

# An Introduction to the Oceanography, Geology, Biogeography, and Fisheries of the Tropical and Subtropical Western Central Atlantic

M.L. Smith, Center for Applied Biodiversity Science, Conservation International, Washington, DC, USA,  
 K.E. Carpenter, Department of Biological Sciences, Old Dominion University, Norfolk, Virginia, USA,  
 R.W. Waller, Center for Applied Biodiversity Science, Conservation International, Washington, DC, USA

This identification guide focuses on marine species occurring in the Western Central Atlantic Ocean including the Gulf of Mexico and Caribbean Sea; these waters collectively comprise FAO Fishing Area 31 (Fig. 1). The western parts of this area have often been referred to as the “wider Caribbean Basin” or, more recently, as the Intra-Americas Sea (e.g., Mooers and Maul, 1998). The latter term draws attention to the fact that marine waters lie at the heart of the Americas and that they constitute an American Mediterranean that has played a key geopolitical role in the development of the surrounding societies.

In geographic terms, the Western Central Atlantic (**WCA**) is one of the most complex parts of the world ocean, consisting of a highly subdivided set of

lithospheric units, deep ocean basins separated by relatively shallow sills, and extensive systems of island platforms, offshore banks, and continental shelves (Figs 2,3). One consequence of this geography is a fine-grained pattern of biological diversification that adds up to the greatest concentration of rare and endemic species in the Atlantic Ocean Basin. Of the 987 fish species treated in detail in these volumes, some 23% are rare or endemic to the study area. Such a high level of endemism stands in contrast to the widespread view that marine species characteristically have large geographic ranges and that they might therefore be buffered against extinction.

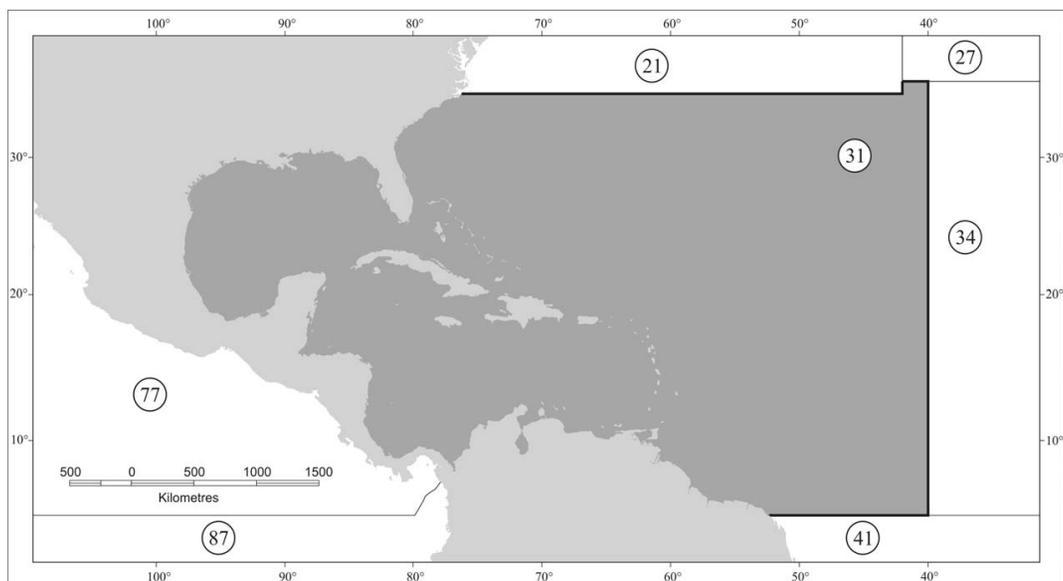


Fig. 1 Area covered by this guide (shaded): FAO Fishing Area 31 or the Western Central Atlantic Ocean (adjacent FAO fishing areas are numbered)

