III.
SANCTUARY
SETTING

This section presents the concept of managing marine resources for biodiversity conservation in the sanctuary. It describes the physical setting of the sanctuary including its geography, geology and oceanography, as well as its connectivity to other parts of the Gulf of Maine. It profiles the primary producers and decomposers essential to the sanctuary's ecosystem function.

BIODIVERSITY CONSERVATION

The environmental condition of the sanctuary is subject to major alterations that are largely due to the effects of human activities. Threats to resource states (e.g., water quality, ecological integrity, habitat complexity) fall into two general categories: those that involve exploitation of resources above a certain level or threshold and those that destroy or degrade marine habitats and the associated biological communities. Exploitation includes both directed harvest and incidental taking of marine life. Threats to habitat include activities leading to physical alteration, various sources of pollution, coastal development and introduction of alien species. Many of these threats are interrelated and have cumulative impacts.

The ability to accurately evaluate the scale and consequences of changes in the sanctuary's resource states (and the subsequent impacts on human society) is challenged by inadequate knowledge of historic baselines for comparison with conditions today. The basic diversity of marine life and the patterns and processes that control the distribution and abundance of marine organisms in the sanctuary is still not well understood. At the same time, exciting new technologies and conceptual advances permit us to implement novel research approaches that seek to reveal fuller understanding of the sanctuary's ecological structure and the diversity and function of its biological communities.

NOAA can and should play a powerful role in protecting this special marine area, increasing public awareness and support for marine conservation, and providing sites for research and monitoring. By changing public attitudes, improving scientific understanding and developing effective models for management, the sanctuary can extend its benefit well beyond the limit of its geographic boundaries. Comprehending the great importance of marine biodiversity, and thereby gaining insights to interpret, explain and main-tain ecological complexity, is the basis for marine resource management in the Stellwagen Bank sanctuary.

EMPHASIS ON COMMUNITY ECOLOGY

Sanctuary management is predicated on the application of science to help formulate understanding of key issues and problems and to infuse the related public dialogue with substantive fact and thought. While many scientific disciplines (e.g., geology, oceanography) are invoked in the process, ultimately, ecology is paramount. While there have arisen a variety of approaches to the study of ecology (e.g., physiological, evolutionary), three basic and classical approaches remain fundamental to the science and are prevalent in the articulation of public policy. These approaches are population ecology, community ecology and ecosystem ecology (Ricklefs and Miller, 2000; Ricklefs, 2001).

Population ecology emphasizes the uniquely biological properties that are embodied in the dynamics of populations. A population consists of many organisms of the same species living together in the same place. Populations differ from organisms in that they are potentially immortal, their numbers being maintained over time by the births and deaths of new individuals that replace those that die. Populations also have properties such as geographic boundaries, densities and variations in size and age composition. Population ecology is essentially the study of the vital rates (births, deaths, recruitment) and biological processes that maintain numbers of animals in a species population. Population ecology is directly relevant to the management of fisheries, forestry and agriculture where rates of removal by harvest need to be balanced against natural means and rates of replenishment.

Community ecology is concerned with understanding the diversity and relative abundances of different species living together in the same place. An ecological community is the

sum of many populations of different species living in the same or similar habitats. The community approach focuses on interactions among multiple populations, which promote and limit the coexistence of species. The focus of community studies is principally on how biotic interactions such as predation and competition in relation to habitat influence the numbers and distributions of organisms. These interactions include feeding relationships, which are responsible for the movement of energy and materials through the ecosystem, providing a link between community and ecosystem approaches. Community ecology has particular relevance to the understanding of the nature of biological diversity and to the management of national marine sanctuaries.

Ecosystem ecology describes the dynamics of energy transformations and material transfers among large assemblages of organisms and the physical environment occupied by those organisms. Ecosystems are large and complex systems, sometimes including many thousands of different kinds of organisms living in a great variety of habitats. In the course of their lives, organisms transform energy and process materials. To accomplish this, organisms must acquire energy and nutrients from their surroundings and rid themselves of unwanted waste products. In doing so, they modify the conditions of the environment and the resources available for other organisms, and they contribute to energy fluxes and the cycling of elements. Ecosystem function results from the activities of organisms as well as from physical and chemical transformations in the seafloor, water column and atmosphere. Ecosystem understanding and approaches to both fishery and sanctuary management are recognized as essential by NOAA.

For purposes of implementing ecosystem-based resource management, the term "ecosystem" needs to be defined. A marine "ecosystem" is a human construct that artificially delineates a related portion of the ocean (Francis *et al.*, 2007) over what can be a variable spatial scale (e.g., Stellwagen Bank sanctuary, Gulf of Maine). In the context of this DMP a marine ecosystem is defined by NOAA (2005:3): "An ecosystem is a geographically specified system of organisms, the environment, and the processes that control its dynamics. Humans are an integral part of an ecosystem. An ecosystem approach to management is management that is adaptive, specified geographically, takes into account ecosystem knowledge and uncertainties, considers multiple external influences, and strives to balance diverse social objectives."

During the public comment phase of sanctuary management plan revision, questions were raised about the respective roles of the National Marine Sanctuary Program and NOAA Fisheries Service. Both parts of NOAA strive to meet a common goal of preserving or restoring the ecological integrity of unique habitats while recognizing that human uses of those habitats must be managed in an environmentally sustainable manner. Both NMSP and NOAA Fisheries Service work towards that goal using the various statutory and regulatory tools at their disposal. Under the Magnuson-Stevens Fishery Conservation and Management Act

(MFCMA), NOAA Fisheries Service strives to provide for sustainable fisheries using principles of population ecology while at the same time conserving the habitat of both target and non-target marine species. While many of the existing fishery management plans focus on single species or multi-species complexes, NOAA Fisheries Service is mandated to consider the broader impact of fishing on the ecosystem and has begun converting many of these plans into ecosystem plans. The NMSP is principally tasked with managing biological communities (together with maritime heritage resources) using the principles of community ecology within explicitly designated areas (under the National Marine Sanctuaries Act (NMSA)). Both take an ecosystem approach to managing fisheries and sanctuaries respectively and when applied in a complementary fashion, both statues can advance the goal of conserving and restoring the ecological integrity of important marine areas.

Conserving biodiversity is central to the implementation of ecosystem-based sanctuary management, an evolving approach that stresses management of the entire sanctuary ecosystem including all biological communities, habitats and species populations, together with all uses. Biodiversity encompasses all levels of organizational complexity in the sanctuary, from genetic diversity to species diversity to community diversity. Maintaining the ecological integrity of the sanctuary and, hence, its sustained production of resources and services requires attention to how the component species interact and how we value those species and interactions.

MANAGING FOR BIODIVERSITY CONSERVATION

In federal waters, marine biodiversity conservation is achieved primarily by the interplay of four national statutes: the MFCMA, MMPA, ESA, and the NMSA. These statutes encompass two main objectives: (1) enable long-term sustainable harvest and/or human use and (2) protect and/or restore species, habitats, biological communities, and/or ecosystems.

The MFCMA was primarily designed to ensure the sustainable harvest of fish and shellfish and has evolved to include the capability to protect the habitat of target and non-target species. Similarly, the MMPA was designed to protect marine mammal species many of which were severely depleted. While offering broad protection to these species to ensure their recovery, the MMPA also regulates sustainable harvest or take in specialized cases. By ensuring that marine mammals are protected as "significant functioning elements of the ecosystem" the MMPA maintains the capability to protect individual animals, species, populations, and the habitats that sustain them. The ESA's mandate overlaps that of the MMPA for marine mammal species facing extinction. The ESA's mandate to protect listed species also includes a mandate to protect distinct animal population units and habitats deemed critical to their survival.

Enacted around the same time, Title III of the Marine Protection, Research and Sanctuaries Act (now NMSA) was the first legislation to focus on comprehensive and area-specific

protection of the marine environment. The NMSA allows uses compatible with the primary purpose of resource protection. The NMSA affords managers the opportunity to consider management measures (e.g., zoned use within designated areas) for the purpose of maintaining "natural biological communities." By including the broad mandate "to protect, and where appropriate, restore and enhance natural habitats, populations, and ecological processes" the NMSA highlights its purpose to provide holistic protection of biodiversity in these special areas. Thus, within designated sanctuaries, NOAA encourages integrated implementation of these four statutes for the purpose of biodiversity conservation.

Of the 3,317 species of marine life documented in the GoM region to date (COML, 2006), there are 41 species of fish that are managed by the regional fishery management councils and the ASMFC, eight species of tuna and shark that are managed separately as highly migratory species, and 12 species of marine mammals and sea turtles managed under the ESA. Additionally, there are 39 species of seabirds

managed under the Migratory Bird Treaty Act. Many other species occur in the GoM which are not subject to direct management plans, including species that are rare but not endangered, and this group is sizeable (see Sidebar). While many of these species could potentially be the subject of direct management, they often gain significant derivative benefits from the directed management actions mentioned above and other actions taken by Federal, State and local partners in the region.

In addition, seven important fish species—Atlantic wolfish, cusk, Atlantic halibut, Atlantic salmon, Atlantic sturgeon, thorny skate and barndoor skate are all on the Species of Concern List for the Endangered Species Act (NOAA 2006). While this designation does not grant any protected status, it indicates that these species warrant attention to insure their populations do not decline further. All of these species currently frequent the sanctuary or once did (salmon and sturgeon). Halibut, salmon, sturgeon and skates are included under various fishery management plans (FMPs). Two of these species (wolfish and cusk), while being considered for inclusion under the Multispecies FMP, have no directed fishery management plan despite continued exploitation of their populations; they are among the top ten species caught by the recreational fishery in the Stellwagen Bank sanctuary (see Table 20 in Recreational Fishing section of this document).

The NMSA is unique in that it allows management actions focused on the protection and conservation of the full spectrum of biological diversity at a unique and significant site (e.g., the Stellwagen Bank sanctuary) and can serve as an important complement to other tools available under the MFCMA and the ESA or MMPA. Congress found that national marine sanctuaries are areas of the marine environment which have special conservation and esthetic qualities (among others). Congress mandated that sanctuaries be designated upon a determination that existing authorities are insufficient or need to be supplemented to protect the resources of that area. Congress directed that national marine sanctuaries be managed to maintain the habitats, and ecological services, of the natural assemblage of living resources that inhabit these areas. Among the purposes and policies of the NMSA is provision of authority for comprehensive conservation and management to maintain the natural biological communities and to protect, restore and enhance natural habitats, populations and ecological processes.

In specifying the management of "natural biological communities," "natural assemblages of living resources" and "natural habitats" rather than focusing on species populations per se, Congress essentially mandated that national marine sanctuaries be managed to protect and conserve biodiversity. In managing for biodiversity conservation, the authorities and protection measures afforded by all relevant statutes should be brought to bear on solving the problems described in this Draft Management Plan (DMP). Given the unique roles that sanctuaries can play in overall resource conservation and management, it is reasonable to anticipate

Rarity

Ecological rarity is defined in a variety of different ways over a range of spatial scales, and the forms that analyses take are highly varied (Kunin and Gaston, 1997). Although definitions of rarity differ in regard to the metrics involved, the concept of rarity is universally accepted and implicitly linked to the practice of managing for biodiversity conservation. Notably, rare species most often are not targeted for economic gain but are impacted as a consequence of activities directed at the exploitation of more abundant species (e.g., Auster 2005; Watling and Auster 2005).

Most species in the GoM might be considered rare based on the relative abundance of their numbers that occur in samples. For example, over a 30-year period (1975-2005), 90% of the numerical abundance of the fish community came from 7-10 species out of a total of 77 species sampled during NOAA Fisheries Service research trawls (Auster *et al.*, 2006). The remaining 67-70 species made up only 10% of the numerical abundance and, therefore, would be considered to have some degree of rarity in the community.

Analysis of such sample data leads to questions about the distribution and abundance of rare species within the sanctuary. For example, are species rare due to human-caused disturbance or are they naturally rare in their associated communities? Answers to this question lead to discussions of the necessity of management and the need for listing under provisions of the ESA. Another question that arises is focused on whether rare species are distributed sparsely and evenly through particular habitats or are they rare in most places and have dense concentrations at limited locations? Answers to this question may indicate the need to manage impacts in centers of species abundance and to insure that potential source populations continue their ecological function.

that the DMP would advocate for a higher level of conservation of living marine resources in the Stellwagen Bank sanctuary than may apply broadly throughout the whole Gulf of Maine. And it is reasonable to expect that human uses such as fishing would be done in a manner that was environmentally sustainable (see Sidebar).

