A Bioregional Classification of the Continental Shelf of Northeastern North America for Conservation Analysis and Planning Based on Representation
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A Bioregional Classification for the Continental Shelf of Northeastern North America for Conservation Analysis and Planning Based on Representation

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Silver Spring, Maryland
July 2007

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ABSTRACT

Understanding how well National Marine Sanctuaries and other marine protected areas represent the diversity of species present within and among the biogeographic regions where they occur is essential for assessing their conservation value and identifying gaps in the protection of biological diversity. One of the first steps in any such assessment should be the development of clearly defined and scientifically justified planning boundaries representing distinct oceanographic conditions and faunal assemblages. Here, we propose a set of boundaries for the continental shelf of northeastern North America defined by subdivisions of the Eastern Temperate Province, based on a review and synthesis (i.e. meta-analysis) of the scientific literature. According to this review, the Eastern Temperate Province is generally divided into the Acadian and Virginian Subprovinces. Broad agreement places the Scotian Shelf, Gulf of Maine, and Bay of Fundy within the Acadian Subprovince. The proper association of Georges Bank is less clear; some investigators consider it part of the Acadian and others part of the Virginian. Disparate perspectives emerge from the analysis of different groups of organisms. Further, while some studies suggest a distinction between the Southern New England shelf and the rest of the Mid-Atlantic Bight, others describe the region as a broad transition zone with no unique characteristics of its own. We suggest there exists sufficient evidence to consider the Scotian Shelf, Gulf of Maine, Georges Bank, Southern New England, and Southern Mid-Atlantic Bight as distinct biogeographic regions from a conservation planning perspective, and present a set of proposed mapped boundaries.

KEY WORDS

biogeography, boundaries, species distributions, physiography, gap analysis
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INTRODUCTION

Understanding how well National Marine Sanctuaries and other types of marine protected areas represent the diversity of species present within and among the biogeographic regions where they occur is essential for assessing their conservation value and identifying gaps in the protection of biological diversity (Auster and Shackell 2000, Roberts et al. 2003). One of the first steps in any such assessment should be the development of a well-defined set of biogeographic boundaries for planning purposes. Biogeographic regions are generally defined by stratifying the marine environment according to a range of oceanographic and biological similarities (Mondor 1997). However, there is no single method of classification (Longhurst 1998). Delineations have been variously based on descriptive analyses of the distribution of particular taxa, patterns of endemism, location of persistent oceanographic conditions that limit distributions, locations of particular physiographic features, and multivariate analyses of selected groups of organisms. Different outcomes have been reached using different approaches. Regardless of conflicts arising from disparate approaches and taxonomic groups, a single set of biogeographic boundaries is necessary for conservation assessments, gap analyses, and for linking the efforts of different groups focused on meeting conservation goals. Here we propose a set of boundaries for the continental shelf of northeastern North America, from the Scotian Shelf off Nova Scotia to Cape Hatteras (Figure 1), based on a review and synthesis (a meta-analysis) of the scientific literature. Use of a single set of boundaries will aid regional analyses focused on the conservation value of a wide variety of marine protected areas in this area, including Stellwagen Bank National Marine Sanctuary (e.g., Recchia 2001).

REGIONAL CONTEXT

The Northwest Atlantic Marine Region (Dunbar 1972) extends from Cape Hatteras along the eastern coast of the United States, northward to Lancaster Sound at the north end of Baffin Island, and then westward to the Bering Strait in Alaska. Dunbar (1988) proposed three principal second order subdivisions based principally on the definition of water masses that included temperature, salinity, origin of water masses, current and tidal patterns, sea-ice cover, vertical stability of the water column, and biological indicators (i.e., species distributions). Zoned north to south, these included the Polar, Subpolar, and Eastern Temperate provinces. Mondor et al. (1995) further subdivided these provinces into ten third order marine biogeographic zones based on the identification of marginal seas. These included four Polar subdivisions (Viscount Melville Sound, Lancaster Sound, Hudson Strait, and Hudson James Bay), three Subpolar subdivisions (North Slope/Beaufort Sea, Labrador Shelf, and Gulf of St. Lawrence), and three Eastern Temperate subdivisions (Grand Banks/Scotian Shelf, Acadian, and Virginian). We focus here on the Eastern Temperate subdivisions (Figure 2).
Figure 1. The Northeast Continental Shelf study area. Location names are referred to in text. Note the location of Stellwagen Bank National Marine Sanctuary in the western Gulf of Maine.