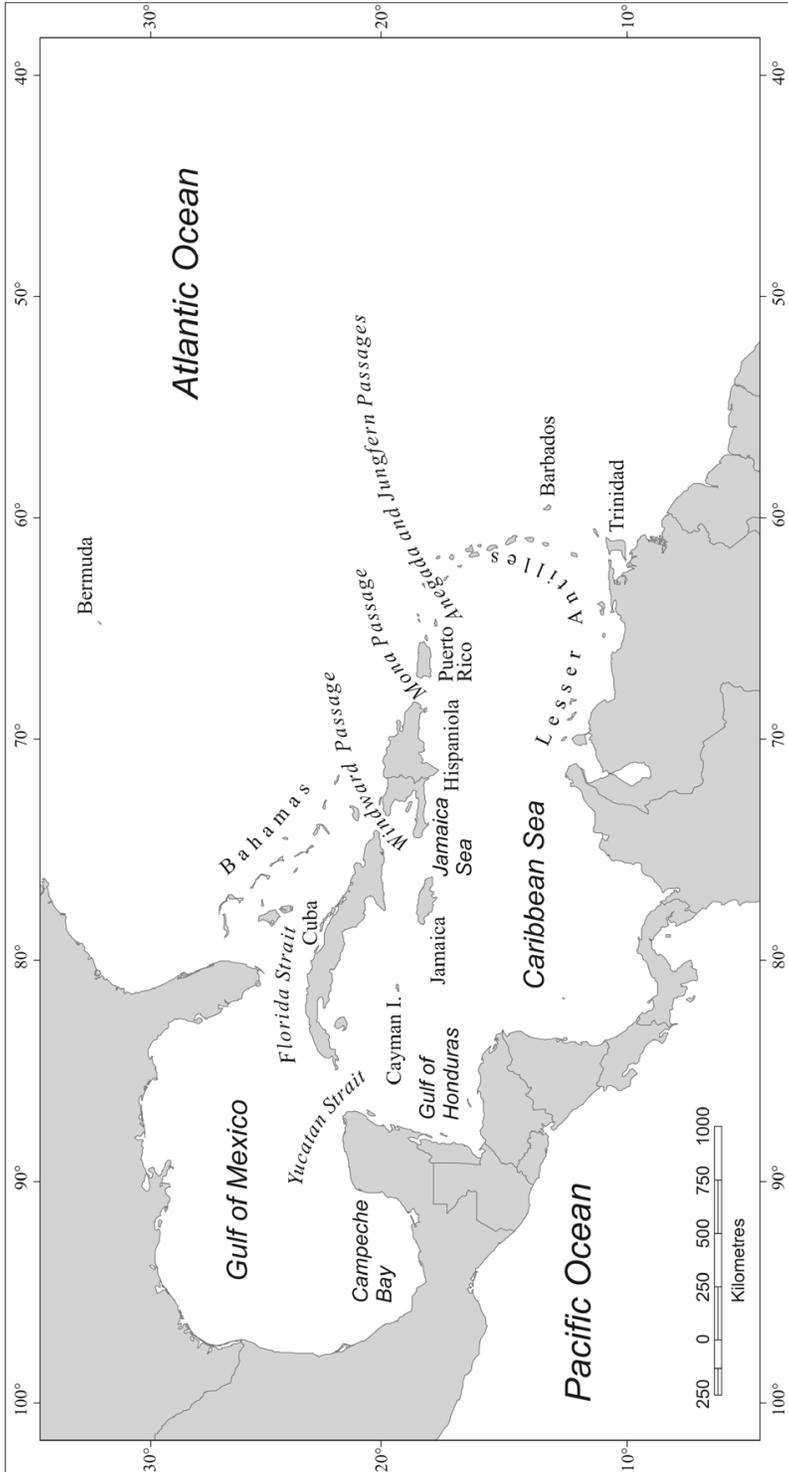
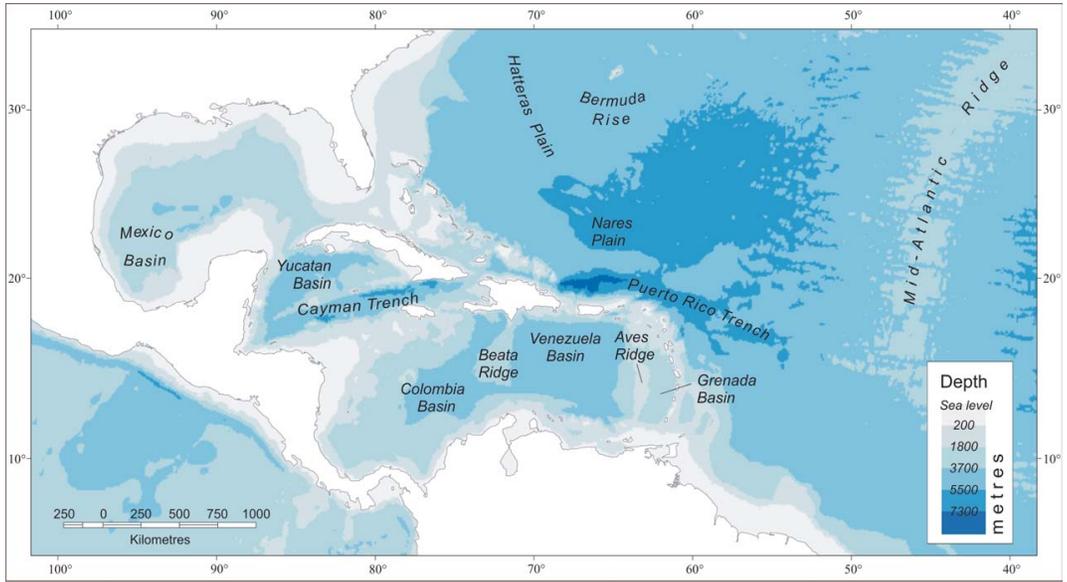