Biodiversity Explained

The ocean is the cradle of biological diversity as life began in the sea. A liter of ocean water contains over a 100 million micro-organisms (Sogin *et al.*, 2006). In fact, micro-organisms represent over 50% of the biomass in the sea. Some micro-organisms produce their own food using sunlight while others are predators, hunting for microbial prey in a fluid and turbid environment. The ocean also contains larger multi-cellular plants, including encrusting species that produce calcareous "skeletons" as well as large fast growing kelps that can produce dense forests rivaling those in tropical jungles. Unlike the land and freshwater realms of our planet, the ocean contains representatives of every major type of animal group (phyla) on earth, from sponges to mammals. Although animals are but a single branch of the tree of life, they are the group with which we are most familiar.

Biological diversity is, simply stated, the variety of life on earth; it is the variability in all living things at all levels of examination (United Nations, 1992). It is inclusive of the millions of plants, animals and microbes; the genes they contain; and the ecosystems they build into the living environment. The definition of "biological diversity" or "biodiversity" deserves some discussion as it can mean different things to different people. The most common meaning refers simply to "species diversity," which is all of the species in a defined area or on earth as a whole, including bacteria, protists, and fungi as well as the multi-cellular organisms (plants, animals).

The genetic variation within species, both among geographically separate populations and among individuals within single populations is termed "genetic diversity." While species diversity by definition includes all of the species, or particular groups of species in an area, genetic diversity refers to the variation within single species. The level of genetic diversity within a population is an indication of the ability of the population to respond to and persist in the face of environmental change.

At the highest levels of complexity, "community diversity" and "ecosystem diversity" refer to the different biological communities and their associations with the physical environment (i.e., the ecosystem) that occur within an area, geographic region or the earth as a whole. The diversity of communities and ecosystems within a region is an indication of the range of evolutionary forces that have influenced species distributions. The range of organisms supported at particular sites provides a benchmark to understand both natural and human-induced change

Species diversity, quantified simply as the number of species in a particular area, is one of the most straightforward means

Concept of Environmentally Sustainable Fishing

The concept of environmentally sustainable fishing is compatible with the goal of managing sanctuary resources for biodiversity conservation. An environmentally sustainable fishery protects the fish and the environment in which they live while allowing responsible use of the species that come from that environment. It is a fishery in which target species populations and associated habitats and biological communities remain functionally intact while ensuring a future for the industry and all those who depend on the fishery for their livelihoods. It is a fishery based on the principle of optimization that incorporates within its goals the maintenance of biodiversity, biological community structure and ecological integrity together with the realization of economically and socially viable fishery production and yield.

An environmentally sustainable fishery is prosecuted in a manner that does not lead to over-fishing or depletion of the exploited resources to a level that imperils their ability to be a long-term functional component of the ecological community and the industry that relies on them. For those populations that are depleted to that level, the fishery is conducted in a manner that demonstrably leads to their recovery to sustainable levels. Environmentally sustainable fishing allows for the maintenance of the structure, productivity, function and biodiversity of the ecosystem, including habitat and associated dependent and ecologically related biological communities. The fishery is conducted in a way that does not lead to trophic (food web) cascades or ecosystem state changes. The fishery does not threaten biological diversity at the genetic, species or population levels and avoids or minimizes mortality of, or injuries to endangered, threatened or protected species. The fishery minimizes bycatch (unintentional capture of non-target species) and reduces the wasteful practice of discarding that bycatch.

The practice of environmentally sustainable fishing is consistent with the 1995 FAO Code of Conduct for Responsible Fisheries (United Nations). Environmentally sustainable fishing is conducted in ways that are consistent with the MFCMA national standards and that are most likely to be compatible with the sanctuary's primary goal of resource protection. Its practice derives from implementation of the principals of ecosystem-based resource management, and its fishery products can gain promotional and market advantage through voluntary certification programs (e.g., Marine Stewardship Council (MSC)). Managing the sanctuary for biodiversity conservation does not imply that fishing should be eliminated and may require the sanctuary to work with its partners, including the Fishery Councils and NOAA Fisheries Service, to modify fishing within the sanctuary in order to conserve biodiversity.

of characterizing biodiversity and is the metric used in this document. Using this measure, there are over 575 species in the Stellwagen Bank sanctuary. Appendix J provides a preliminary list of species, ordered by phylum, currently known to occur within the sanctuary boundaries. The list is incomplete as it does not include many pelagic planktonic species that are difficult to capture and identify. NOAA intends to augment this list as more is learned about the diversity of species in the sanctuary.

BIOGEOGRAPHIC CONTEXT

GULF OF MAINE (GoFM) LARGE MARINE ECOSYSTEM (LME)

The GoM LME forms a distinctive sub-region of the North American continental shelf in the northwest Atlantic Ocean, based not only on topography and circulation but on the communities of organisms that inhabit the area (Sherman *et al.*, 1996). The GoM LME is located at the southerly end of the Acadian biogeographic province, which also includes the Bay of Fundy and the Scotian Shelf. The Stellwagen Bank sanctuary is the only national marine sanctuary in the Acadian biogeographic province.

Georges Bank is included in the Acadian biogeographic province by some scientists but in the Virginian biogeographic province to the south by others. The affinity to one or the other biogeographic province is based on differences in the distributions of major groups of organism, patterns of endemism or oceanographic features (Cook and Auster, 2007). Many scientists view Georges Bank, as well as the southern New England Shelf and mid-Atlantic Bight, as a broad transition zone with no unique biogeographic characteristics.

The Stellwagen Bank sanctuary is located in the southwest part of the GoM LME and has depths that range from 20 to greater than 200 m. The shallower parts of the sanctuary support species that are primarily coastal in origin while the deeper waters support species more characteristic of northern and deeper marine communities. Seafloor topography in the western GoM blocks the flow of Maine deep water from the north and east, thereby excluding species that reside in conditions characteristic of Maine deep water environments from sanctuary waters.

The diversity of organisms that occur in the Stellwagen Bank sanctuary is a subset of the species that occur within the larger GoM LME. While not all species found in the GoM LME occur within its boundaries, the sanctuary contains a representative sample of many of the species in the region. Because of the wide range of depths (that cross major water column boundaries) and the high diversity of habitat types (e.g., mud, sand, gravel, boulder), the sanctuary exhibits a wide range of communities and species in a relatively small area (Auster *et al.*, 2001; Auster, 2002; Cook and Auster, 2006).

The GoM LME is relatively species poor when compared to other shelf ecosystems in the world ocean. For example, while the GoM has 652 species of fish (GoM Register of Marine Species at http://www.usm.maine.edu/gulfofmaine-census/Docs/About/GoMRMSClassification/index.htm; downloaded 8 August 2006), the tropical seas off northern Australia and Indonesia contain over 2,000 species of fish (Allen and Steene, 1999)—a diversity hotspot with the greatest number of fish species on earth.

BIODIVERSITY COLDSPOT

Biodiversity "hotspots" are regions of the world with unusually high concentrations of endemic species (species that are found nowhere else on Earth) and that, by the original definition (Myers, 1988), also suffer severe habitat destruction. Today the term is more loosely applied to areas having the perceived biological quality of high species richness. The term is used in practice to identify areas of the world that should be managed to protect biodiversity (Myers *et al.*, 2000).

By this definition, hotspots occur almost exclusively at lower latitudes in tropical and subtropical climes. Temperate places in the world that may be relatively species poor can also have high biological value, when those values are defined differently. Such places are considered to be biodiversity "coldspots" (Kareiva and Marvier, 2003). Coldspots take on particular and unique importance when they can be linked in additive fashion to become part of a regional network that fully characterizes and effectively maintains functioning ecosystems.

The Stellwagen Bank sanctuary is an important biodiversity coldspot. The sanctuary area is one of thirty priority sites for networked marine ecosystem conservation in New England and Maritime Canada that were identified through an extensive science-based approach (Crawford and Smith, 2006). That study is the foundation for a systematic effort to conserve and network high-quality and enduring examples representative of the full range of communities, habitats, environmental gradients and ecological processes in the GoM and northeast continental shelf. The sanctuary was a particularly important contributor for meeting a range of network goals, including demersal fish goals (89%), marine mammal goals (73%) and benthic habitat and seascape goals (80%).

So while the GoM region is not a global hotspot of biological diversity (*sensu* Myers, 1988), it does contain species endemic to the region, species which are the products of evolutionary forces that act selectively within the region. Hence the GoM LME contains a unique fauna based on a number of species occurring nowhere else, some having a distinct genetic composition if they are a subset of a wider ranging species, and others occurring within unique communities or habitats and having a unique ecological role when compared to other regions.

FUNDAMENTAL CONCEPTS OF BIODIVERSITY

HISTORICAL BASELINES

To the extent possible, an understanding of the historic abundance and diversity of organisms in the Stellwagen Bank sanctuary area is essential to effectively manage for

biodiversity conservation. Long-term population trends of economically important fish species, as well as marked changes in the ecosystem through time, can be used to make empirical estimates of key metrics. While historical baselines may be insufficient by themselves to set realistic targets for restoration efforts, they add useful perspective for consideration of what the goals and policies should be (e.g. Roberts, 2007; Bolster, 2008).

The phenomenon of "shifting baselines" as described by Pauly (1995) and Jackson *et al*. (2001), whereby standards of resource condition degrade through time, directs us towards the importance of historical perspectives as tools for determining long-term trends and setting baselines for comparison. Historical baselines can help avoid underestimations of ecosystem capacity or biased policy decisions resulting from lack of historical context. For example, Rosenberg *et al*. (2005) used fishing logs from the mid-19th century to model Atlantic cod biomass on the Scotian Shelf of Canada in 1852.
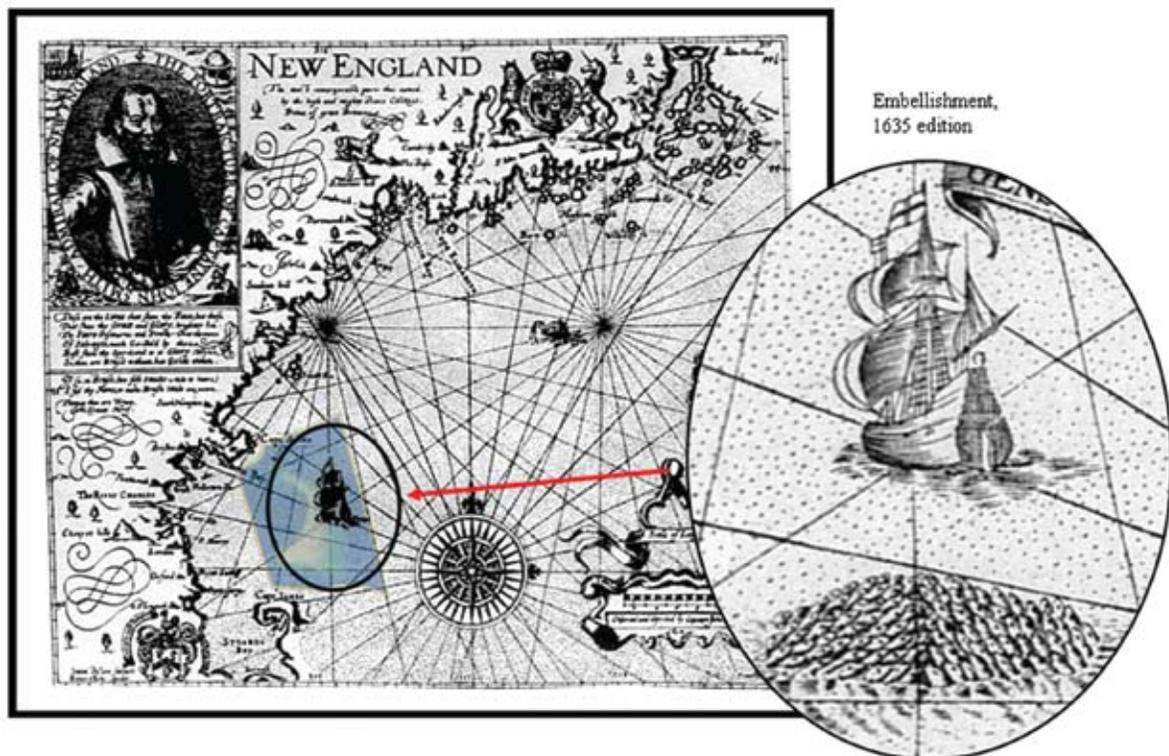
Using daily catch records, fleet activity and communication with other vessels, Rosenberg *et al*. (2005) inferred fishing capacity of the Beverly (Massachusetts) fishing fleet, and related the change in catch per unit fishing effort between 1852 and 1859 to a population dynamics model. This analysis allowed for estimation of original biomass prior to

1852 of 1.26 million metric tons of Atlantic cod. The 2002 biomass estimate, determined by Canada's Department of Fisheries and Oceans was approximately 3,000 metric tons, a decline of 99.7% from the population biomass of 1852. Growth of cod populations due to recent conservation efforts does not bring numbers of fish close to historical biomass.

