1 Introduction

1.1 Definition of Deep-Sea Fishes

Life on earth is dependent on energy from the Sun, which warms the biosphere and provides direct input through photosynthesis creating the chemical energy that supports living processes. Deep-sea fishes are species that live at depths greater than 200 m beyond the effective range of solar radiation. The heat of the Sun is absorbed in the uppermost one or two metres of the ocean; sufficient light for photosynthesis reaches a maximum depth of 100–150 m in clear open ocean waters (Ryther, 1956). Deep-sea fishes hence live remote from their main source of energy and must somehow indirectly access surface-derived food (Herring, 2002), with many species developing extraordinary adaptations to cope with the reduced food supply at depth.

Defining a strict upper depth boundary for deep-sea fishes is problematic. Below 1000 m, the oceans are totally devoid of solar light, the temperature is generally less than 4°C and there is no doubt that fishes living in these cold dark conditions can be considered to be deep-sea species. However between 200 and 1000 m there is a transition zone where, although there may be sufficient light for vision using highly sensitive specially adapted eyes, life is more or less untenable for normal surface-dwelling fishes. This zone contains some of the most interesting deep-sea fishes that are obviously different from shallow species. Despite living deep, many species have buoyant eggs that float to the surface so that larvae can develop in the plentiful food supply in the surface layers. In the open ocean many deep-sea fishes migrate towards the surface at night and descend again at dawn to pass the day in darkness and the cold waters below. Thus deep-sea fishes do not necessarily pass their entire life cycle in the deep sea, and adults may not be restricted entirely to depths greater than 200 m.

Conversely many shallow-water species are capable of moving deeper than 200 m. For example, although the Atlantic Cod (*Gadus morhua*) has been recorded as far down as 600 m_{fbd} depth and the Atlantic Herring (*Clupea harengus*) down to 364 m_{fbd}, these species would never be considered to be deep-sea fishes. These are the maximum depths recorded for the species in the online database FishBase (Froese and Pauly, 2016), which in this volume are denoted by the suffix 'fbd', denoting '*fish base depth*'.

Early researchers recognised the difficulties of defining a fixed depth horizon for deep-sea fishes. Albert Günther (1887) of the London Natural History Museum, for the purposes of his report on deep-sea fishes captured during the voyage of the HMS *Challenger* around the world 1873–1876, had initially agreed with Professor Charles Wyville Thomson of Edinburgh University that a depth of 300–350 fathoms (572–640 m) should be considered as the boundary between surface and deep-sea fishes. However, as species that were unmistakably deep-sea species were being discovered at shallower depths in the North Atlantic, he finally adopted 100 fathoms (183 m) as the upper boundary delineating the deep sea, not very different from the present defined limit of 200 m. Goode and Bean (1895) wrote that the limit of 100 fathoms is ordinarily used to define deep-sea fishes and the 200 m limit is now recognised by the United Nations, Food and Agriculture Organisation, Fisheries and Aquaculture Department who define deep-sea fisheries as taking place at great depths (between 200 and 2000 m; FAO, 2014).

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For bottom-living or demersal fishes the 200 m depth horizon coincides with the depth of the shelf break, the edge of the continental shelf where the seafloor begins to slope off down to the abyss. Thus 200 m defines the boundary between coastal shelf-dwelling neritic species and deep-sea species of the continental slope. This distinction is clearest in the North Atlantic in areas such as the Celtic Sea area, west of the British Isles, where the depth reaches 200 m over 300 km offshore (Fig. 1.1a), defining a clear boundary between productive shelf seas and the deep sea. However elsewhere, the 200 m depth boundary is less clear. The most important fishing area in New Zealand waters is the Chatham Rise off the east coast of South Island (Fig. 1.1b). Much of the Rise is about 400 m deep and is populated by shelf-seas species with truly deep-sea species *Centrophorus squamosus* (Leafscale gulper shark) and *Mora moro* (Common mora) occurring at the outer edges of the Chatham Rise at depths greater than 500 m (McMillan et al., 2011). Off the east of Japan there is a shelf break at around 200 m before the seafloor slopes off down to great depths in the Japan Trench (Fig. 1.1c). However at oceanic islands such as Oahu in the Hawaiian Islands there is no distinctive 200 m depth horizon; the seafloor slopes down from the beach at Honolulu and reaches 500 m depth approximately 5 km offshore (Fig. 1.1d).