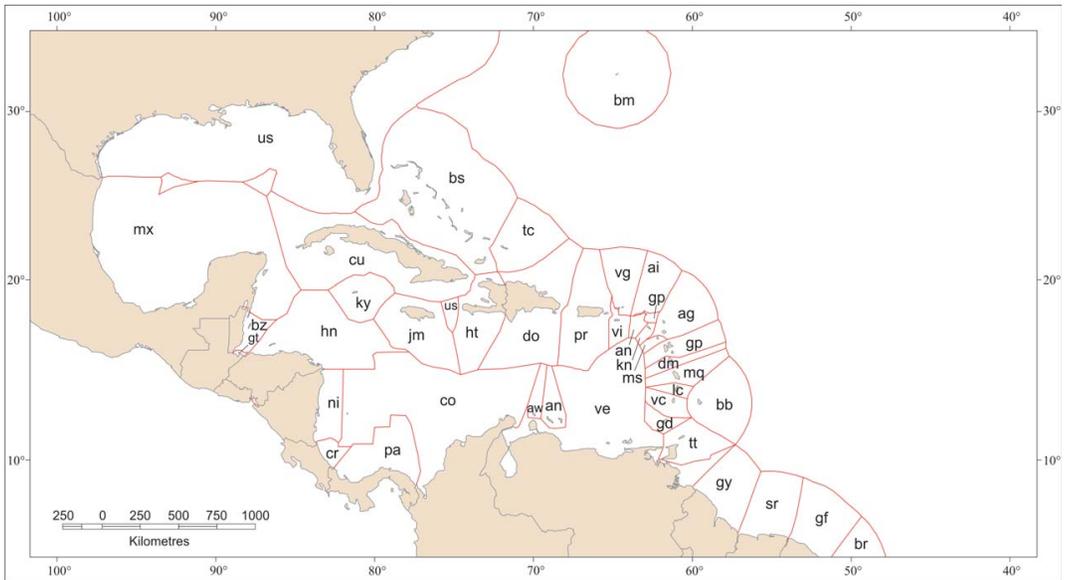
Fig. 2 The major seas, gulfs, and island groups of the Western Central Atlantic



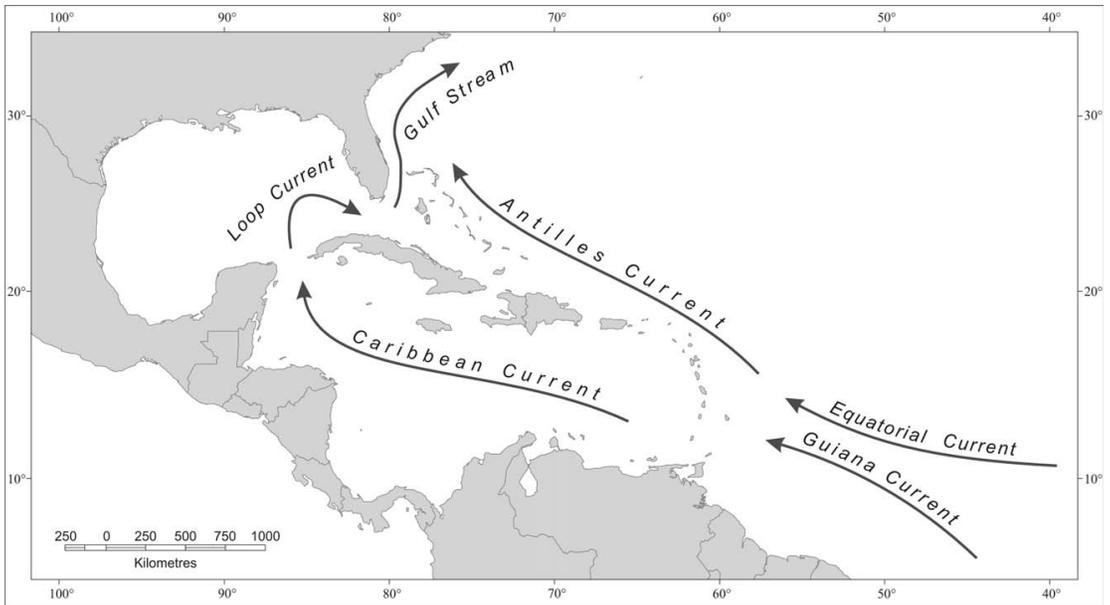
**Fig. 3** Depth patterns showing major submarine basins and ridges

The geographic intricacies that resulted in the region’s high levels of biological richness are also associated with social and political diversity. The Western Central Atlantic includes the world’s greatest concentration of small countries, and they represent the full range of the world’s major political systems. All of the Caribbean Sea and nearly all of the Gulf of Mexico are included within one or another of the region’s 42 jurisdictional units (Fig. 4), the largest

number found in any ocean area of this size. When the Exclusive Economic Zones are compared to the geographic and ecological features of the same area (Figs 2,3,5), it becomes clear that the countries of the region are faced with managing the biological outcomes of oceanic and ecological processes that operate on a scale that is far larger than any of the region’s individual management units.



**Fig. 4** Maritime boundaries in the Western Central Atlantic Ocean demarcating the Exclusive Economic Zones (EEZs) of the Western Central Atlantic states. Two open areas in the Gulf of Mexico represent “doughnut holes,” that is, international waters beyond the EEZs of Mexico, the USA, and Cuba. Country codes are explained in “Map Data Sources” [Modified from Sullivan Sealey and Bustamante, 1999]



**Fig. 5 Major surface currents**

This guide expands upon the FAO Species Identification Sheets for Fishery Purposes, Western Central Atlantic (Fischer, 1978). All species accounts with distribution maps have been revised and updated, and the number of species treated in detail has increased from 533 to 1 172. This guide is the geographic complement to the FAO identification guide to the Eastern Central Atlantic (Fischer et al., 1981); together, the two guides provide coverage of subtropical and tropical marine species across the Atlantic with the exception of Brazilian waters.