Determination of historical baselines of ecosystem condition are required to make appropriate conservation decisions. Without a historical baseline, there is the risk that managers and the public mistakenly assume that recent condition of the resource in question is an appropriate reference point on which to base target restoration measures when, in fact, this reference point represents a significantly degraded condition. Absent historical context to gauge ecological potential, restoring the sanctuary's resources may result in serious underestimation of the system's capacity to respond.

The GoM cod project focuses on the collection and analysis of historical data of fish populations in the GoM including the sanctuary area (Rosenberg *et al*., 2005). The first phase of this project was aimed at the collection and review of historical sources providing biological indicators and population trends for fishes in the sanctuary. Data indicate that the sanctuary area was identified as a site of high biological productivity from the earliest times (Figure 6). The

FIGURE 6. EXPLORER JOHN SMITH'S *MAP OF NEW ENGLAND*, 1616, WITH STELLWAGEN BANK AND THE SANCTUARY AREA (SHADED BLUE) SUPERIMPOSED.

The ship was positioned over Stellwagen Bank (and within the boundaries of what today is the Stellwagen Bank sanctuary) and was an early convention to identify good fishing grounds. In the 1635 revised edition, the map was embellished with a pyramid of "cod heads" under the ship to depict the area as being especially good fishing. Courtesy: Karen Alexander, GoM cod project, University of New Hampshire.

second phase will incorporate the data into a Geographical Information System (GIS) database, as well as analyze the data in order to determine historical trends in fish diversity and population abundance. The Sidebar on researching historical trends offers background for work ongoing in the sanctuary.

TROPHIC INTERACTIONS

Food Webs

Other than primary producers and chemosynthetic organisms that make their own food from inorganic sources, all other organisms must consume others to sustain life processes, grow and reproduce. The range of interactions of species feeding on one another is referred to as a food or trophic web. The food web is a conceptual model of how the ecosystem functions.

Species are grouped according to trophic level (TL) as primary producers (like phytoplankton and algae), primary consumers (those that feed on primary producers), secondary consumers (those that feed on organisms that feed on primary producers), and up through higher TL predators (like sharks and tunas and humans) as well as the tremendous diversity of microbial organisms that either prey on other microscopic prey or decompose organic material in microbial food webs. While this is a highly simplistic view of the major types of trophic interactions that occur within natural communities, the true nature of such interactions are highly complex when many species are involved.

For the GoM region, which includes the Stellwagen Bank sanctuary, Link (2002) developed a food web model that was composed of 81 "trophic compartments" from detritivores and phytoplankton through to human predators (Figure 7). Some nodes of this food web are actual species (like Atlantic cod and silver hake) while other nodes are designated as trophic groups (like copepods and sponges). The food web is most detailed for fishes and their interactions with primary prey and reveals a highly complex and interconnected set of relationships.

This food web, based on relationships between predators and prey from across the northeast continental shelf (northwest Atlantic ocean), is in sharp contrast to food webs developed in more discrete and complex habitats such as coastal kelp forests and coral reefs. It is in such distinct habitat types that trophic

Researching Historical Trends

Context. European settlement marked the beginning of documented exploitation of marine resources in Massachusetts Bay. Explorations of the New England region reported the abundance of fish as far back as 1602, when Bartholomew Gosnold visited the sanctuary area. The abundant marine resources provided surrounding settlements with close, protected fishing grounds to make a living. From Plymouth to Gloucester, regional fishing camps grew into towns dependant on the local fisheries. As early as 1670, concerns arose over the coastal fisheries resources. Licensing fees and limits on the taking of particular fish species, such as mackerel, came about in the Plymouth colony. However, open ocean resources were viewed as "inexhaustible," a view held until relatively recent times.

The early 19th century brought about rising concerns over declines in fish species and populations. In 1839, David Humpheys Storer reported concerns of fisherman over changes in "composition, size, and distribution of the region's fish populations." Louis Agassiz established the Museum of Comparative Zoology at Harvard University, collecting samples and investigating the biology of fishes of the GoM. Human activity, such as damming rivers, and pollution had significant effects on fish populations, particularly anadramous species such as alewife, shad and salmon, as did directed fishing pressures.
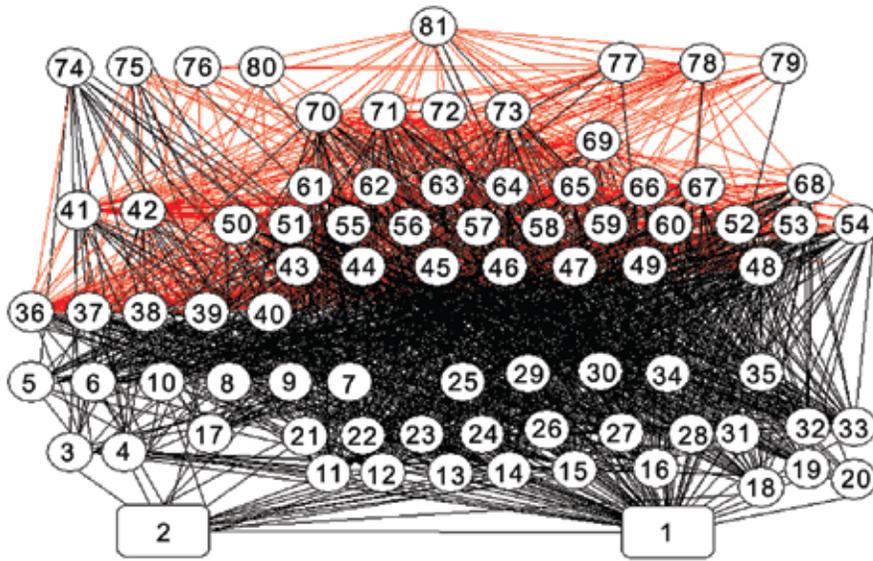
The federal government established the U.S. Fish Commission in 1871 to investigate the declines of fisheries of the area and research the biology and oceanography of the regional marine ecosystem. This Commission was replaced by the U.S. Fish and Wildlife Service in 1940. The federal government did not impose fishing restrictions on the banks or any offshore areas of New England until the mid 20th century. In 1970, the National Marine Fisheries Service became a part of the NOAA.

Sources of Information. Baselines based on historical data and trends are essential to decision-making agencies needing to compare present resource conditions to those of the past. Sources of these historical data range from personal journals of sailors aboard fishing vessels, to documents annually reported to the federal government. Maps, journals or log books, letters and interviews taken directly from fishermen throughout the history of this area provide specific quantitative fish counts, areas of high catch and trends of catch throughout years of fishing, as well as observations and insight into the lives of fishermen and their thoughts on changing environmental conditions.

Private business records from many fishermen provide some on the most detailed information with names, bait used, catch and other personal information. Newspapers from local fishing towns, as well as census data from the Commonwealth of Massachusetts, provide detailed information on vessels owned and run in the region, giving insight into fleet size and investments or products of the fisheries in the area.

Scientifically collected data from government research vessels through the U.S. Fish Commission, local government or local scientific societies such as the Boston Society of Natural History, are available in serial sets published as early as 1834. Federal statistics collected from fishermen on a monthly basis (in the later half on the 19th century) provide data on types of fish caught, landings, numbers of crew members and fishing methods. Legislative documents from as early as the 17th century and right up through the 20th century provide information on regulations focused on local fishing activities. These various forms of historical documentation provide many pieces to a puzzle that must be carefully pieced together, producing baseline context for conservation decision making.

FIGURE 7. SPECIES AND TROPHIC INTERACTIONS OF THE NORTHWEST ATLANTIC FOOD WEB.

This tangled "bird's nest" represents interactions at the approximate trophic level (TL) of each species, with increasing TL towards the top of the web. The left side of the web generally typifies pelagic organisms, and the right to middle represents more benthic/demersal oriented organisms. Species interactions in the top half of the web are dominated by predation on fish.

1 = detritus, 2 = phytoplankton, 3 = *Calanus* sp., 4 = other copepods, 5 = ctenophores (comb jellies), 6 = chaetognatha (arrow worms), 7 = jellyfish, 8 = euphasiids, 9 = *Crangon* sp., 10 = mysids, 11 = pandalids (shrimp), 12 = other decapods, 13 = gammarids (amphipods), 14 = hyperiids, 15 caprellids, 16 = isopods, 17 = pteropods, 18 = cumaceans, 19 = mantis shrimps, 20 = tunicates (sea squirts), 21 = porifera (sponges) , 22 = cancer crabs, 23= other crabs, 24 = lobster, 25 = hydroids, 26 = corals and anemones, 27 = polychaetes, 28 = other worms, 29 = starfish, 30 = brittlestars, 31 = sea cucumbers, 32 = scallops, 33 = clams and mussels, 34 = snails, 35 = urchins, 36 = sand lance, 37 = Atlantic herring, 38 = alewife, 39 = Atlantic mackerel, 40 = butterfish, 41 = loligo (squid), 42 = illex, 43 = pollock, 44 = silver hake, 45 = spotted hake, 46 =white hake, 47 = red hake, 48 = Atlantic cod, 49 = haddock, 50 = sea raven, 51 = longhorn sculpin, 52 = little skate, 53 = winter skate, 54 = thorny skate, 55 = ocean pout, 56 = cusk, 57 = wolfish, 58 = cunner, 59 = sea robins, 60 = redfish, 61 = yellowtail flounder, 62 = windowpane flounder, 63 = summer flounder, 64 = witch flounder, 65 = four-spot flounder, 66 = winter flounder, 67 = American plaice, 68 = American halibut, 69 = smooth dogfish, 70 = spiny dogfish, 71 = goosefish, 72 = weakfish, 73 = bluefish, 74 = baleen whales, 75 = toothed whales and porpoises, 76 = seals, 77 = migratory scombrids (tunas), 78 = migratory sharks, 79 = migratory billfish, 80 = birds, 81 = humans (adapted from Link, 2002).

cascades have been shown to regularly occur when these communities are disturbed by human activities.
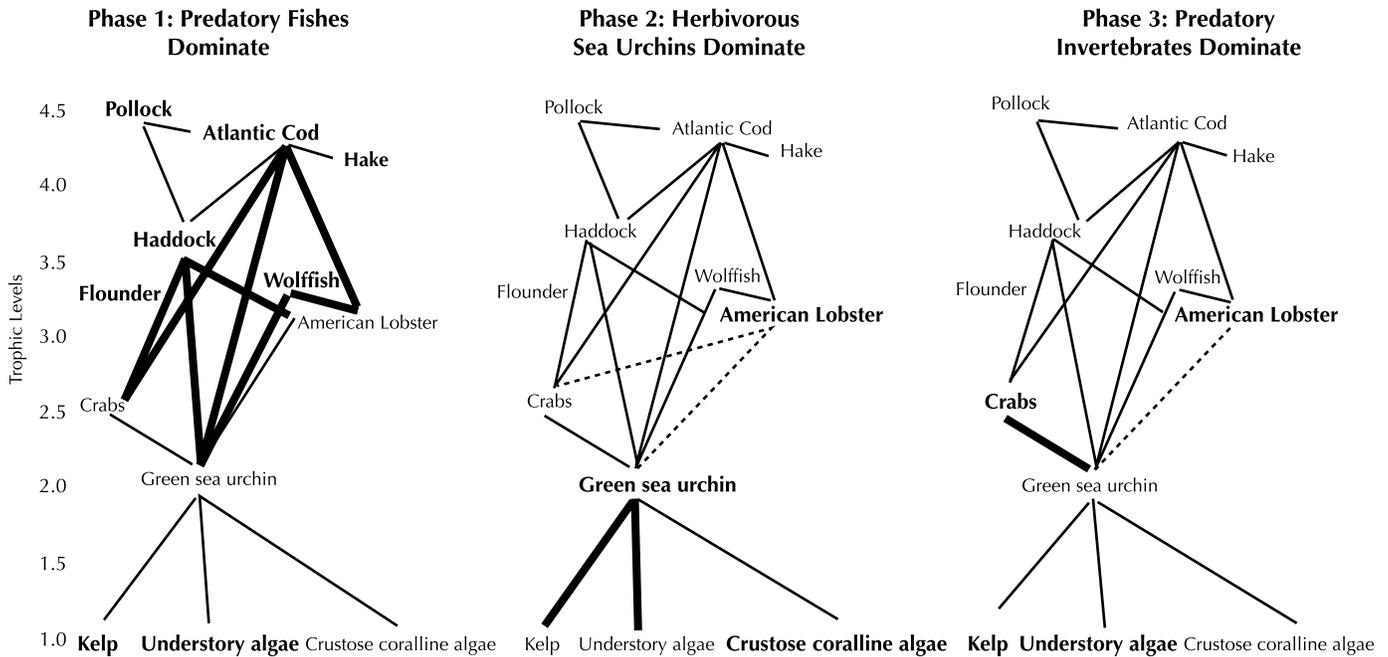
Trophic Cascades

Trophic cascades occur when change in the abundance of a particular species affects the abundance of species at two or more lower TLs. For coastal kelp forests in the GoM, Steneck *et al.*, (2004) defined trophic relationships that were significantly more limited and well defined than those for the northeast continental shelf (Figure 8). The effects of human exploitation over the last century produced trophic cascades in the kelp forests by reducing predators such as cod and other gadids (phase 1). This reduced predation pressure, primarily on green sea urchins, resulting in urchin dominated communities that decimated kelp forests and shifted the dominant primary producers to species of coralline algae (phase 2). Overexploitation of urchins in the late 1980s and early 1990s resulted in the recovery of kelp forests and increased abundances of crabs and lobsters (phase 3). Similarly, over-exploitation of piscivores and herbivores has caused trophic cascades on coral reefs shifting the system from one dominated by corals to one dominated by algae (Jackson *et al.*, 2001).