Figure 2. Marine provinces and subprovinces of the Northeast Continental Shelf.
Eastern Temperate Subdivisions

Prior to 1970, three general biogeographic schemes had evolved to characterize the northwest Atlantic south to Cape Hatteras (Hazel 1970; based on a review of 17 papers from 1838 to 1966). Many studies used patterns of mean annual ocean surface temperature to define the boundaries of biogeographic regions or faunal provinces (e.g., Coomans 1962). However, information on geographic patterns in the assemblages of organisms was based primarily on inshore faunas. Some authors (including Mondor 1995) considered the Eastern Temperate (also known as the Boreal or Cold Temperate) Province to include the continental shelf from Newfoundland to Cape Hatteras while others described a boundary at Cape Cod between the Eastern Temperate and the Warm Temperate (also known as the Trans-Atlantic) Province to the south. Some classification schemes divide the Warm Temperate Province into two subprovinces (i.e., the Virginian, from Cape Cod to Cape Hatteras, and the Carolinian, from Cape Hatteras to Cape Canaveral). In some cases, the Virginian Subprovince was classified as a transition zone, lacking a unique fauna of its own (e.g., Coomans 1962).

Later studies tended to further subdivide these large regions. Based on his definition of water masses, Dunbar (1972) found the Gulf of Maine and Bay of Fundy to represent a distinct region, what he called the Acadian subdivision of the Eastern Temperate Province, with a northern boundary at the Scotian Shelf and a southern boundary at Cape Cod. He also described a strong boundary between the Scotian Shelf and Georges Bank defined by the Northeast Channel, which reaches depths over 300 m. The Virginian subdivision of this province continued south from there. Ingham et al. (1982) identified the Gulf of Maine, Georges Bank, Southern New England, and southern Mid-Atlantic Bight as separate regions based on distinct bathymetry and circulation (Figure 3). Whereas the Gulf of Maine was characterized by a cyclonic gyre and a seasonally stratified three layer water mass system over the deep basins, Georges Bank was dominated by mixed water with an anticyclonic gyre over the shallower bottom.

Sherman et al. (1996) compared and contrasted productivity, zooplankton, and fish species composition for Georges Bank, Gulf of Maine, Southern New England, and the southern Mid-Atlantic Bight, according to the regions described by Ingham et al. (1982). All regions were found to differ in patterns of primary productivity, experiencing peaks and declines at different times of the year. Dominant zooplankton species changed during the year in each region and the dominant species differed. These authors also described a boundary for fishes at Cape Cod. They noted that most fish species occurring between Cape Cod and Cape Hatteras are migrants. About 15% are boreal with principal abundances north of Cape Cod; 75% range north of Cape Hatteras only in summer. Most inshore-offshore migration also occurs between Cape Cod and Cape Hatteras as most species in this region have temperature tolerances that are exceeded by the normal inshore seasonal temperature cycle. Resident species move offshore and south as inshore areas become too cold in winter. The divisions described by Ingham et al. (1982) and Sherman et al. (1996) were further supported by Longhurst (1998), based on his analysis of the distribution of pelagic primary productivity.
Figure 3. Bathymetry and major surface currents on the Northeast Continental Shelf.

Theroux and Wigley (1998) compared assemblages of benthic macro-invertebrates in the Gulf of Maine, Georges Bank, Southern New England, and the Scotian Shelf, and two subregions below 150 m on the continental slope. Average density and biomass of these organisms were substantially higher on Georges Bank and in Southern New England than the Gulf of Maine and Scotian Shelf. Theroux and Wigley related these differences to variation in mean annual temperature among regions (8.6°C for Georges Bank, 5.7°C for the Gulf of Maine, and 4.6°C for the Scotian Shelf), and to annual variations in temperature within regions, these being greatest on Georges Bank and in Southern New England, and less in the Gulf of Maine) and on the Scotian Shelf. Variation in temperature is especially important, as density and biomass are highest in areas with high annual ranges in temperature, and lowest in areas with low annual ranges, although this is probably influenced also by other chemical and physical properties of water masses. Theroux and Wigley observed large differences among regions in the composition and abundance of major groups of organisms such as decapods, holothurians, and bivalves. The Gulf of Maine was distinguished from Georges Bank by the presence of small groups of Arctic and Subarctic species that do not appear on Georges Bank, and by an absence of many of the tropical and subtropical species that do occur on Georges Bank and in Southern New England.
In agreement with Dunbar (1972), Theroux and Wigley (1998) described a strong boundary between Georges Bank and the Scotian Shelf among benthic macro-invertebrates of the continental shelf. They found that even for species that maintain breeding populations in other boreal and temperate transition zones, Georges Bank represents a distinct entity, with populations differing and separated from those on the Scotian Shelf by the deep Northeast Channel, what they referred to as “a formidable barrier to most benthic and demersal animals”.