The distributional data presented in the species accounts comprises the most extensive set of geospatial information so far assembled on marine biodiversity for the region, and the range maps will therefore be of interest in the search for, and explanation of, general patterns of distribution, species richness, and endemism. This chapter provides an introduction to the physical and geohistorical setting that creates the basic constraints for the evolution of such patterns. Particular attention is called to the water masses and currents which show a clear structure throughout the region, but especially so in the Caribbean Sea and Gulf of Mexico where their configurations are constrained by ridges, archipelagos, and the continental margins. They provide a marked physical and chemical structure that influences the distributions of many of the region's species.

### Physical Topography

The dominant geomorphological feature in the eastern reaches of the WCA is the Mid-Atlantic Ridge which slopes westward to abyssal plains (including the Nares and Hatteras Plains) at depths typically ranging from 5 000 to over 7 000 m (Fig. 3). In

the north, the plains are interrupted by the Bermuda Rise which is crowned by the world's northern-most coral reefs around the Bermuda Islands (Smith-Vaniz et al., 2001). Topographic features in these parts of the WCA are generally similar to those of most parts of the North Atlantic Basin (see maps in Earle, 2001), and the plains are broadly open to deep-water circulation. In contrast, the central and western parts of the WCA are broken into a very complex set of sub-basins that are surrounded by ridges and trenches that are inferred to have been generated primarily by interactions between the Caribbean tectonic plate and the surrounding North American and South American plates.

The Caribbean Sea constitutes the largest marginal sea of the Atlantic Ocean with a surface area of  $2.52 \times 10^6 \text{ km}^2$  and volume of  $6.48 \times 10^6 \text{ km}^3$  (twice that of the Mediterranean). It is separated from the open Atlantic by ridges that emerge, in places, as the Greater and Lesser Antilles islands. Passages between the islands allow exchange of water only at relatively shallow depths. The deepest passages and sills between the Caribbean and Atlantic are the Windward (1 540 m), Jungfern (1 815 m), and Anegada (1 910 m) Passages. The Caribbean Sea itself occupies five principal basins that have been separated from each other at various depths in the past (see below) and that are presently separated at depth by submerged ridges. These basins divide the deep circulation and hold water with significant residence times (NAS, 1990). From east to west, they are the Grenada Basin (typical depth about 3 000 m), Venezuela Basin (5 000 m), Colombia Basin (4 000 m), Cayman

Trench (6 000 m), and Yucatán Basin (5 000 m). The Caribbean is connected to the Gulf of Mexico through the Yucatán Channel which allows passage of water to the channel's maximum sill depth of 2 040 m. The Gulf is a single basin with typical depths of about 3 000 m. It has been suggested that the deeper waters of the Gulf of Mexico (greater than 1 500 m) have rather long residence times (300 to 500 years) and are only infrequently exchanged with adjacent water bodies (NAS, 1990).

## Oceanography

### Water Masses and Currents

The waters of the WCA are strongly structured as a system of discrete water masses and currents. Water masses are relatively coherent bodies of water that have a common history of formation and that can often be identified at great distances from their points of origin on the basis of characteristics of temperature, salinity, and oxygen content. The fundamental water masses of the WCA are described below in a general sequence from the bottom to the surface (based on Wright and Worthington, 1970; Emery and Meincke, 1986; Mooers and Maul, 1998; and Baum, 2001).

Antarctic Bottom Water is formed in the Weddell and Ross Seas with temperatures ranging from  $-0.8$  to  $0^{\circ}\text{C}$  and salinities from 34.6 to 34.7‰. It is the densest water in the free ocean (that is, outside of regional basins where denser water is blocked by sills, such as in the Mediterranean or Norway seas). Antarctic Bottom Water spreads across the Nares and Hatteras Plains, forming the deepest water mass in most of the WCA, but ridges prevent it from entering the Caribbean basins and Gulf of Mexico.

North Atlantic Deep Water is marked by relatively high oxygen levels (greater than 5.5 ml/l) and salinity greater than 34.9‰. This water mass originates primarily in the Greenland-Iceland-Norway seas and spreads into the Atlantic as dense overflows through sills on either side of Iceland to fill the depth range from about 1 000 to 4 000 m. Its upper layers enter all sub-basins of the Caribbean and Gulf of Mexico.

Antarctic Intermediate Water originates from a circumpolar layer with most of the Atlantic component coming from the Drake Passage and Falkland Current. It fills the basins of the Caribbean and Gulf of Mexico at depths ranging from about 500 to 1 000 m and can be recognized in those basins by a distinct salinity minimum at 34‰ (NAS, 1990).

Subtropical Underwater originates in the tropical central Atlantic and sinks to about 200 to 500 m as it enters the Caribbean. It is readily recognized in the Caribbean and eastern Gulf of Mexico by its high salinity, 36.7‰.