One of the underlying assumptions of the trophic relationships discussed above is that interactions of species within particular habitat patches (e.g., kelp forests, coral reefs) is tightly linked to those habitats, and that interactions with species outside of those habitats is weak (i.e., not "leaky"). While made an explicit assumption of many trophic web models, this is not necessarily the case in less complex and more spatially extensive habitats such as those of the offshore GoM, including the Stellwagen Bank sanctuary. For example, approximately half of the fish species in communities on deep boulder reefs in the sanctuary are either seasonal residents or transients (Auster and Lindholm, 2006), suggesting that such habitats are quite "leaky" and that predator-prey interactions extend beyond their boundaries.

Given the high levels of exploitation of fish species on the northeast continental shelf, the concern is that regional or shelf-wide trophic cascades could occur, resulting in long-term changes in the shelf ecosystem including that of the sanctuary. Such cascades have already occurred in more discrete habitats in the nearshore environment of the GoM (Jackson *et al.*, 2001; Steneck, 2004). However, an analysis of patterns in the abundance of fish species within particular trophic guilds (groups of species that feed on the same kinds of prey, e.g., piscivores, benthivores, crab eaters, echinoderm eaters, planktivores, shrimp-fish eaters) on the northeast continental shelf revealed that most trophic guilds remained remarkably stable over the four-decade time series studied, despite large changes in the abundance of

FIGURE 8. TROPHIC CASCADES IN KELP FORESTS ALONG THE COAST OF MAINE.

All species determined to have been abundant at one time were plotted with their assigned TL. Abundant species are shown in bold face; rare or low-abundance species are shown in smaller regular type. Most trophic linkages (TL-*lines connecting species*) have been demonstrated with ecological studies. Apex fish predators (all above TL 3.2) feed on invertebrates (TL less than 3). Predatory invertebrates (TL 2.5-3.0) feed on the herbivorous sea urchin (TL 2), which feeds on algae (all TL 1). Interaction strengths correspond to the width of trophic linkage lines. Some species are weak interactors in this system, for example flounder have no identifiable trophic linkage with other species in this system. Note: Lobster's trophic linkages are weak despite their abundance in recent years because they feed primarily on lobster bait in the trap fishery (Steneck, unpublished) (adapted from Steneck *et al.*, 2004).

individual species (such as Atlantic cod) within the guilds (Auster and Link, in preparation).

These data suggest that there is a form of compensation in the way fish communities within the GoM and the sanctuary respond to exploitation and that in habitats and landscapes where significant connectivity occurs, a level of protection against trophic cascades exists. This is not to say that trophic cascades could not occur in the sanctuary. For example, data suggest a trophic cascade has occurred in the nearshore kelp communities of the GoM and on the Scotian Shelf to the north, attributed to extreme reductions in the abundance of top predators (Steneck *et al.*, 2004; Frank *et al.*, 2005). However in the offshore GoM, researchers have shown that compensation in the abundances of species within trophic guilds, including piscivores, may buffer the potential for trophic cascades (Auster and Link, in preparation).

Structuring Biological Communities

While trophic cascades *per se* among fish communities may not have occurred on the northeast continental shelf, despite the extreme effects of overexploitation on individual species, competitive interactions due to changes in the populations of exploited species have impacted the composition of GoM fish communities. For example, the decline in cod and flounders due to fishing likely resulted in

a competitive release allowing extreme increases in skates and spiny dogfish on Georges Bank (Fogarty and Murawski, 1998). Consider also the documented decrease in mean TL in the northeast continental shelf fishery landings for the hundred-year period, 1901-2003 (Figure 9).

The abundance and distribution of preferred prey species has played a significant, perhaps critical, role in structuring the distribution of baleen whale populations in the GoM (Payne *et al.*, 1990). The distribution of humpback whales has been shown to be significantly correlated with the number of sand lance obtained from standardized trawl tows (Payne, et. al., 1986). Humpback whale sightings from 1978-1986 showed a shift in distribution from the upper GoM-lower Bay of Fundy region to the southwestern GoM concurrently with an increase in sand lance in this area during the same period. This shift in distribution coincided with a dramatic increase in the concentrations of sand lance throughout the shelf waters of the eastern United States. The sand lance populations apparently expanded in response to the collapse of the Atlantic herring stocks in the mid-1970s due to over-fishing from foreign, distant water factory fleets (Meyer *et al.*, 1979; Sherman *et al.*, 1981).

Significant changes in the biomass of sand lance and the abundance of copepods have co-occurred with a shift in the occurrence and abundance of four species of baleen whales (northern right, humpback, sei and fin) in the south-

ern GoM (Payne *et al.*, 1990). Peak years in the abundance of the copepod *Calanus finmarchicus* were the lowest years in abundance for sand lance. Right whales and sei whales were common in the region only during 1986, when *C. finmarchicus* reached a regional maximum and sand lance were at a regional minimum. These distributional shifts in cetaceans have been characterized as an ecological response to human-induced changes in the abundance of herring and mackerel due to over-harvesting and a compensatory response by sand lance (Payne *et al.*, 1990).

Since the elimination of foreign fisheries on the northeast continental slope in the late 1970s, Atlantic herring populations were able to re-colonize much of the area's spawning habitat during the period from 1988-1993 (US DOC, NOAA, 1993a). During 1992-1993, the abundance of sand lance was well below the average for previous years. This change in the abundance of species which feed at the same TL is referred to as a "biomass flip". This shift in the abundance and distribution of cetacean prey could possibly trigger a similar shift in the distribution of humpbacks and other cetaceans that feed on these small pelagic species. Many species of marine mammals and predatory fish follow the movements and abundance of their prey, which in turn may be linked to physical oceanographic conditions including circulation patterns, water temperature and salinity as well as local depletion of prey species due to targeted fishing activity.
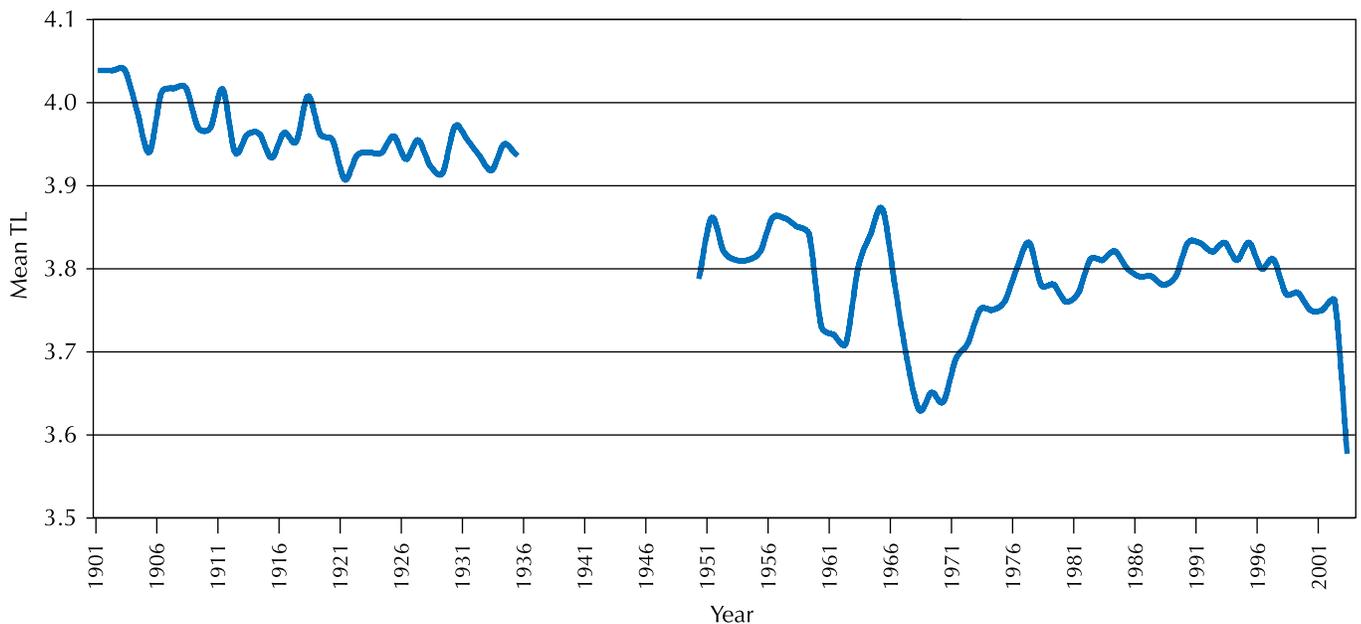
Climate change may have the most unpredictable effects on community structure and trophic interactions. Many species are at the southern or northern limits of their distributions in the sanctuary area. Small increases in water temperature may result in significant increases in more warm temperate species and the loss of cold water taxa. Long-term trends in warming have already resulted in shifts in the distribution of fishes in the GoM (Garrison, 2001).

HABITATS

A variety of habitats occur within the sanctuary. The underwater landscape is a patchwork of habitat features that are composed of both geologic and biologic components. Habitat is defined as the location occupied by an organism, population or community. It is the physical part of the community structure in which an organism finds its home, and includes the sum total of all the environmental conditions present in the specific place occupied by an organism. Habitats can be found on the seafloor or in the water column. Seafloor habitats are formed by the physical substrata in an area or by the combination of physical substrate and inhabiting organisms (biogenic habitats), such as anemones attached to a boulder.