Data on the abundance and distribution of demersal fishes have been collected annually in fishery independent trawl surveys by the National Marine Fisheries Service since 1963 and by the Canada Department of Fisheries and Oceans since 1970. To reduce the chances of biased population estimates, the surveys of both nations divide the continental shelf into strata for random sampling, with strata defined by depth and temperature (Grosslein 1969, Clark and Brown 1977). Depth strata include four zones: 27-55 m, 56-110 m, 111-183 m, and > 183 m. Divisions between two strata are made down the middle of the Great South Channel.

Using nine years of trawl survey data (1963-1974), Colvocoresses and Musick (1984) demonstrated consistent patterns of composition and distribution among demersal fishes with the use of cluster analysis. These included four relatively constant and well defined areas of faunal homogeneity in the spring and five more general areas in the fall. Spring assemblages included: 1) a northern inner shelf group from shore to 68-80 m from Cape Cod to Delaware Bay; 2) a mid shelf group from Cape Cod to Hudson Canyon in deeper waters from 60-80 m to 150 m; 3) a southern mid shelf group from Delaware Bay to Cape Hatteras at depths from 60 to 150 m; and 4) an outer shelf group at depths exceeding 150 m. Their analysis therefore agrees with Theroux and Wigley’s (1998) finding of a boundary at 150 m. Fall assemblages occupied similar latitudinal ranges, but tended to occur in the shallower depths. In particular, the northern mid-shelf group occurred at depths between 60 and 90 m, the southern inner and mid shelf group occurred only to 60 m, and the outer shelf group occurred from 60-90 m and 150 m.

Georges Bank and Southern New England

Work by numerous authors corroborate Cape Cod as a barrier to many species, both warm-water and cold-water forms, including ectoprocta, bryozoa (Schopf 1968) opistobranch mollusks (Hazel 1970), gammaridean amphipods (Watling 1979), sea stars (Franz et al. 1981), fishes (Mahon and Sandeman 1985), and benthic macro-invertebrates (Wigley and Burns 1971, Williams and Wigley 1977, Theroux and Wigley 1983, Theroux and Grosslein 1987, Theroux and Wigley 1998). However, there exists some ambiguity as to just where the break occurs on the shelf, depending on which biological characteristics (e.g., faunal composition, patterns of endemism, and population structure) are examined, and whether studies were conducted inshore or offshore. Theroux and Grosslein (1987) studied benthic macro-invertebrates in the western North Atlantic, south of the Scotia Shelf. They noted that zoogeographers have tended to focus on coastal features like Cape Cod, rather than offshore barriers, as ecological boundaries because inshore faunas have been studied more extensively. In their analysis, they found that the
large majority of species off Nova Scotia and in the Gulf of Maine consisted of boreal forms, whereas Georges Bank had a significant component of temperate transitional or Virginian species because of its higher seasonal maximum water temperatures (which preclude reproduction and/or growth of many subarctic or boreal species).

Based on these results, Theroux and Grosslein (1987) concluded that much of Georges Bank belongs to the Warm Temperate Province, noting “A critical point here is that Cape Cod forms the inshore part of this faunal boundary while Georges Bank forms the offshore part”. They described the American Atlantic Boreal Region (i.e., the Eastern Temperate Province) as delimited by 5° and 10° C isotherms (annual mean surface temperature). The 10° isotherm cuts across the north-eastern part of Georges Bank. Under this scheme, Georges Bank forms an unbroken extension of Southern New England with no sharp change in depth or water temperature before the Northeast Channel where the steepest gradients in these features occur.

Briggs (1974) on the other hand, developed a classification system in which provinces on the shelf were identified primarily on the basis of endemism. By his criteria, all of Georges Bank was considered to be part of the Eastern Temperate Province. This classic work, which modified the earlier classification of Eckman (1953), remains the principal authority of marine biogeography the world over. Ingham’s (1982) analysis of oceanographic characteristics tends to support Briggs’ conclusions regarding Georges Bank, in that he considered this region and the Gulf of Maine to form a coupled ecosystem with prominent characteristics distinguishing it from Southern New England.