The relatively shallow sills surrounding the Caribbean Sea restrict the connection to the deep-water masses of the open Atlantic. The uppermost part of North Atlantic Deep Water can enter the Caribbean through the Windward Passage (1 540 m) and the Anegada and Jungfern Passages (1 800 m). Antarctic Intermediate Water can enter at several points that have sill depths from 800 to 1 400 m. The two water masses mix upon entering just above sill depth and the mixture fills the lower reaches of the Caribbean basins with a distinctive and remarkably uniform bottom water. It passes subsequently through the Yucatán Strait into the Gulf of Mexico at about 2 000 m.

The movement of high-density, polar-sourced water masses into the WCA and its sub-basins must be compensated by displacement of water of equal mass, and this density balance is a primary feature of circulation on an Atlantic-wide scale. The precise course of return flow is controlled in part by the Coriolis force and, at the surface, by the trade winds and seasonal tropical storms. The most obvious circulatory feature of the WCA is its "western boundary current," a generic term for intensification of the western limb of the subtropical gyres in each major ocean basin. Stommel (1948) established that western boundary currents (e.g., the Caribbean Current/Gulf Stream in the North Atlantic or the Kuroshio in the North Pacific) are the inevitable consequences of three conditions: a rotating earth, a meridional boundary, and a zonal wind stress pattern. These conditions have prevailed to some degree in the WCA since the Central American Isthmus began to be elevated in the middle Miocene. Modern circulation became established with full emergence of the Panamanian Isthmus in the Pliocene.

At the point where the western boundary current enters the WCA, it includes components of the North Equatorial Current and the Guiana Current (Fig. 5). Upon encountering the Antilles, it splits into two branches. The Antilles Current skirts the Antilles on the Atlantic side to merge eventually with the Florida Current. The second part flows through several passages in the Windward Islands to become the Caribbean Current, a warm and powerful body of water that increases in velocity as it flows along the western margins of the Caribbean to the Yucatán Channel. The trajectories of satellite-tracked drifters show that the Caribbean Current should be referred to only in a statistical sense, as it consists of meanders, eddies and filaments of currents under a general pattern of movement (Gallegos, 1996). It and the Antilles Current are sometimes referred to as the roots of the Gulf Stream (Mooers and Maul, 1998).

The Caribbean Current enters the Gulf of Mexico through the Yucatán Channel to become the Loop Current, a much more coherent feature that can be traced as a swift and narrow stream flowing northward into the Gulf of Mexico and then looping back to exit through the Straits of Florida where it is known as the Florida Current. It is rejoined by the Antilles Current to become the Gulf Stream.

### Paleoceanography

The present-day circulation patterns in the WCA are relatively young, having been established in association with the closure of the Central American Seaway, and it is likely that the basic distribution of marine biodiversity in the region reflects patterns of circulation and topography that are significantly older. On a global basis, the fundamental pattern of ocean circulation has evolved from one dominated by circulation at tropical latitudes (that is, through the former seaway between North and South America; Fig. 6) to today's condition of circum-Antarctic circulation, via the southern ocean (Roth et al., 2000). The key developments in this evolution, including late Cenozoic climatic changes, were triggered by the appearance of barriers to circulation at various depths in the area now occupied by the WCA. The record of pelagic sediments shows that the Inter-American seaway was generally open at all depths for a period of some 20 million years following separation of the Americas in the middle Mesozoic, that there have been occasional incomplete barriers to circulation (e.g., deep ridges and/or incomplete island chains), especially during the Oligocene and Miocene, and that the Caribbean or its sub-basins have been connected alternately to the Atlantic or the Pacific at different times.

The history of isolation of Atlantic and Pacific water masses can be inferred from remarkable detail from pelagic sediments that reflect the characteristics of the over-lying water masses that produced the deposits. The Ocean Drilling Program (ODP) and its precursor, the Deep Sea Drilling Project (DSDP), have resulted in an array of 160 drilling sites in the WCA and nearby waters (Fig. 7) that provide a record of changes in the region's water masses over a period extending to the middle Mesozoic (see numerous reports in *Proceedings of the Ocean Drilling Program, Scientific Results* and specific citations below).

With respect to deep-water circulation, past barriers can be inferred from the accumulation of siliceous sediments because the Atlantic and Pacific differ in processes of silica dissolution and transport (Broecker, 1974; Donnelly, 1985, 1989). When the low-latitude seaway between the Americas is closed (as is the case today), deep water that originates in the Atlantic flows into the Pacific only via the seas around Antarctica, carrying silica from the Atlantic to the Pacific. The deep water of Atlantic origin upwells in the Pacific, and the dissolved silica is immediately taken up by siliceous organisms in shallow waters. These in turn contribute a fraction of the silica in their skeletons to Pacific deep-sea sediments. Return flow to the Atlantic occurs near the surface and therefore consists of water from which silica has been removed. The result is a net accumulation of silica in Pacific water masses and their sediments. Whenever conditions like those of today prevail (i.e., deep-water circulation takes place only via the southern ocean), then Atlantic waters and their pelagic sediments are silica-poor relative to those of the Pacific at the same time.