Confusingly, in the English language the term ‘deep-sea fishing’ is also often used to refer to fishing distant from the shore, despite the fact that the fish being captured are usually shallow or surface-dwelling species. Holdsworth (1874) stated that British deep-sea trawlers rarely fish so much as 50 fathoms (92 m) deep. From the 1890s onward steam-powered trawlers from England began to fish for cod off Iceland, Greenland, Bear Island, the White Sea off Russia, and across the Atlantic off Newfoundland and were known as deep-sea trawlers; the leading British fishermen’s welfare organisation (founded 1881) is still known as the Royal National Mission to Deep Sea Fishermen. Few of the fishermen supported by the organisation were ever engaged in catching truly deep-sea fish. Similarly recreational sports fishermen often are said to engage in deep-sea fishing which Coghlan (2008) defines as a form of marine tourism involving overnight travel offshore. The species sought by such recreational anglers are the big-game fish: marlin, billfish, mackerel, tuna, dolphin-fish and sailfish, all open ocean surface-dwelling fishes (Pepperell, 2010).

For the purposes of this text, deep-sea fishes are considered to be species that live a large proportion of their lives at depths greater than 200 m. Nevertheless depth overlaps between shallow and deep-sea species do occur, and some deep-sea fisheries may exploit a mixture of shallow and deep-sea species. Only fishes of the globally interconnected oceans and seas including the Arctic Ocean, Red Sea and Mediterranean Sea are considered. Inland seas and lakes, although deep (e.g. Caspian Sea, maximum depth 1025 m, and Lake Baikal, maximum depth 1,642 m) are not considered.

1.2 The Structure of the World’s Ocean Basins

1.2.1 Ocean Depth Zones

Zonation of species with increasing altitude is a familiar phenomenon on land, from low-lying grasslands to upland forests and increasingly barren slopes above the treeline up to the snow-capped peaks of mountains. When deep-sea fishes were first discovered by Risso (1810), it was immediately apparent that a similar zonation occurs in the deep sea with different species of fishes living at different depths. Indeed, Risso (1826) went on to describe the zonation of flora and fauna from the summits of the Alps to the depths of the Mediterranean Sea. Deep-sea fishes show remarkable fidelity to their preferred depth zones (Merrett and Haedrich, 1997), so in order to understand their distribution it is important to know about the shapes of the ocean basins. In particular, (a) How much area is there of different depths? (b) Is the area fragmented or continuous? (c) What is the distance between patches of the same