Habitat features provide shelter from predators and the flow of tidal and storm generated currents, serve as sites that enhance capture of prey such as drifting zooplankton, and serve as foci for spawning activities including egg laying and brooding young. All organisms have particular habitat
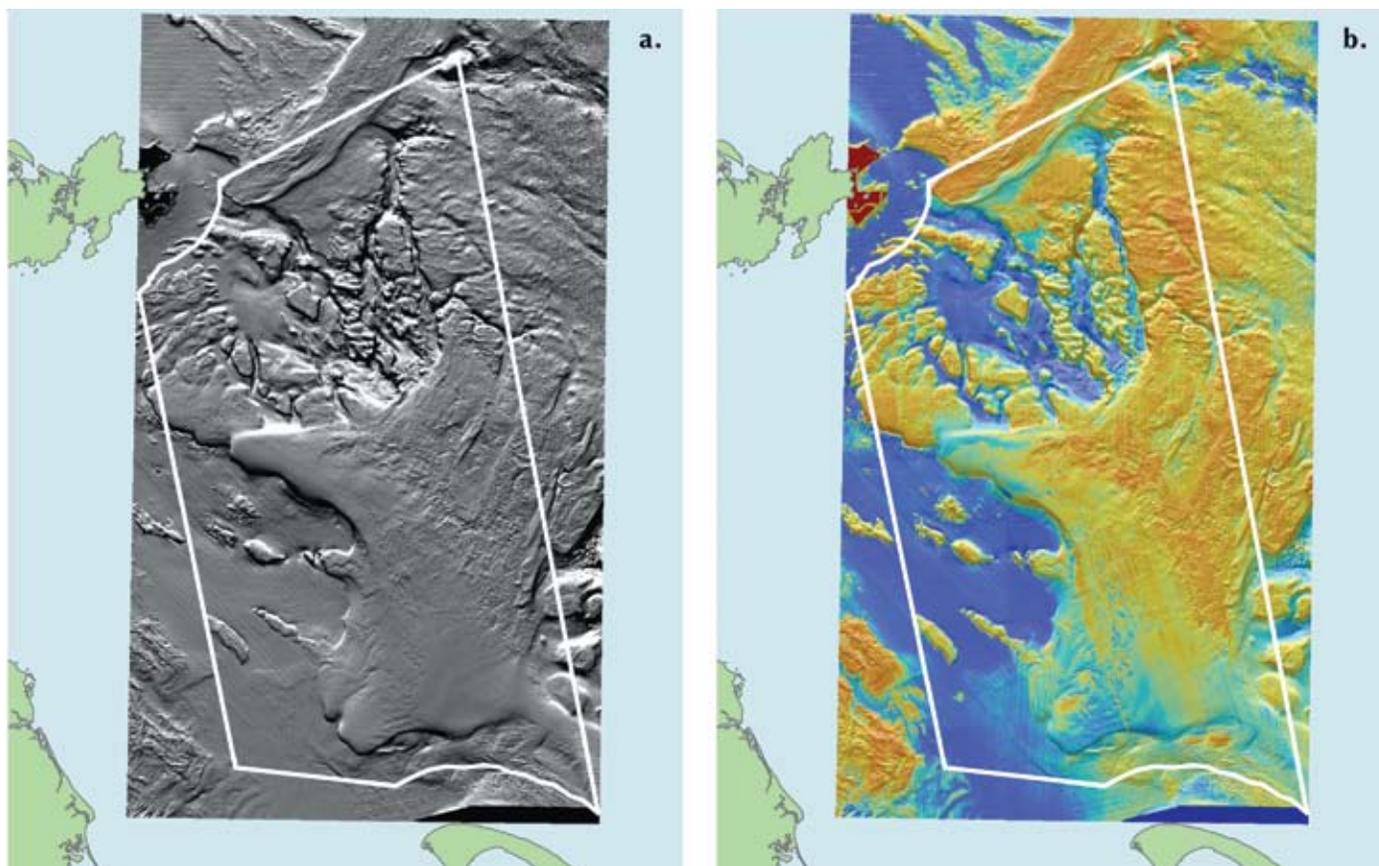
FIGURE 9. HISTORIC REDUCTION IN MEAN TLS IN FISHERY LANDINGS IN THE GOM FROM STATISTICAL BULLETIN LANDINGS DATA (1901–1935) AND LME NORTHEAST U.S. CONTINENTAL SHELF LANDINGS (1950–2003).

Fishing pressure over the past century has reduced the mean TL of landings in the GoM region, a long-term trend that continues through the present. This figure serves as an example of a historical baseline of ecosystem condition. Trophic level indicates position in the food chain determined by the number of energy-transfer steps to that level. By convention, plants have a TL = 1, herbivores TL = 2, and so on up to a TL = 5 such as for killer whales. Courtesy: Stephan Claussen, GoM cod project, University of New Hampshire.

FIGURE 10. MULTI-BEAM SONAR IMAGE OF THE STELLWAGEN BANK SANCTUARY AREA SHOWING (a) SUN-ILLUMINATED SEAFLOOR TOPOGRAPHY AND (b) BACKSCATTER INTENSITY OF SEDIMENTS.

Source: USGS.

requirements and the important attributes of "habitat" vary between species and between the various life history stages within species.

Regional topography and surficial seabed features of the sanctuary have been mapped in great detail based on multi-beam echo sounder imagery and on extensive ground-truthing with video and photographic imagery and geological and biological sampling. Habitat characterization produces descriptors of habitats based on geological, biological, chemical and oceanographic observations. Habitat classification produces a set of habitat types based on a suite of standard descriptors of topographical, geological, biological, natural, and anthropogenic features and processes. Habitat mapping is the spatial representation of described and classified habitat units (Valentine *et al.*, 2005). The development of a new seabed classification scheme has made it possible to map habitats based on substrate texture, seabed dynam-

ics, the complexity of physical and biological structures on the seabed, and fauna (Valentine *et al.*, 2005).

The simplest classification of habitats in the Stellwagen Bank sanctuary that can be discerned is based on the multi-beam echo sounder imagery which reveals backscatter intensity—a measure of the hardness of the substrate (Figure 10). Based on this imagery, the sanctuary contains three basic physical habitat types: gravel, sand and mud with the following coverage: 34%, 28% and 38%, respectively. Bedrock outcrop and piled boulder reefs are other important physical habitats. Bedrock outcrop is found only on Sanctuary Hill in the northeastern-most corner of the sanctuary; piled boulder reefs are extensively associated with sand and gravel areas of the sanctuary (Valentine *et al.*, 2001). Imagery from ground-truthing and physical sampling reveals that each of the three basic habitat types can be further subdivided into more descriptive categories such as mobile rippled coarse-grained sand, for example (Valentine *et al.*, 2005).

PHYSICAL SETTING

The physical setting of the sanctuary is the structural foundation for its biological processes. The first set of sanctuary regulations that were established when the sanctuary was designated was intended to prevent Stellwagen Bank from being mined for its sand and gravel resources. Minerals extraction has enormous potential to adversely impact the ecosystem functions of the sanctuary by physically altering the surface profile of Stellwagen Bank and its attendant oceanography. Exploring for, developing or producing industrial materials such as oil and gas within the sanctuary are strictly prohibited. Other regulations prevent the drilling into, dredging or otherwise altering the seabed of the sanctuary or constructing, placing or abandoning any structure, material or other matter on the seabed of the sanctuary, except as exempted as an incidental result of traditional fishing operations, for example.

An understanding of the physical setting—the linkages between its geography, geology and oceanography—enables understanding of how regional, large-scale processes of the GoM ecosystem connect with and directly impact the local biodiversity patterns and processes at the scale of the sanctuary. For example, the habitats of marine mammals are affected by the physical and chemical properties of the water through which they swim and communicate, the topography and substrate type of the ocean bottom and water column characteristics where they feed, the physical state of the ocean surface where they breath, and the numerous factors influencing the distribution of food organisms (including temperature, salinity, currents and winds) that determine their distribution and local abundance.

GEOGRAPHY

The Stellwagen Bank sanctuary stretches between Cape Cod and Cape Ann at the mouth of Massachusetts Bay and is virtually the size of the state of Rhode Island (Figure 11). It covers 842 square-miles (2,182 km2) of marine waters and is located entirely within federal jurisdiction. At its greatest distance from the coast, the sanctuary is located approximately 25 nautical miles east of Boston, Massachusetts, and 3 nautical miles off Cape Ann and Cape Cod. On a regional scale, the sanctuary is a part of the GoM LME.

The sanctuary is a topographically diverse area that encompasses the submerged Stellwagen Bank and Basin, Tilles Bank and Basin and a portion of Jeffreys Ledge in the southern GoM. The GoM is a large gulf of the Atlantic Ocean on the northeastern coast of North America, roughly between Cape Cod in Massachusetts to the south and Cape Sable Island on the southern tip of Nova Scotia to the northeast (Figure 12). It includes the entire coastlines of the States of New Hampshire and Maine, as well as Massachusetts from the north side of Cape Cod, and the southern and western coastlines of the Canadian provinces of New Brunswick and Nova Scotia, respectively. Massachusetts Bay and the Bay of Fundy are included within the GoM LME.

There are three major basins contained within the GoM: Wilkinson Basin to the west, Jordan Basin in the northeast, and Georges Basin in the south, which are isolated from each other beneath the 650 ft. (200 m) isobath. Georges Basin, just north of Georges Bank, is the deepest of the three at just over 1,200 ft. (370 m) and generates a pocket at the end of the Northeast Channel, a deep fissure between Georges Bank and Browns Bank, the southwestern edge of the Nova Scotian Shelf. The Northeast Channel is the major channel between the GoM and the rest of the Northwest Atlantic. A secondary, shallower connection to the rest of the Atlantic is the Great South Channel, located between Georges Bank and the Nantucket Shoals. The sanctuary's geographic location relative to the arctic and temperate regions of the Northwest Atlantic makes it an obvious focus for biodiversity research.

GEOLOGY

Stellwagen Bank is the most prominent geological feature in the sanctuary and is one of only two shallow (less than 20 m

depth) sandy banks in the Gulf of Maine (GoM)—the other one being Georges Bank. Stellwagen Bank is a glacially-deposited feature, curved in a southeast-to-northwest direction for almost 32.2 km; it measures 18.75 miles in length and roughly 6.25 miles across at its widest point, at the southern-most portion of the bank (Figure 11). The seabed of the sanctuary is a complex of geomorphic features and substrate types that formed by 1) glacial ice movement, 2) erosion and deposition of sediments during ice melting and sea level rise, and 3) reworking by modern currents (Valentine et al., 2005).

Like Cape Cod and the islands of Martha's Vineyard and Nantucket, Stellwagen Bank and other submerged banks and ledges off the northeastern United States coast were created by the advance and retreat of glaciers. Stellwagen Bank owes much of its existence to the Laurentide Ice Sheet that advanced out of Canada and into southern New England approximately 21,000 years ago (Oldale, 1993,1994). As the ice sheet advanced, it was shaped into huge lobes. One ice lobe was formed by what is now Cape Cod Bay; the other by the present-day Great South Channel, located to the southeast of Cape Cod. The advance of ice over the continental land mass ground the land into fragments and carried them along with the movement of the ice.

With general climatic warming between 18,000 and 15,000 years ago, the glaciers began to melt and retreat from their coverage. The ice lobes became more pronounced, and retreated at differing rates, depending on the depths of topographical depressions within which they moved. During this process enormous amounts of pulverized continental land were released from the melting ice. These land fragments, or "outwash" from the two ice lobes formed much of the present-day Cape Cod peninsula. Retreat of the ice lobe formed by the Great South Channel was sufficiently slow that much of the land fragments it carried melted out and was deposited on the sea floor. These materials formed the submerged elevation now known as Stellwagen Bank

Through the continual evolution and refinement of technologies for mapping the seafloor, the characterization of the sanctuary landscape is also continuously evolving (Valentine et al., 2001). Multi-beam imagery provides a level of resolution of landscape features that has been unattainable with lower resolution bathymetric and seafloor geological surveys. Multi-beam imagery provides a highly detailed picture of the seafloor landscape, providing detailed bathymetry. Most multi-beam systems also provide a measure of acoustic backscatter. Using backscatter data, the relative hardness of a substrate can be determined by the strength of the acoustic signal reflectance.

The USGS completed an initial series of 18 seafloor topographic maps (scale 1:25,000) in 1997 that covers the entire sanctuary. The data were collected using a hull-mounted multi-beam system. This map series was followed by sun-illuminated versions of the multi-beam maps in 2001. Additional backscatter and sediment characterization maps are in preparation that will also cover the sanctuary.

The entirety of the sanctuary as well as a surrounding buffer area has been mapped using multi-beam sonar (approximately 1,100 nm2 in total) at a vertical resolution of approximately 25 cm and a horizontal resolution of approximately 10 m. Figure 10 shows the sun-illuminated seafloor topography and acoustic backscatter sediment maps of the sanctuary. Substrate type is color coded and superimposed over the bathymetry. The sanctuary multi-beam map, in conjunction with extensive ground truthing (e.g., video, still photos, sediment samples), provides the most complete characterization of the seafloor in the GoM. For more information on seafloor maps of the Stellwagen Bank sanctuary go to http://woodshole.er.usgs.gov/project-pages/stellwagen/stellwagenbank.html.

This section served as an introduction to the gross geological features and processes of the sanctuary area. Descriptions of additional geological aspects of the sanctuary are provided in subsequent discussions of landscapes and physical and biogenic habitats.

OCEANOGRAPHY

Ocean circulation through and around the Stellwagen Bank sanctuary drives the dynamic biology of the area, and that circulation is greatly influenced by the sanctuary's location within the greater GoM. While Stellwagen Bank is an important feature driving local water circulation, the sanctuary's water properties and dispersal mechanisms are largely determined by large-scale oceanographic patterns. To gain perspective, it is necessary to understand these large-scale patterns and how they influence the smaller-scale unit of the sanctuary. Many processes (tides, currents, sea surface temperature, internal waves, thermal fronts, etc.) comprise the oceanographic character of the region and their interactions drive large and small-scale biological dynamics.