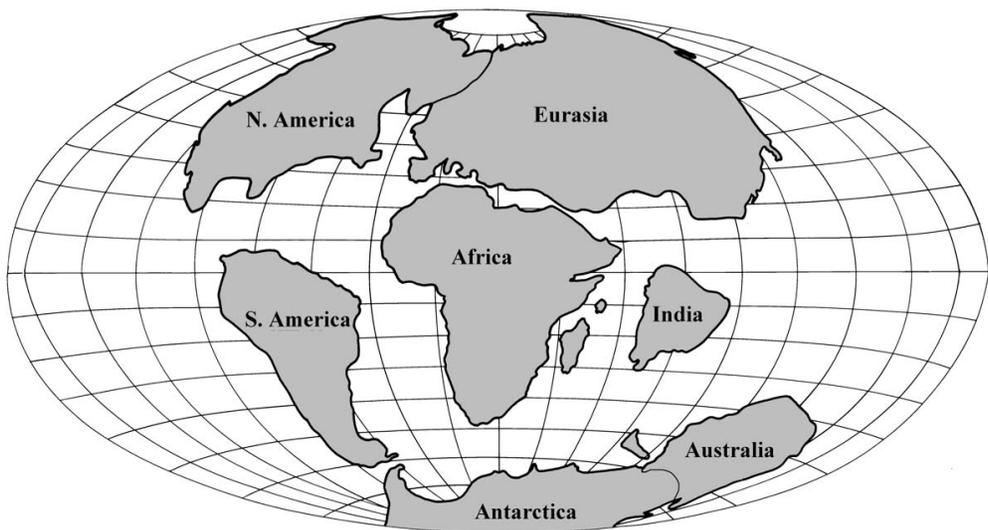
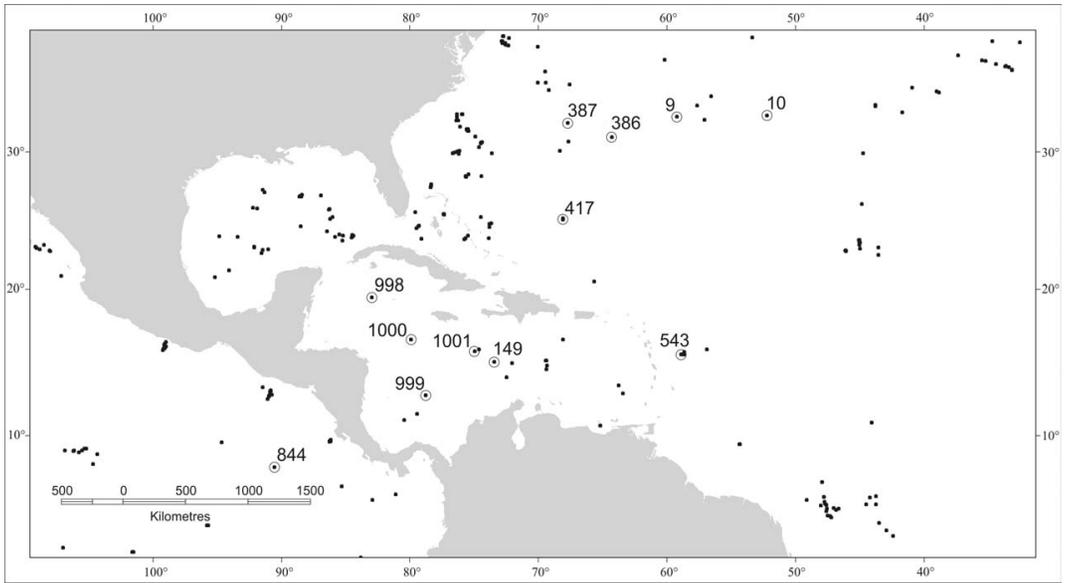


Fig. 6 Position of the continents and inter-oceanic seaways 65 million years ago



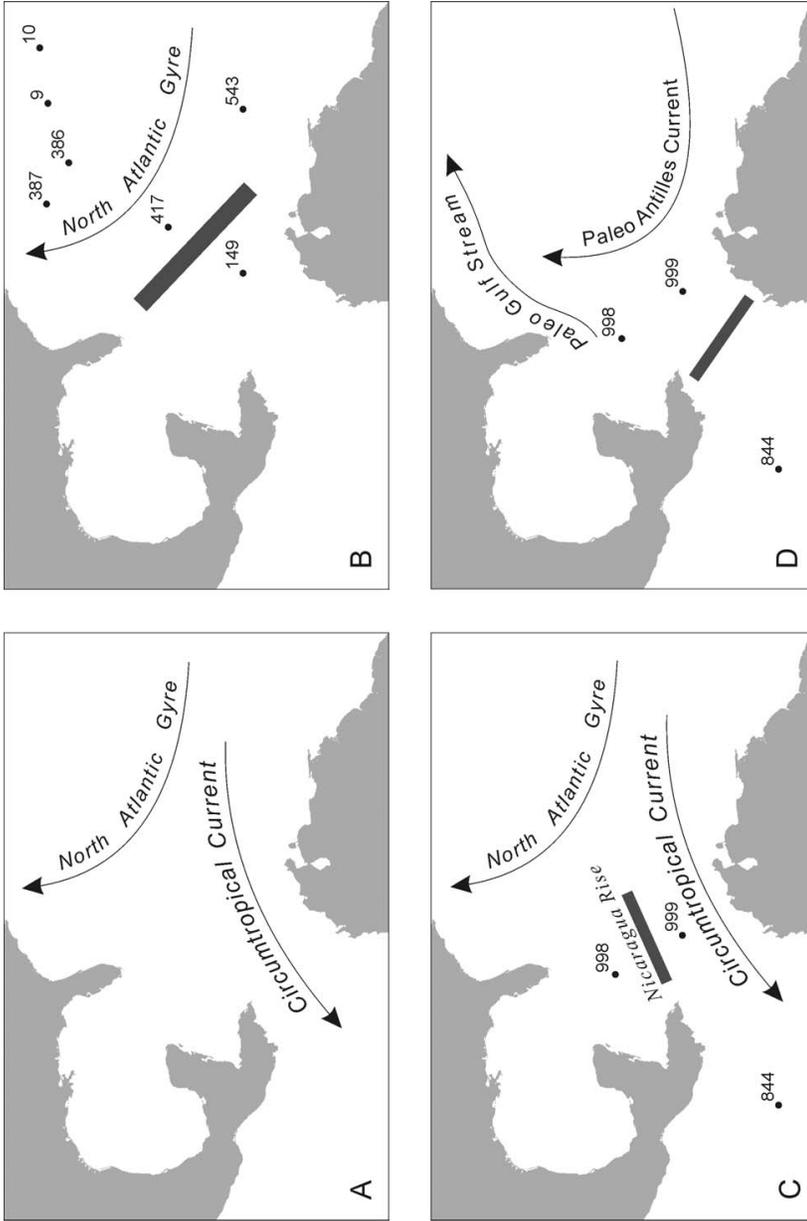
**Fig. 7 Site locations of the Deep Sea Drilling Program and Ocean Drilling Program. Numbered sites are referred to in the text (site 846 lies off the map south of the Galapagos Islands)**