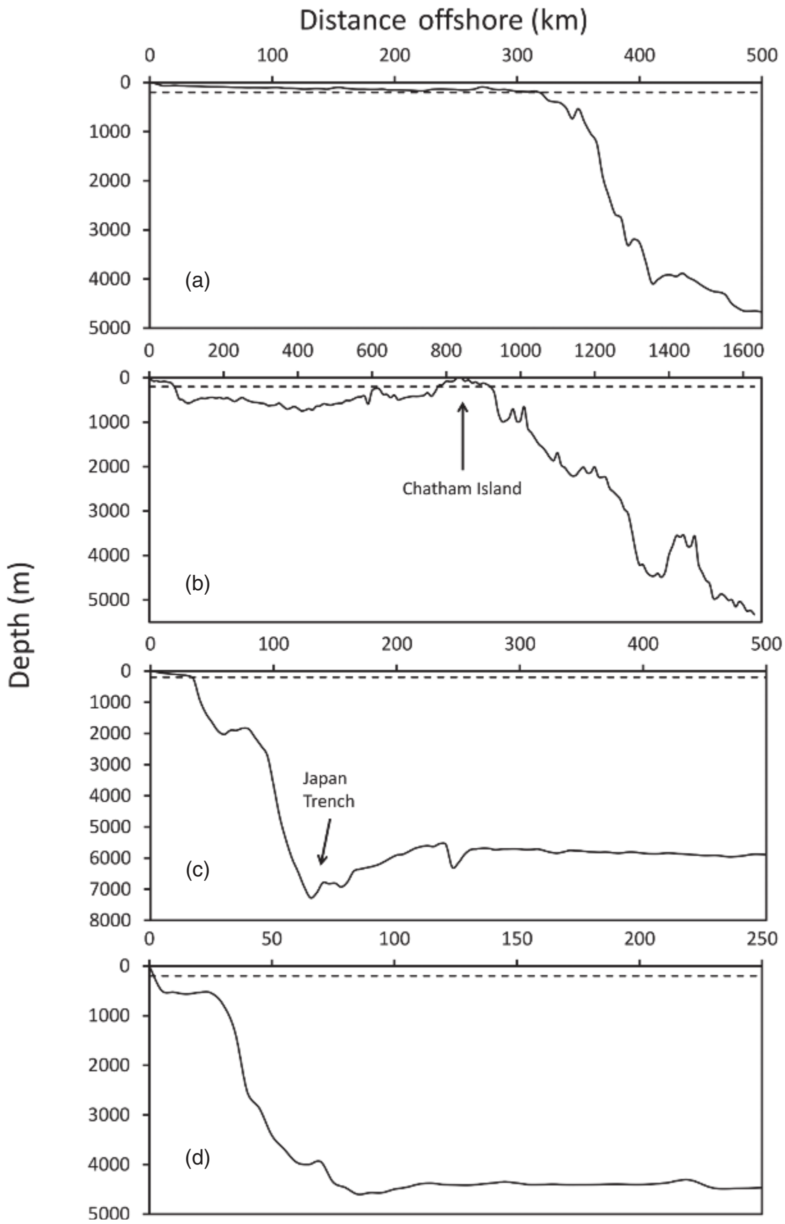

Figure 1.1 Seafloor depth profiles at different locations around the world. The horizontal dashed line is the generally recognised 200 m upper depth limit for deep-sea fishes. The solid line is the seafloor.

(a) Celtic Sea, NE Atlantic Ocean, Transect from Land's End (50.065°N 5.716°W), Cornwall, England, heading 234°.

(b) Chatham Rise, SW Pacific Ocean, Transect from Banks Peninsula (43.820°S 173.103°E) Christchurch, South Island, New Zealand, heading 94° passing through the Chatham Islands.

(c) Japan Trench, NW Pacific Ocean, Transect from Coshi (37.713°N 140.878°E) Honshu Island, Japan, heading 102°.

(d) Hawaii, N Pacific Ocean, Transect from Honolulu (21.278°N 157.835°E), Oahu Island, Hawaiian Islands, heading 215°.

depth? This section of the book seeks to answer those questions and to describe the characteristics of the seafloor.

The oceans and seas occupy 360.663 million km^2 of the earth's surface, equivalent to 70.55 per cent of the area of the planet (Costello et al., 2010). Most of this is deep sea, with the total area deeper than 200 m amounting to 65.26 per cent of the earth surface area. The average depth of the ocean is 3729 m, and its total volume is 1.335819 $\times$ 10^9 km^3. It is convenient to divide the seafloor into four depth categories: 0–200 m – shallows around land masses, mostly continental shelves; 200–3,000 m – the bathyal zone comprising slopes around continents, islands, seamounts and ridges; 3,000–6,000 m – the abyssal zone, mostly abyssal plains; depths greater than 6,000 m – the hadal zone, trenches and deep basins. The hypsographic curve (Fig. 1.2) shows that the abyssal zone is the largest and accounts for 53.2 per cent of the surface of the earth. The hadal zone, between 6,000 m and its maximum ocean depth 10,990 m at the Challenger Deep in the Pacific Ocean, accounts for 45 per cent of the ocean depth range but less than 0.5 per cent of total ocean area.

