from Nova Scotia to Massachusetts; and between the coast and the interior of the Gulf? How do community types and functional groups relate to ecosystem function in these various environments, and how are these related to services that society depends on? Nested within this are some of the more small-scale questions about the specific biodiversity patterns and processes within communities, including their dynamics, responses to and recovery from disturbance, and what is needed to conserve them. Monitoring for function and identifying indicators must become part of integrated ocean observing, assessment, and education. We need the ability to detect change, distinguish between natural and anthropogenic forcing, and respond in an informed way, which includes precautionary steps, previous experience (from here and elsewhere), and assessed risk.

To gain a better understanding of how ecosystem function and adaptability may be linked to biodiversity, we need the means to conduct experimental investigations at a range of scales. Consolidating some regional research capacities within “defined ocean spaces” where ecological structure and function can be assessed across different temporal and spatial scales, along with evaluation of comprehensive data integration and modeling techniques, could represent a key step toward testing and implementing EBM approaches across the region.

Understanding the inextricable links between human interactions and the natural system is the basis of ecosystem management. Because EBM regulates human activities, public literacy at local, regional, national, and international levels is fundamental to its implementation (Novacek 2008). Biologist Rachel Carson’s popular books of the mid-twentieth century, *The Sea Around Us* (Carson 1951) and *Silent Spring* (Carson 1962), helped create a societal shift toward support of the environmental policies of the 1960s and 1970s. Scientists must convey to the public and policy-makers the connection between biodiversity and the sustainability of goods and services provided by ecosystems. To build an ecosystem-literate public, one must first acknowledge that there is truly no “general public”, but collections of individuals with varying backgrounds, interests, and values. Now, more than ever in human history, societies supported by marine ecosystems – in the Gulf of Maine region and around the world – are made up of direct and indirect stakeholders with different socio-cultural values, economic concerns, and perceived connections to the natural world. Recognizing this human diversity is essential to building public support for research and acceptance of indicated management actions.

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