When the low-latitude seaway is open to deep-water circulation between the Americas, silica-laden waters return to the Atlantic so that sediments in both ocean basins have similar silica content. The chronological record of silica at core sites therefore provides a basis for detecting former deep-water barriers between them.

Other parameters provide the basis for corroboration or for detection of circulation patterns at different depths. Ancient water masses can be compared on the basis of the paleodepth at which calcareous microfossil debris dissolves in deep water (Lyle et al., 1995; Roth et al., 2000) or in terms of the biotic composition of nannofossil assemblages that reflect connections in shallow waters (e.g., Kameo and Sato, 2000). Analyses of these phenomena at ODP sites in and around the WCA provide the following outline of the opening and closing of seaways and of the consequent re-organization of ocean circulation.

Cores from widely distributed sites show that both Pacific and Atlantic water masses in and near the WCA carried a high silica content during the latest Cretaceous and early Cenozoic (Donnelly, 1985), i.e., the Inter-American Seaway was open to effective circulation at all depths. Throughout this period (and until the middle Miocene), the Circum-Tropical Current was well developed and flowed from the North Atlantic into the Pacific between the American continents. Given that no meridional boundary was yet in existence and that the Atlantic Ocean was narrower than it is today, the gyral circulation system in the North Atlantic was only weakly established.

During the Eocene, sediments in the Pacific and Caribbean were similar to each other in having high levels of silica, but silica content had plummeted in Atlantic sediments. This implies that Caribbean and Pacific waters were still confluent at depth, but that deep Atlantic waters were segregated by a deep-water barrier in the position of the Antilles or Aves Ridge, either of which was in position to separate the deep water masses over-lying the respective sets of drilling sites (Site 149 in the Caribbean and Sites 9, 10, 386, 387, 417, 543 in the Atlantic; Figs 7, 8b). This was followed in the early Miocene by a decrease in the silica content of Caribbean sediments, showing that the exchange of deep water between the Caribbean and Pacific was becoming restricted by the elevation of submerged structures in the position of present Central America. Although these structures rose into waters shallower than 1500 m (Donnelly, 1989), the Inter-American Seaway remained open to surface circulation into the middle Miocene, as shown by shared assemblages of shallow-water nannofossils at Sites 999 (Caribbean) and 844 and 846 (Pacific) (Roth et al., 2000; Kameo and Sato, 2000). During much of the Miocene, the northern and southern basins of the Caribbean were separated by the Nicaragua Rise, inferred in part from differences in calcareous coccolith assemblages at Sites 998 (Cayman Trench) and 999 (Colombia Basin). The Rise stood in the way of a western boundary current and helped shunt the Circum-Tropical Current into the eastern Pacific (Fig. 8).



**Fig. 8** Summary of paleoceanographic evolution of the WCA. Coastlines are for orientation and are not contemporaneous with the depicted events. Solid bars indicate position of barriers to circulation. **A**) Early Cenozoic: Silica content is high in sediments at broadly distributed Pacific and Atlantic drilling sites (Donnelly, 1985). The Inter-American Seaway is open; the Circumtropical Current is well developed; and the North Atlantic Gyre is weak. **B**) Eocene: Silica content is high in Caribbean sediments (site 149), but low in Atlantic sediments (e.g., sites 9, 10, 386, 387, 417, 543) (Donnelly, 1989). The Caribbean and Pacific are confluent at all depths, but are separated from deep-water circulation with the Atlantic by developing ridges (Antilles and/or Aves Ridges). **C**) Early Miocene: Shallow-water coccolith assemblages are similar in the Pacific (site 844) and Colombian (site 999) Basins, but distinctive in the Yucatan Basin (site 998) (Kameo and Sato, 2000). The Inter-American Seaway is open, and a barrier in the position of the Nicaragua Rise shunts a strong Circumtropical Current into the Pacific. **D**) Middle Miocene: Coccolith assemblages are similar within the Caribbean Basin and different from those in the Pacific (Kameo and Sato, 2000). The Nicaragua Rise has foundered and the Inter-American Seaway is temporarily closed for the first time