The boundaries between these zones cannot be sharply defined, and terminology varies between different authorities and according to whether physiographic or ecological principles are applied (Fig. 1.3). Gage and Tyler (1991) used the ecological depth zones; bathyal (200–2000 m), abyssal (2000–6000 m) and hadal (>6000 m). For describing the depth distribution of demersal fishes around the North Atlantic basin Haedrich and Merrett (1988) developed a scale with 750 m depth increments, upper middle and lower slope extending down to 2250 m and the rise (upper, middle and lower) extending

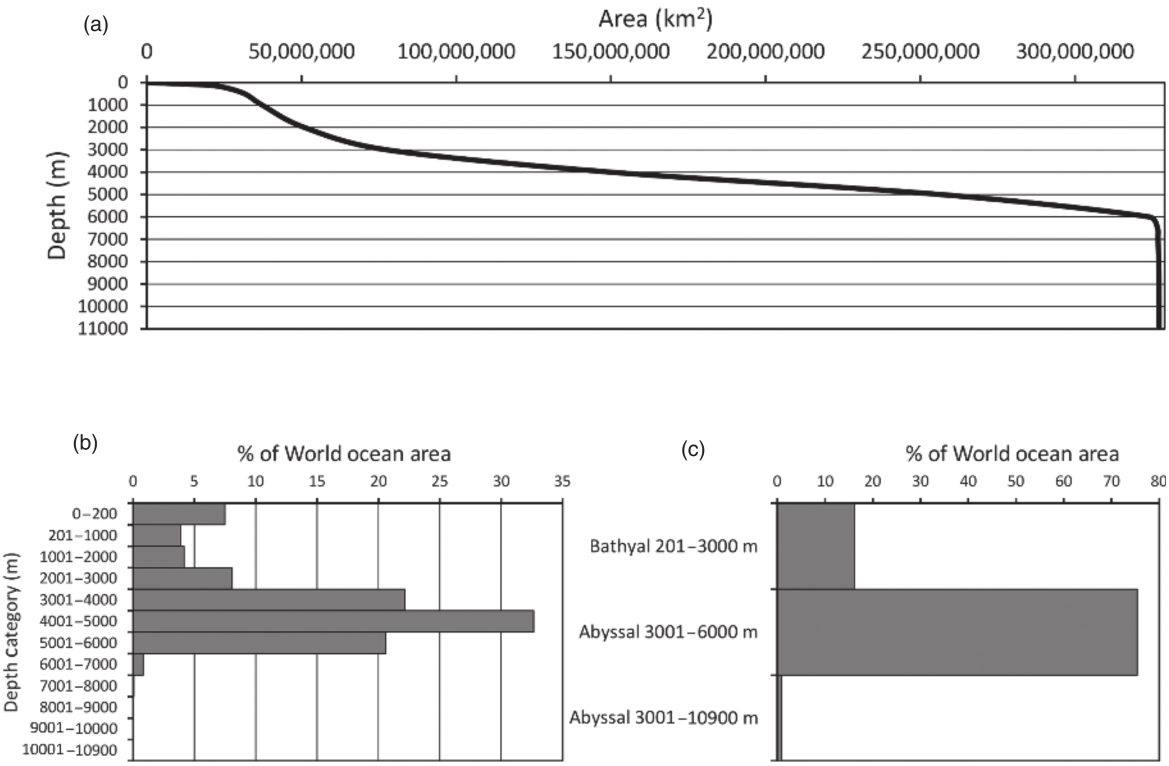

Figure 1.2 Distribution of depths in the oceans. (a) The hypsographic curve based on the GEBCO global bathymetry showing cumulative area with increasing depth. (b) Percentage of world ocean floor area at 1000 m depth increments (except the 0–200 m continental shelf, nominally continental shelf). (c) Percentage of world ocean floor in the three main deep-sea depth categories.