Some demersal fish species such as yellowtail flounder (Cadrin 2000) and winter flounder (Nitschke et al. 2000) are known to have distinct Southern New England and Georges Bank subpopulations. Differing life history parameters and little mixing between subpopulations suggests the presence of a strong physical barrier between these regions. Using multivariate analysis, Brown et al. (1996) also suggest a break between Georges Bank and Southern New England for some species of demersal fishes. They analyzed fish assemblages using data from the research trawl survey for the region between Cape Chidley in northern Canada and Cape Hatteras. Methods included visual inspection of distribution maps, Principal Components Analysis, and Cluster Analysis. Visual inspection suggested four bank and slope species assemblages occurring at depths less than 200 m. These included a northern group extending from the Scotian Shelf to Cape Chidley, a south-temperate group from the mid-Atlantic Bight to the Grand Banks, a southern group from the southern Gulf of Saint Lawrence to Cape Hatteras, and a north-temperate group from Georges Bank (inclusive) to Cape Chidley. The latter group exhibited a range limit in the area of the Great South Channel. Principal Components Analysis suggested a sole biogeographic boundary in the Grand Banks area, but Cluster Analysis suggested a break at Cape Cod, with five (of 17) cluster groups occurring exclusively south of this region, the others mostly to the north.

Although Theroux and Wigley (1998) analyzed Georges Bank and Southern New England separately, their results suggested a northern boundary for many benthic macro-invertebrate species that extends east across the northern end of the Great South Channel
at depths of 50-100 m and continues along the northern margin of Georges Bank and then southeasterly along the western boundary of the Northeast Channel. This boundary would separate Georges Bank and Southern New England from the Gulf of Maine but not from each other. However, it differs from that described earlier by Theroux and Grosslein (1987) in that it does not bisect Georges Bank.

**Proposed Planning Boundaries**

It is often the case that different methods of classification produce different results. When similar methods are used, different outcomes can arise depending on the choice of taxa. However, even for similar methods and taxa, results can vary depending on how data are grouped or the spatial extent of the analyses (e.g., Colvocoresses and Musick 1983, Brown et al. 1996). Despite the potential for disagreement based on the use of different methods and data sets, there appears to be a reasonably strong consensus for the existence of five distinct biogeographic regions on the continental shelf of the eastern United States and Nova Scotia, including the Scotian Shelf, Gulf of Maine, Georges Bank, Southern New England, and southern Mid-Atlantic Bight. Each is characterized by a unique combination of oceanographic conditions, physiographic features, fish species assemblages, and a wide variety of invertebrate taxa. While most studies recognize these five regions as distinct, they differ somewhat in how they group them at a broader scale. The boundary at Cape Cod appears to be so strong that some authorities consider it to be a break between two major provinces, the Eastern Temperate and Warm Temperate. Others consider it to be a boundary between subprovinces of the Eastern Temperate Province. The distinction is not terribly important from a regional conservation perspective because smaller, ecologically distinctive regions within these larger areas are clearly apparent.

The principal area of dispute is Georges Bank. Theroux and his colleagues (e.g., Theroux and Wigley 1983, 1998; Theroux and Grosslein 1987) suggest that Georges Bank faunas are largely an extension of Southern New England’s, based on mean maximum sea surface temperatures and the distribution of boreal and southern forms of benthic macro-invertebrates. However, other comparisons based on primary and secondary productivity, fish species assemblages and population structure, bathymetry and circulation, and patterns of endemism (e.g., Ingham et al. 1982, Sherman et al. 1996, Longhurst 1998, Briggs 1974, Brown et al. 1996, Colvocoresses and Musick 1984) suggest that the two regions are distinct.

Recognizing finer order divisions would be the most conservative approach for planning a system of representative marine protected areas. Capturing representative endemism is particularly important for the conservation of biodiversity. The designation of protected areas on Georges Bank as well as Southern New England would help ensure that the greatest number of species unique to those areas were protected. For this reason, and because a number of biogeographic assessments support doing so, we recognize Georges Bank as a unique biogeographic region for planning purposes. Similarly, although some classifications consider the entire Virginian subprovince a transition zone, we consider
Southern New England and the southern Mid-Atlantic Bight to be distinct, based on evidence provided by Ingham et al. (1982) and Sherman et al. 1996.

These five regions correspond in spatial scale with fourth-order subdivisions defined by Dunbar (1972). While many individual investigations support the recognition of distinct bioregions at this scale, relatively few make suggestions about where exactly to draw boundary lines. This is probably due to the fact that boundaries are rarely sharp divisions and can shift somewhat between seasons and over longer time scales. For example, the latitudinal position of the point where the Gulf Stream breaks from the North American coastline in the vicinity of Cape Hatteras ranges from 30-40 km during the year (Hogg and Johns 1995). Nonetheless, it is necessary to draw lines for mapping and planning purposes. Based on the information available in this review, we propose the following set of boundaries (Figure 4). Precise placement was guided by divisions between sampling strata for demersal fishes where other information was not available.