An in-depth description of the sanctuary area's physical oceanography is provided in "An ecological characterization of the Stellwagen Bank National Marine Sanctuary region" (NOAA, 2006). Drawing from that document, a general description of the key oceanographic features that shape the sanctuary environment follows and includes discussion of general patterns of circulation at different geographic scales and the role of internal waves. A key attribute of the sanctuary's physical oceanography is its regional connectivity with other parts of the GoM. This connectivity is important in understanding the sanctuary's ecological role in supplying and receiving larval recruits across the region, as well as the paths taken by pollutants and contaminants in relation to the sanctuary.

GENERAL PATTERNS OF CIRCULATION

GULF OF MAINE CIRCULATION

A combination of physical and oceanographic characteristics in the GoM results in cycles of biological productivity that support exceptionally large and diverse populations of fish, that in turn attract and support seasonal populations of cetaceans and seabirds. Bounded by underwater offshore banks, the prevailing counterclockwise circulation results

from ocean currents, freshwater inflow, and the configuration of shoreline and underwater topography which together create a nearly self-contained oceanographic system (Figure 12).

The interior GoM has cyclonic circulation regions situated over three deep basins—Georges, Jordan and Wilkinson. The gyres are influenced by the deep inflow of saline waters through the Northeast Channel and forced by topography (Hannah *et al.*, 1996; Lynch, 1999). The dominant temporal variability in the gyres or between gyres is on the order of months (Xue *et al.*, 2000). The current patterns in the GoM are greatly affected by the physical characteristics of the gulf and its coastline.

In general, cold water enters the gulf over the Scotian Shelf, Browns Bank and through the Northeast Channel. Water flows around Nova Scotia and into the Bay of Fundy. The coast then deflects currents southwestward forming the GoM gyre, which rotates counterclockwise, moving surface waters about 7 nm per day. Tidal fluctuations and shallow water over Georges Bank form a secondary, clockwise-spinning gyre. Water leaves the Gulf through the Great South Channel and over the eastern portion of Georges Bank. It takes about three months for surface water to completely circle the GoM. Deep waters also circulate, but much more slowly, taking about a year to complete the circuit (Xue *et al.*, 1999).

Current speed and direction can

The image shows the glacially-deposited Stellwagen Bank within the boundaries of the national marine sanctuary. Source: NOAA/NOS.

vary spatially and temporally throughout the GoM. Over 20 buoys are stationed throughout the Gulf that collect hourly oceanographic and meteorological data as part of the Gulf of Maine Ocean Observing System (GoMOOS). For more information, visit URL http://gomoos.org/buoy/buoy_data.shtml. Hourly current speeds were obtained from the GoMOOS Buoy A during 2002-2006 to examine monthly and inter-annual patterns. During this time period, mean current speed was highest (and most variable) during April and May and lowest speeds were observed during the summer and fall.
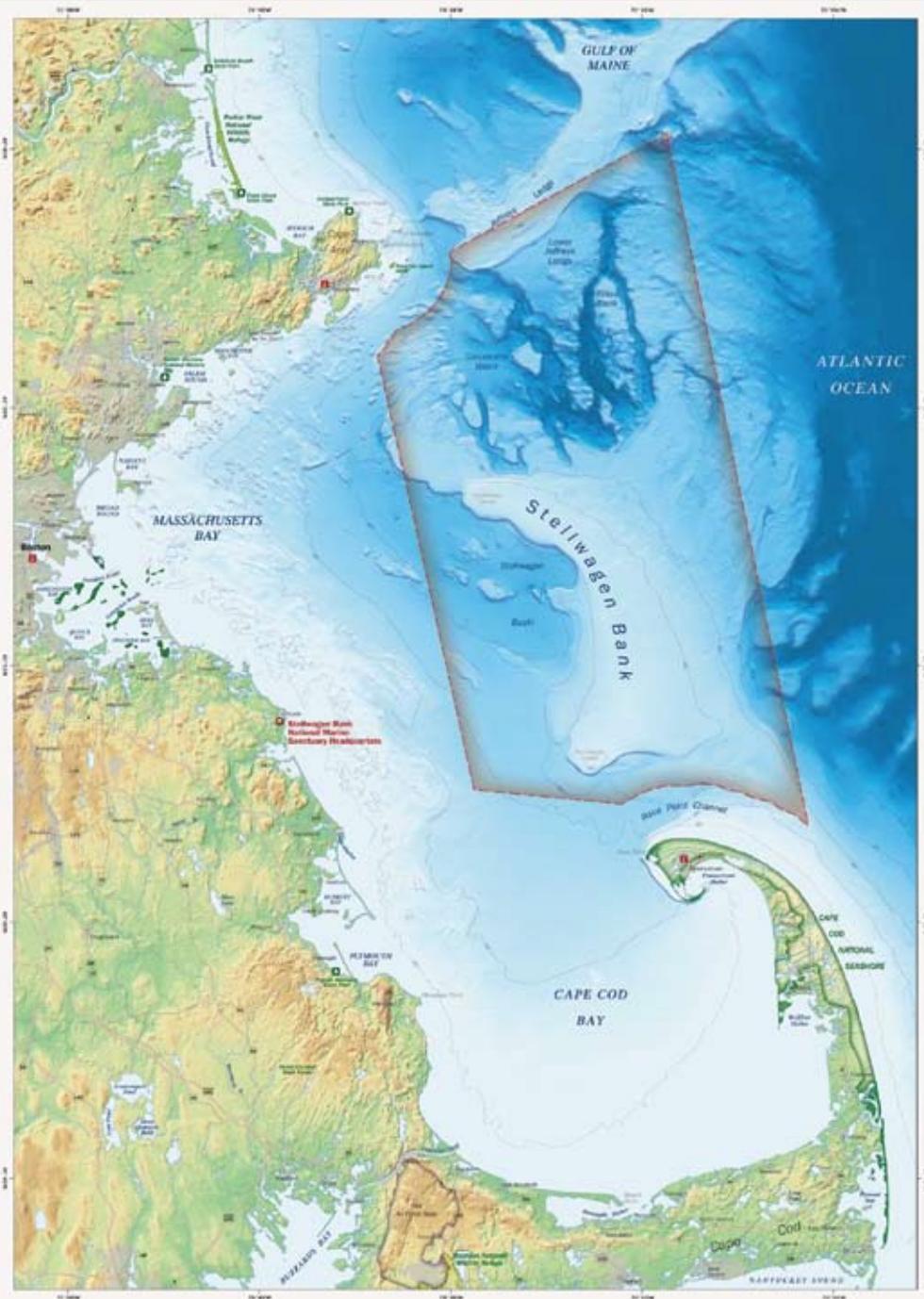
Massachusetts Bay Circulation

Circulation in Massachusetts Bay (Figure 13) is controlled by the large-scale circulation in the GoM, localized wind forcing, and freshwater inflow (Signell *et al.*, 2000). The Maine Coastal Current (MCC) flows south at 5–15 cm/s along the Maine and New Hampshire shoreline. A weak branch (2–5

cm/s) occurs near Cape Ann. Usually the MCC flows south along the eastern edge of Stellwagen Bank and east of Cape Cod (Normandeau Associates, 1975; Vermersch *et al.*, 1979; Blumberg *et al.*, 1993; Bumpus, 1973; Lynch *et al.*, 1997). However, as explained below, the MCC can strongly influence the circulation pattern in Massachusetts Bay and Cape Cod Bay depending on the season (Figure 13).

The circulation pattern can be altered by seasonal wind and runoff events (Signell *et al.*, 2000). The main current joins smaller coastal currents and flows southward, often penetrating deep into Cape Cod Bay (Jiang and Zhou, 2004). Seasonal variation in stratification occurs in Massachusetts Bay, with well-mixed conditions during winter and strong stratification during summer (Geyer *et al.*, 1992). The stratification greatly reduces vertical exchange between surface and bottom waters and isolates the bottom water from the direct influence of wind stress and river runoff (Signell *et al.*, 2000).
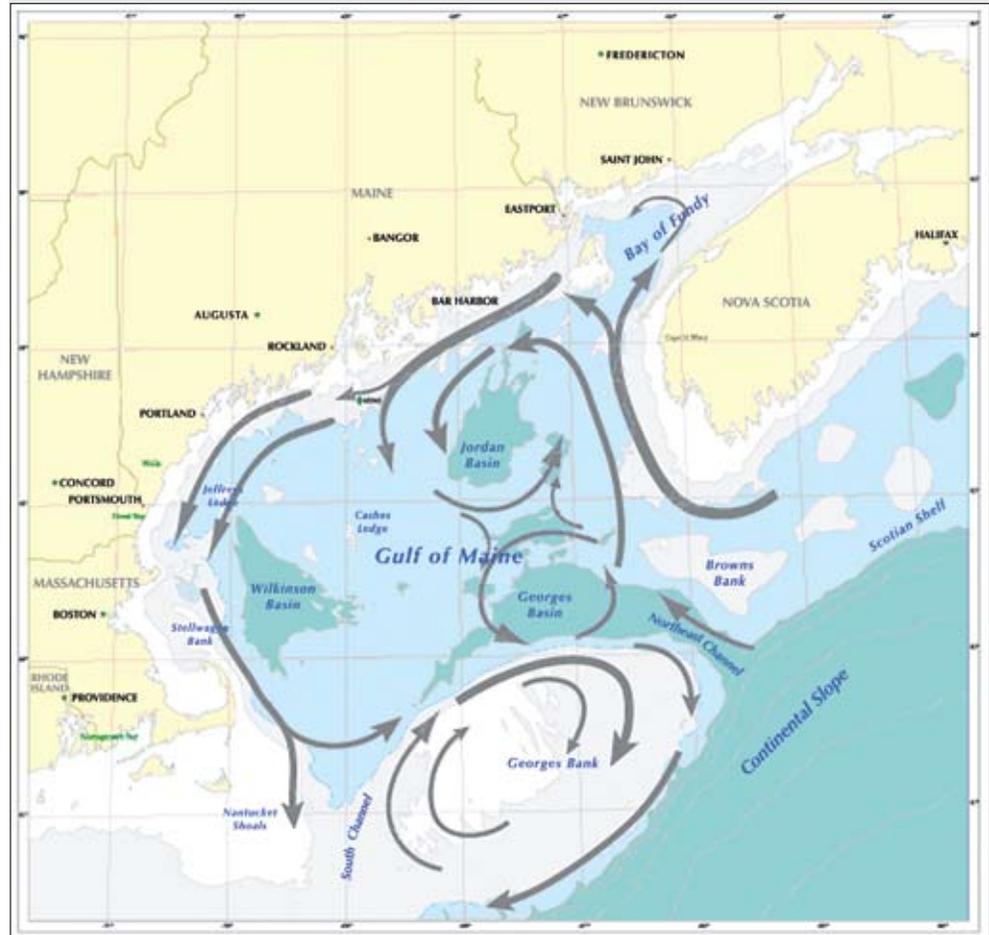
The seasonal variations of stratification, wind stress, and river discharge change the nature of transport and dispersion processes in Massachusetts Bay. During winter, strong northerly winds enhance the counter-clockwise circulation along the shoreline and northward flow in the deeper portions of the Bay (Butman, 1975; Brickley, 1994). In the spring, shallow (5–15 m) fresh water plumes enter the Bay, commonly generating strong currents (20–30 cm/s) with 10–30 km spatial scales (Butman, 1976; Lee, 1992). Summer conditions stratify the water column and frequent southwesterly winds can result in localized upwelling along the western and northern coast. During the fall, mean circulation reverses and flows northward as the result of strong cooling (Geyer *et al.*, 1992).