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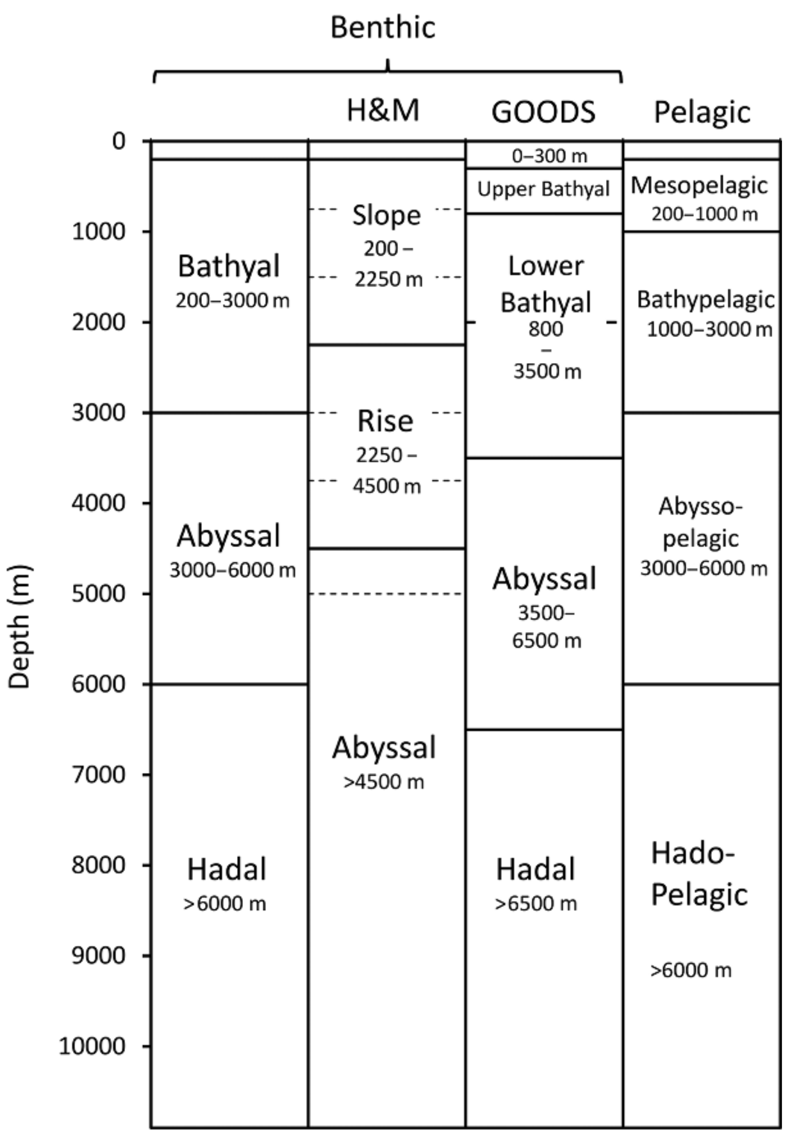

Figure 1.3 Deep-sea depth zones; nomenclature according to different authorities. The first column shows the benthic scheme used in this volume. H&M is according to Haedrich and Merrett (1988) with upper middle and lower subdivisions within each depth band. GOODS is according to UNESCO (2009). Pelagic nomenclature is in the final column.

down to 4500 m. All depths greater than 4500 m were considered abyssal, and there was no hadal zone to consider in their study. This scheme accords well with the observed boundaries between deep-sea fish species assemblages and is appropriate for passive ocean margin typical of the North Atlantic (Fig. 1.3). The Global Open Ocean and Deep Seabed (GOODS) – Biogeographic Classification, (UNESCO, 2009) offers an alternative scheme in which the boundaries are defined by differences in mainly invertebrate faunal assemblages. The deep sea is defined as the seafloor below 200–300 m, and owing to the detection of bathyal and abyssal fauna at greater depths than previously recognised, the boundaries of zones have been moved 500 m deeper to 3500 m and 6500 m, respectively (Fig. 1.3).