1. **The Scotian Shelf** extends from southern Newfoundland to the southern tip of Nova Scotia. Following results obtained by Theroux and Wigley (1998) for benthic macroinvertebrate assemblages, and lacking any additional information, the boundary is set at the 100-meter isobath along the northern edge of the Northeast Channel, which separates it from the Gulf of Maine. The outer boundary of the Scotian shelf follows the 150 m isobath that delineates the shelf.
break per results obtained for benthic macroinvertebrates by Theroux and Wigley (1998) and demersal fish species assemblages by Colvocoresses and Musick (1984).

2. **The Gulf of Maine**, including the Bay of Fundy and the Northeast channel, is bound by the Scotian Shelf and Georges Bank at depths of 100 m, following the distribution of benthic macroinvertebrate assemblages examined by Theroux and Wigley (1998).

3. **Georges Bank** is bound in the north by the Northeast Channel, a physical feature that separates water masses of the Scotian Shelf and Gulf of Maine (Dunbar 1972) and benthic macroinvertebrate assemblages (Theroux and Wigley 1998). The northern boundary extends from the Northeast Channel to the Great South Channel at depths of 100 m per the distribution of benthic macroinvertebrate assemblages (Theroux and Wigley 1998). The southern boundary is defined by the 150 m isobath delineating the shelf break following results obtained for benthic macroinvertebrates (Theroux and Wigley 1998) and demersal fish species assemblages by (Colvocoresses and Musick 1984).


5. **The southern Mid-Atlantic Bight** extends from Hudson Canyon in the north, following results obtained for demersal fish faunal assemblages by Colvocoresses and Musick (1984), to Cape Hatteras in the south. Cape Hatteras is a well known biogeographic boundary created by abrupt latitudinal differences in water temperature where the south flowing Labrador Current meets the northeast movement of the Gulf Stream (Cerame-Vivas and Gray, 1966)

The ecological and oceanographic distinctiveness of these five regions suggest that any network of marine protected areas aimed at conserving biological diversity on the northeastern continental shelf include at least one site from each region. Within regions, the location and number of sites should be chosen with the aim of representing all habitat types. Often, from a purely biological perspective, there exist numerous scenarios involving tradeoffs between size and number of sites that can accomplish similar goals of representation (e.g., Cook and Auster 2005). Representation may be redundant where species cross boundaries, but such redundancy can help ensure the regional continuation of species and stability of populations impacted by local catastrophes.

Numerous marine protected areas have been established on the eastern continental shelf of North America, both in the United States and Canada, providing various types
and levels of protection to biological organisms. These include year round and seasonal
fishery closures, which largely protect benthic habitats from disturbance by mobile
trawling gear, mesh size control areas for protection of juvenile fish, critical habitat
protection for marine mammals, and others. National Marine Sanctuaries provide
protection from a wide range of extractive activities, but some currently permit most
forms of fishing, including the use of fishing gears that alter seafloor habitats.

Stellwagen Bank National Marine Sanctuary in the western Gulf of Maine is
currently the only national marine sanctuary within the Eastern Temperate Province of
the United States. The set of boundaries we propose can be useful to sanctuary
management in that they define the species pool that should be represented within the
region. With knowledge of the location and types of protection afforded by the sanctuary
and other protected areas in the Gulf of Maine, Gap Analysis could be used to identify
which species and communities (and associated habitats) are in greater need of
representation or protection on a bioregional basis. This information could be used by
sanctuary management to determine how well protection within the sanctuary meets
larger regional goals of representation and enhance the level of protection afforded those
species and communities in need, where the opportunity exists. Such information would
also be useful for greater coordination among agencies in regional management efforts.

Finally, fourth order subdivisions of marine biogeographic realms, including
those proposed in this paper, represent the level at which regional marine planning is
currently being developed by Parks Canada for Canada’s national system of marine
protected areas, and by UNESCO’s Man and the Biosphere Program for the United States
(Agardy 1988, McCormick-Ray et al. 1988). These two national efforts make up the
northwest Atlantic portion of the IUCN’s Global Representative System of Marine
Protected Areas program (Kelleher et al. 1995). Using a common set of biogeographic
boundaries for ongoing conservation analysis and planning efforts will ensure that results
of various efforts can be compared and contrasted with a high level of ecological
consistency.

ACKNOWLEDGEMENTS

This work was supported by grants from the Conservation Law Foundation,
Oceana, NOAA’s Undersea Research Program, Stellwagen Bank National Marine
Sanctuary and the Census of Marine Life Gulf of Maine Program. We thank three
anonymous referees and Kathy Broughton for comments that improved the quality of the
manuscript. The views expressed herein are those of the authors and do not necessarily
reflect the views of the funding agencies.
LITERATURE CITED


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