Significance to the Sanctuary

These broad-scale circulation patterns significantly affect water column mixing and transport mechanisms in the sanctuary. Mixing on the continental shelf is an important process for redistributing nutrients, sediments, freshwater, pollutants, plankton and fish larvae (Carter *et al.*, 2005). Stellwagen Bank serves as a boundary between the GoM to the east and Massachusetts Bay to the west and is an important determinant of the water properties within Massachusetts Bay. The sanctuary is located along the major path of

the Maine coastal current, while also receiving surface and subsurface flows from Massachusetts Bay (Figures 12 and 13).
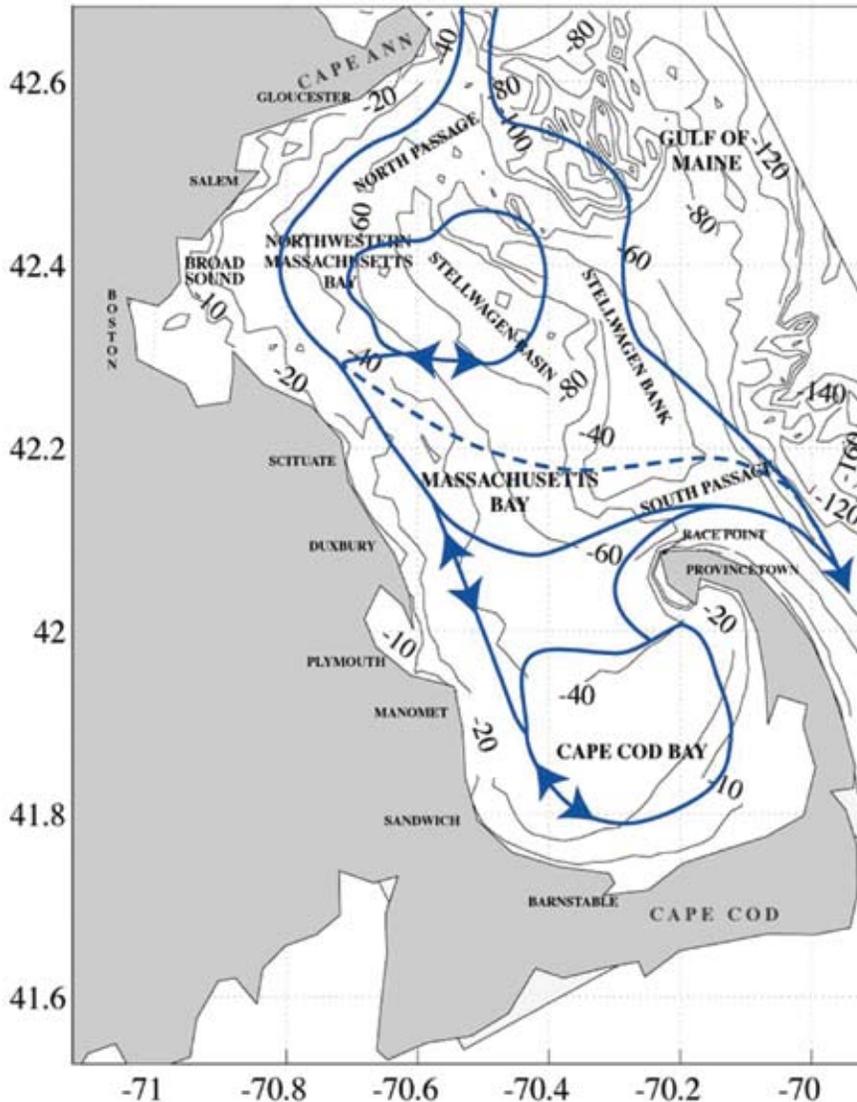
The physical oceanographic processes at work in Massachusetts Bay are critical to the generation of biological productivity and maintenance of biological diversity in the sanctuary. These ecological qualities are in turn important to sustaining local fishing and recreation industries and for resource conservation efforts. Understanding circulation patterns helps to identify biological sources to and exports from the sanctuary in the form of larval recruits or zooplankton concentrations and provides insight into the transport and deposition of sediments and "red tide" spores as well as potentially harmful contaminants from local sewage discharges.

INTERNAL WAVES

Internal waves are particularly important for internal mixing and localized transport within the sanctuary area (Figure 14). Stellwagen Bank (most notably) and Cashes Ledge are biologically productive as a result of internal wave dynamics (Sherman *et al.*, 1996). Internal waves are literally waves under the ocean's surface that occur at the interface between two water layers of differing densities (Brown *et al.*,

Solid lines represent most common patterns; dashed lines represent less common patterns. Source: Lermusiaux (2003).

phytoplankton downward to benthic communities (Witman *et al.*, 1993). This mechanism may also serve as vertical transport for passively dispersed larvae of benthic invertebrates and fish (Witman *et al.*, 1993; Meekan *et al.*, 2006).

Strong convergence of internal waves at the bottom causes sediment re-suspension (Boczar-Karaiewicz *et al.*, 1991), including recently settled invertebrate larvae and toxic algae cysts (Scotti and Pineda, 2004). The existence of trapped cores (pockets of water) between internal wave crests also suggests internal waves are a prime candidate for concentrating and transporting larvae which nourish benthic communities (Scotti and Pineda, 2004). Internal waves, and potentially other related transport mechanisms, have a significant influence on ecological processes in the sanctuary (Scotti and Pineda, 2004).

Internal waves can have additional benthic impact by re-suspending sediments. Recent evidence (Butman *et al.*, in preparation) has shown that benthic currents associated with internal waves caused sediment re-suspension within Stellwagen Basin at depths between 50-85 m. Net transport direction was offshore and currents were of considerable speed to carry sediments 5-20 km. Thus, sediments in shallower portions of Massachusetts Bay are frequently re-suspended and carried offshore and are typically deposited in the deeper Stellwagen Basin. Due to weaker current flows, sediments re-suspended in Stellwagen Basin do not typically leave the basin, but are re-deposited (Butman *et al.*, in preparation).

1989). They occur when seasonally stratified water is forced over abrupt topographic features, such as banks or ledges, by diurnal tides. Internal waves disappear as they approach shallow water (typically 25 to 40 m in depth) because of decreasing depth (Jackson and Apel, 2004). Internal waves usually occur in Massachusetts Bay between May and October when the water column is stratified.

Internal waves contribute to the energetics of the upper ocean in many ways; in particular, they enhance mixing and nutrient availability (Jackson and Apel, 2004). Plankton distribution exhibits strong vertical displacements and mixing associated with the passage of internal wave packets (Haury *et al.*, 1979). The ability of internal waves to mix stratified water layers during the summer provides a mechanism for benthic-pelagic trophic coupling by moving

Synthetic Aperture Radar (SAR) can detect internal waves by emitting pulses of microwave energy, producing a two-dimensional radar backscatter map of the roughness of the ocean surface (Apel and Jackson, 2004). In SAR imagery, internal waves appear as packets or groups of waves characterized by alternating bright and dark bands and decreasing wavelengths from front to back of each packet, indicating direction of propagation. While wave packet size is variable, imagery from Massachusetts Bay and surrounding waters has shown high density (number of packets/km2) internal waves within the Stellwagen Bank sanctuary area (Figure 14).

CONNECTIVITY

The GoM connects the New England states (Massachusetts, New Hampshire, and Maine) and the Canadian provinces
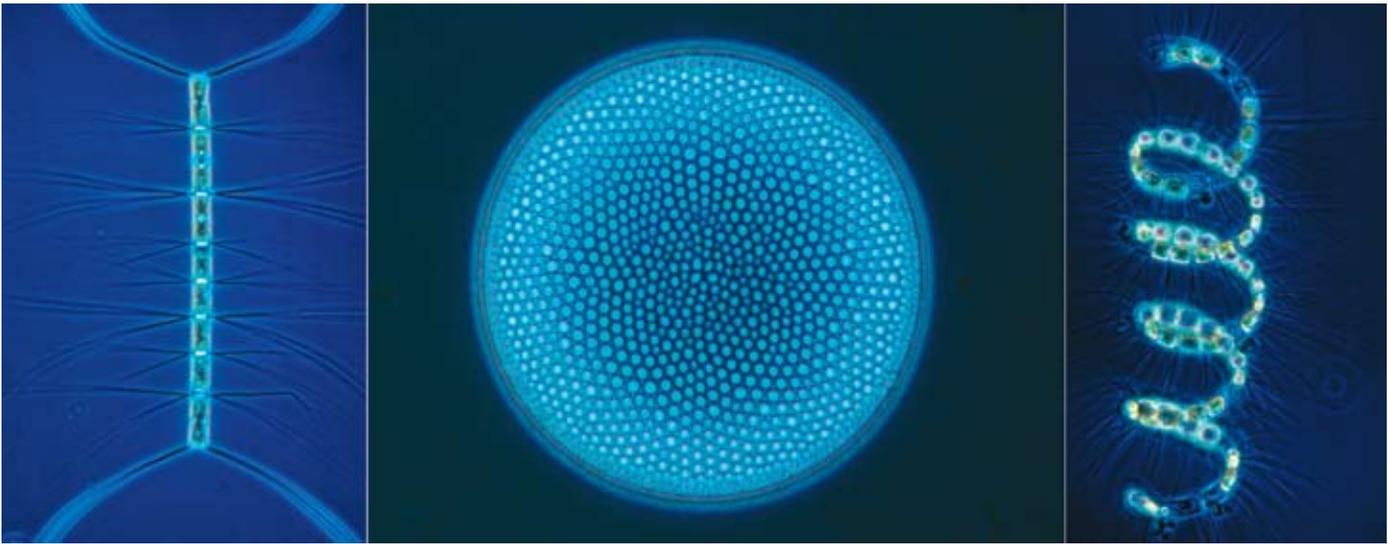
(New Brunswick and Nova Scotia) with 93,239 km2 of ocean along 19,424 km of shoreline. Stellwagen Bank sanctuary is integrally connected with the rest of the GoM through water circulation. The sanctuary both receives water and associated particles (larvae, plankton, etc.) via the Maine Coastal Current and disperses water and particles to areas to the south (Great South Channel) and east (Georges Bank). A recent example of this connectivity occurred when one of the sanctuary's acoustic recording units deployed on the bottom broke free and drifted to Georges Bank where it was retrieved by the USGS. Additionally, this connectivity has been shown through the use of telemetered drifter buoys.

NOAA Fisheries Service NEFSC has deployed telemetered drifter buoys for several years throughout the GoM to serve as proxies for the transport of American lobster larvae which remain in the water column as plankton for approximately one month. Many of the buoys deployed in or near the Stellwagen Bank sanctuary have revealed how complex the surface currents are in Massachusetts Bay and how strong the connection is between the sanctuary and areas to the east and south, such as Georges Bank and outer Cape Cod and the Islands (Figure 15). These drifter tracks correspond well with the generalized circulation depicted in Figure 12. The implication of this connectivity is that the sanctuary serves as both a source (for export) and a sink (for import) for larvae of most fish and invertebrate species throughout the southwestern and central GoM.

FIGURE 14. SYNTHETIC APERTURE RADAR (SAR) IMAGE OF INTERNAL WAVE EVENTS IN MASSACHUSETTS BAY ON AUGUST 7, 2003.

Three internal wave packets are obvious as curvilinear features in the sanctuary area north of Cape Cod. Image courtesy of European Space Agency, processed by Jose da Silva, Univ. of Lisbon. Envisat ASAR, 7 August 2003 2:30 GMT; image precision mode.

(a) Track of drifter buoy 65208 deployed on May 2004 off of Isle au Haut, Maine, revealing connectivity between the south-west margin of the GoM, the sanctuary and Georges Bank; (b) Track of drifter buoy 65207 deployed on June 27, 2006, off of Boston Harbor revealing connectivity between the sanctuary and the interior GoM; and (c) Track of drifter buoy 55202 deployed on June 13, 2005, off of Cape Ann, Massachusetts, revealing connectivity between the sanctuary and the islands south of Cape Cod. Courtesy: James Manning, NOAA Fisheries Service/NEFSC.

PRIMARY PRODUCERS AND DECOMPOSERS

Marine bacteria, protists (e.g., algae, phytoplankton, protozoans) and fungi are crucially important at many levels of ecosystem function. By most accounts vascular plants and seaweeds do not occur in the sanctuary, but microscopic organisms are astronomically numerous and make up the bulk of the primary producers and decomposers, fixing carbon and recycling nutrients through a variety of biochemical processes. These microscopic organisms are actively engaged in all processes of biologically induced energy transfer through all ecosystem pathways involving all TLs, biological communities and habitats. While the species diversity of this group of organisms is poorly documented, their great importance as a functioning element of the sanctuary ecosystem merits their acknowledgement in this document.

Investigations of biodiversity are complicated by the paucity of knowledge of certain taxonomic groups, particularly those in the following three categories (prokaryotes, protists and fungi). What one taxonomist considers a species may be only a subspecies to another. The greater scientific body relies on the expertise of taxonomists in their fields of specialization as to what level of phenotypic and genetic variation is sufficient to warrant species status. In addition, many taxonomic groups such as the marine bacteria and fungi have received little attention in relation to their species diversity. Instead, one must consider their generic or functional diversity. With such disparities, the study of biodiversity in these groups is just beginning; an annotated technical summary follows. Scientific nomenclature not explained in the text is described in the glossary of this document.

These organisms are mostly found in or on the sediments and plankton of the sanctuary. Plankton consists of microscopic drifting organisms that inhabit the water column. The plankton is primarily divided into broad functional (trophic level) groups consisting of bacterioplankton, phytoplankton and zooplankton. Bacterioplankton are bacteria and archaea which play the role of decomposers and recyclers.

Phytoplankton are largely pro- or eukaryotic algae that live in the upper water column where there is sufficient light to support photosynthesis; they serve as the primary producers. However, the TL of some phytoplankton is not straightforward, and some species, e.g., certain dinoflagellates are mixotrophic (producers or consumers) depending on environmental conditions. Zooplankton are small protozoans or metazoans (e.g., crustaceans and other animals) that feed on other plankton and serve as the primary consumers in the ecosystem.