The Inter-American Seaway was substantially, though temporarily, closed for the first time at the transition from middle to late Miocene, based on divergence of nannofossil assemblages in younger layers at Caribbean Site 999 and Pacific Sites 844 and 846 (Roth et al., 2000), but inter-ocean surface exchange was again taking place in the latest Miocene (Kameo and Sato, 2000). Final closure of the Inter-American Seaway by complete emergence of the Isthmus of Panama in the Pliocene was originally documented using diverse geological evidence (Duque-Claro, 1990; Coates et al., 1992) and by foraminiferal studies at sites on both sides of the Isthmus (Keigwin, 1978; Keller et al., 1989). The date of closure has been further constrained to the late Pliocene (2.76 ~ 2.51 Ma) based on provincialism of microfossil assemblages in the western Caribbean (Sites 989 and 999) and eastern equatorial Pacific (Sites 844, 846, and 850) (Kameo and Sato, 2000).

Foundering of the Nicaragua Rise in the middle Miocene opened a new gateway for the North Atlantic's western boundary current inside the Caribbean basin (Droxler et al., 1992; Roth et al., 2000) and is linked to the initiation of the North Atlantic Deep Water. As the Inter-American Seaway gradually closed, the strengthening Caribbean Current transported warm, saline waters of the Caribbean to the northern Atlantic via the Loop Current, Florida Current, and Gulf Stream, all of which were becoming established late in the middle

Miocene. During this transition, the Caribbean region acted as a discriminating valve in which the opening and closing of gateways at different depths modified the global circulation pattern (Roth et al., 2000) and triggered the global climatic changes of the Pliocene (Raymo et al., 1989).

### Tectonic Setting

Four major lithospheric plates underlie the Western Central Atlantic (Fig. 9). These include a small part of the African Plate to the east of the mid-Atlantic spreading boundary, all of the Caribbean Plate, and parts of the North American and South American Plates. In addition, two lithospheric units in the eastern Pacific, the Cocos and Nazca Plates, were involved in key tectonic processes that created the WCA's western margins. The North and South American plates are moving generally westward from the mid-Atlantic spreading boundary, while the Cocos and Nazca plates are moving generally eastward from their spreading boundary with the Pacific plate. This means that the larger lithospheric units that surround the Caribbean plate are all converging upon it from the east or west, and this compression is offset by subduction at its eastern and western extremities that has resulted in the formation of the trenches and volcanic arcs of the Antilles and Central America. On its northern and southern boundaries, the continental plates are moving past the Caribbean plate.

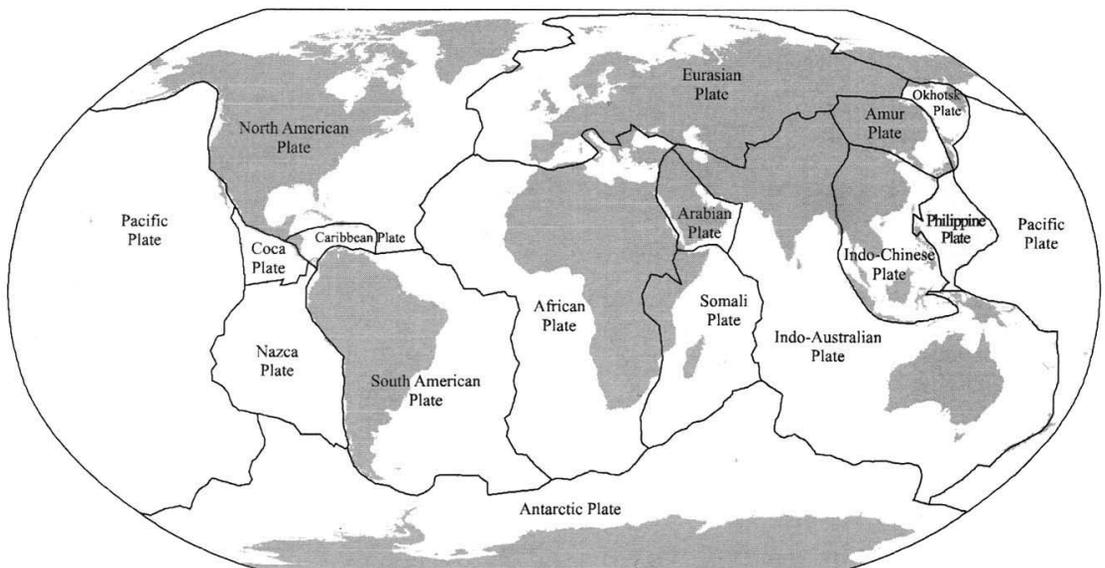


Fig. 9 Major lithospheric plates of the world