Zooplankton are not addressed separately in this document because of the extensive treatment that would require, but their ecosystem role as primary consumers of phytoplankton and prey for organisms at higher TLs is enormously important. Certain species, such as the Calanoid copepod *Calanus finmarchius* is prey both for fish (e.g., sand lance) and whales (e.g., North Atlantic right whale) in the sanctuary.

Viruses, another group of microscopic organisms, also are not given any treatment here because virus diversity has not been addressed in the Northwestern Atlantic (Fuhrman, 1999). Viruses are known primarily as pathogens and little is known of their ecology. The topic is of pragmatic importance due to the likelihood for transport or accidental introduction of exotic pathogens and the complicated density dependant functions of disease. The role of virus particles as pathogens and gene vectors in nature makes the lack or near absence of data on their distribution in the GoM an acute problem, but only a general concern for sanctuary management at this time because there are no overt problems.

PROKARYOTES

Prokaryotes (bacteria and archaea, the latter group not distinguished in this review) are the biochemical specialists of the ecosystem. Each bacterium consists of a simple, single cell, lacking a nucleus and chromosomes to organize its DNA. Nonetheless, bacteria accomplish many unique

biochemical transformations due to the enormous range of their metabolic capabilities. Only a very small amount (perhaps less than 1%) of all microbial diversity has been studied (Colwell *et al.*, 1995). Thus, it would be impossible to include a list of prokaryote species found in the sanctuary. The official list of the described bacteria is contained in the *International Journal of Systematic Bacteriology*. In marine communities, some taxonomic categories are studied considerably more than others.

Margulis and Schwartz (1998) provide a description of the major prokaryotic lineages and functional groups and describe their intimate relationships with higher organisms. The prokaryotes are involved in virtually every metabolic pathway and every link in the marine food web (e.g., Cavanaugh, 1994; Dubilier *et al.*, 1999; Hinrichs *et al.*, 1999). Bacteria drive and regulate a seemingly infinite number of marine processes (e.g., Schlitz and Cohen, 1984; Schropp *et al.*, 1987; Hines *et al.*, 1991) and y*et al*most nothing is known of their distribution or diversity. Bacteria in the North Atlantic, as everywhere, are the key operators of biological processes in marine sediments (Chepurnova *et al.*, 1987; Christensen and Rowe, 1984; Lyons *et al.*, 1980; Vetriani *et al.*, 1999) and constitute a significant portion of the primary producers within the euphotic zone (Ducklow, 1999). The evolution and species diversity of certain of these groups has been considered (Kawasaki *et al.*, 1993), while others have been ignored or await description. Rath *et al.* (1998) discuss the biological diversity of marine snow communities.

In marine ecosystems, like most others, prokaryotes play a significant role as pathogens (Colquhoun *et al.*, 1998; Cook and Lynch, 1999; Greger and Goodrich, 1999; Lewis *et al.*, 1992; Linn and Krieg, 1978; Schropp *et al.*, 1987; Tall *et al.*, 1999). The ecology, physiology and evolution of bacteria are discussed in every issue of the *Journal of Fish Diseases*, yet a synthesis and overview of prokaryote ecology in the marine environment is lacking and probably premature because of all that is still unknown.

Bacterial communities are governed by distinct temporal cycles (Balch, 1981; Glover *et al.*, 1985b; Keller *et al.*, 1982, 1999), inherent behavioral variances (Dalton *et al.*, 1996) and site-specific environmental variables (Cuhel *et al.*, 1983; Ducklow *et al.*, 1992; Ducklow *et al.*, 1993; Nold and Zwart, 1998). Spatial variances in bacterial community structure are apparent across landscapes (Mullins *et al.*, 1995; Murray *et al.*, 1999; Zubkov *et al.*, 1998) and across ocean strata (Gutvejb *et al.*, 1987; Townsend and Cammen, 1985). Some researchers have investigated the ecology of specific prokaryotes (Balch *et al.*, 1992; Fredrickson *et al.*, 1999; McHatton, 1999; Rieley *et al.*, 1999), but such studies are rare when weighed against the overall diversity and functional importance of the group.

Several studies have considered the genetic diversity of marine prokaryotes (Field *et al.*, 1997; Fuhrman and Ouverney, 1998; Giovannoni *et al.*, 1996; Zumarraga *et al.*, 1999), but these results are difficult to interpret in light of the species definition dilemma. The picoplankton or

ultraplankton (0.2-2 micrometers in size) are given separate status by some. Glover *et al.*, (1985a) and Murphy and Haugen (1985) suggest that cyanobacteria (formerly referred to as blue-green algae) are the most important segment of the bacterioplankton in unproductive sites, since cyanobacteria are known for their resourcefulness in acquiring nitrogen under oligotrophic conditions. Murphy and Haugen (1985) cover the vertical distribution and abundance of the cyanobacteria. Glover *et al.* (1985a, 1985b) include them in discussion of the picoplankton, as do Murphy and Haugen (1985). Genetic work suggests this group is globally intermixed (Mullins *et al.*, 1995).

Davis *et al.*, (1978) showed that marine waters contain approximately equal amounts of heterotrophic and autotrophic picoplankton. A heterotroph is an organism that requires organic substances to get its carbon for growth and development; it is known as a consumer in the food chain. An autotroph is an organism capable of synthesizing its own food from inorganic substances, using light or chemical energy; it is known as a producer in the food chain. These general studies are only first insights into the functional diversity of marine prokaryotes. No studies have related this topic directly to the sanctuary.

Wichels *et al.* (1998) discuss bacteriophage (a virus that infects bacteria) diversity in the North Sea. One would expect similar levels of diversity in the sanctuary, but the constituent species from that region may be quite different.

PROTISTS

Protists are an extremely diverse group of mostly single-celled eukaryotes—organisms having nuclear membranes and other cell organelles—ranging from slime molds and protozoans to phytoplankton and red, brown and green algae. The protists are a paraphyletic grade, rather than a natural group, and do not have much in common besides a relatively simple organization (unicellular, or multicellular without highly specialized tissues). Protists were traditionally subdivided into several groups based on similarities to higher kingdoms: the animal-like protozoa, the plant-like algae, and the fungus-like slime molds. While these groups have been replaced by phylogenetic classifications, they are still useful as an informal way to characterize this assemblage of organisms.

Several authors have described the macrophytes (large aquatic plants) and phytoplankton assemblages of the northeast region. Villalard-Bohnsack (1995) presents an illustrated key to the seaweeds. South and Tittley (1986) developed a checklist of the benthic algae for the whole North Atlantic. Bigelow (1924) gives an overall description of the offshore plankton from the GoM. A comprehensive discussion is given by Taylor (1957) for the northwestern Atlantic and addresses geographic distribution of algal species within that region. Marshall and Cohn (1982b, 1983) discuss general patterns of distribution and diversity of the algae. A more recent discussion of the topic is given in Silva (1992). Vadas and Steneck (1988) outline the geographical zonation

of benthic algal species, and Townsend and Cammen (1985) showed zonation along vertical strata of the open ocean.

Mathieson (1989) includes some discussion of the distribution and diversity of the Rhodophta (red algae); their taxonomy is unresolved. Taylor (1957) includes most species one would encounter in the region. Mathieson (1989) includes discussion of the distribution and diversity of the Phaeophyta (brown algae) as well. South and Tittley (1986) include some discussion of the distribution of benthic Phaeophytes. There is currently no text dedicated to this group, and there is no research relating the specific diversity or distribution of the Phaeophyta relative to the sanctuary. Mathieson (1989) discusses the distribution and diversity of the Chlorophyta (green algae). Taylor (1957) covers the green algae in his descriptions, and this dated work is still one of the most complete. There are no published descriptions or records for these macrophytes from the Stellwagen Bank sanctuary.

Cahoon *et al*. (1993) discussed the productivity of benthic micro-algae on Stellwagen Bank, one of the few studies to address the *habitus* of this ocean feature. Protist productivity is at least partially governed by physical oceanographic processes, and several authors consider this relationship in the region of the sanctuary (Townsend *et al*., 1987; Franks, 1990; Townsend, 1991; Kerkhof *et al*., 1999). A more detailed examination is provided by Matta and Marshall (1983). Ducklow *et al*. (1992, 1993) discuss the growth of the protists during a plankton bloom, an important food web phenomenon.

In addition to physical-spatial variances, seasonal environmental variances play a significant role in growth, productivity (Durbin *et al*., 1995b; Keller *et al*., 1982) and patterns of diversity (Marshall and Cohn, 1982) of the protists. Mathieson (1989) discusses seasonal variance and its relation to reproduction of the protists in the GoM. Glover *et al*. (1985b) cover diurnal variations in the photosynthetic rates. Environmental and biological variances at all time scales may affect protist diversity.

Diatoms are a major group of eukaryotic algae and one of the most common types of phytoplankton. Most diatoms are unicellular, although some form chains or simple colonies; a characteristic feature of diatom cells is that they are encased within a cell wall made of silica. The general distribution of diatoms is covered in Marshall (1984). Over 1,000 species have been described. Several authors address the diatoms in their general discussion of marine algae (Bigelow, 1924; Marshall and Cohn, 1982; Sears and Cooper, 1978; Taylor, 1957). Round *et al*. (1990) describe the diatom genera and their biology, and include the marine groups.

Dinoflagellates are a large group of flagellate algae; most are marine plankton. About half of all dinoflagellates are photosynthetic, and these make up the largest group of eukaryotic algae aside from the diatoms. The dinoflagellates are most famous for their toxic blooms, i.e., "red tides" (Franks and Anderson, 1992). The blooms are so deadly they have even killed large whales (Geraci *et al*., 1989). Tomas (1995) is the most recent comprehensive text for the diatoms and dinoflagellates. Tomas (1997) covers the marine phytoplankton on the whole, including species level descriptions of the most common representatives of the major groups.

Other than the general summaries of the microbial communities discussed above, there are virtually no works that address the Cryptophyta (unicellular flagellate phytoplankton similar to dinoflagellates) as they relate to Stellwagen Bank or the GoM. Genetic variance in the coccolithosphores is discussed by Edvardsen and Medlin (1998), and the major groups have been described (Throndsen *et al*., 1993). Coccolithopores are species of planktonic single-celled algae that produce and encase themselves in coccoliths, which are individual plates of calcium carbonate. The coccoliths, which are dispersed after death or continuously shed by some species, settle to the sea floor and become part of the sediments. Coccoliths are the main constituent of chalk deposits such as the white cliffs of Dover.

Foraminifera are amoeboid protozoans with reticulating pseudopods (fine strands of cytoplasm) that branch and merge to form a dynamic net; they typically produce a mineral shell or "test." They can be planktonic or benthic. A number of forms retain unicellular algae and conduct photosynthesis. These organisms play a critical role in both primary production and transport of minerals, energy and nutrients to benthic communities. Corliss and Emerson (1990) addressed the distribution of benthic foraminifera. Settling foraminifera (components of marine snow) have been associated with diverse bacterial assemblages (Rath *et al*., 1998) and their diversity is of considerable interest to paleontologists. The foraminifera Families and Genera have been carefully delineated for marine communities (Hemleben *et al*., 1989; Sen Gupta, 1999), though new groups are regularly being discovered and described.

Stoecker *et al*. (1989) discuss the distribution of heterotrophic protists on Georges Bank and briefly address the Choanoflagellida, Rhizopoda, Actinopoda, Microspora, Ciliophora and Sporozoa (groups of motile unicellular or colonial protozoans). This is perhaps the only peer-reviewed study of its kind and there is no definitive text in print on the heterotrophic protists elsewhere in the GoM or the northwestern Atlantic. The Sporozoans are parasites of organisms which are found within the sanctuary (Sherburne and Bean, 1979; Lom *et al*., 1980; Bachere and Grizel, 1982). The Ciliophora are of special interest both as food for many marine larvae and as symbionts with higher taxa (i.e., Dupuy *et al*., 1999).

FUNGI

Cavaliere (1977) provides one of the first descriptions of marine fungi (Kohlmeyer and Volkmann-Kohlmeyer, 1991); Ho *et al*. (1991) provide some of the more recent taxonomical revisions. Some taxa have been found in association with Foraminifera and marine snow (Kohlmeyer, 1985). Several taxa are known to be parasitic (Studies, 1980). There are no recent descriptions of marine fungi from the GoM or Stellwagen Bank. In general, marine fungi have been greatly ignored by scientists relative to most groups.