For the pelagic realm, the ocean remote from the shore and not in contact with the seafloor, it is convenient to use similar depth limits as for the seafloor. Thus the epipelagic zone is from the surface to 200 m depth within which during daylight photosynthesis occurs, fish can hunt their prey by conventional visual means and many species have coloured patterns. The mesopelagic zone, from 200 to 1000 m, is a twilight zone reaching down to the maximum depth of penetration of solar light in clear oceanic water. Low-intensity diffuse monochromatic down-welling light, insufficient for photosynthesis, is nevertheless sufficient for visual function by many organisms, including mesopelagic fishes. Below 1000 m there is total darkness other than occasional bioluminescent flashes with the Bathypelagic zone from 1000 to 3000 m and the Abyssopelagic zone from 3000 to 6000 m (Merrett and Haedrich, 1997). However, in practice there is no distinct boundary in midwater at 3000 m, and unless otherwise qualified the term 'bathypelagic' commonly refers to any depth greater than 1000 m. Hado-pelagic is used to refer to depths greater than 6000 m. (Fig. 1.3)

1.2.2 Ocean Basin Formation, Slopes, Plains, Ridges, Islands and Seamounts

The shape of the ocean basins derives from the basic structure of the earth's crust, with the relatively low-density continental crust floating on denser mantle rocks and surrounded by thinner oceanic crust (Fig. 1.4). The continental crust, made up of granitic rocks, is of ancient origin and occupies about 40 per cent of the earth's surface. The oceanic crust, made up of basaltic rock, is continuously renewed at the mid-ocean ridges so that most of the ocean floor is less than 150 Ma old. Upward extrusion of magma raises the seafloor in mid-ocean creating shallow areas and volcanic islands such as the Azores and Iceland in the Atlantic Ocean. Summits that do not reach the sea surface are termed seamounts. Newly created seafloor moves away symmetrically either side of the mid-axial rift valley, and, as it cools the crust thins, deepening the ocean with increasing distance from the mid-ocean spreading centre. Volcanic islands and seamounts created by eruptions at the spreading centre are transported away from the mid-ocean ridge as if on a conveyor belt, gradually decreasing in altitude (or increasing in depth) as the crust sinks and the summit is eroded over time (Fig. 1.5). Chains of large seamounts can be formed where the moving oceanic crust passes over a hotspot or mantle plume where successive eruptions raise one volcanic summit after another. In the North Atlantic, the New England seamount chain with more than 20 peaks rising from the abyssal seafloor stretches over 1000 km from the Mid-Atlantic Ridge to Georges Bank. In the North Pacific Ocean the Hawaiian and Emperor seamount

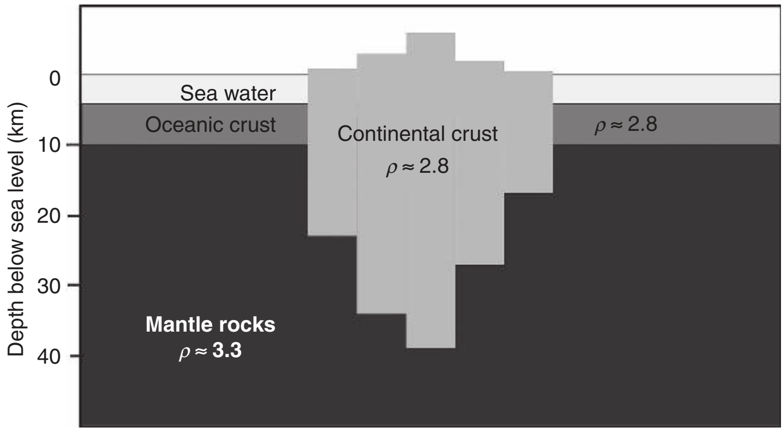

Figure 1.4 Schematic diagram of a section through a continent showing continental crust floating on dense mantle rocks surrounded by thinner oceanic crust creating deep ocean of average depth ≈ 4000 m. Continental slopes and sediment deposits are omitted for simplicity.

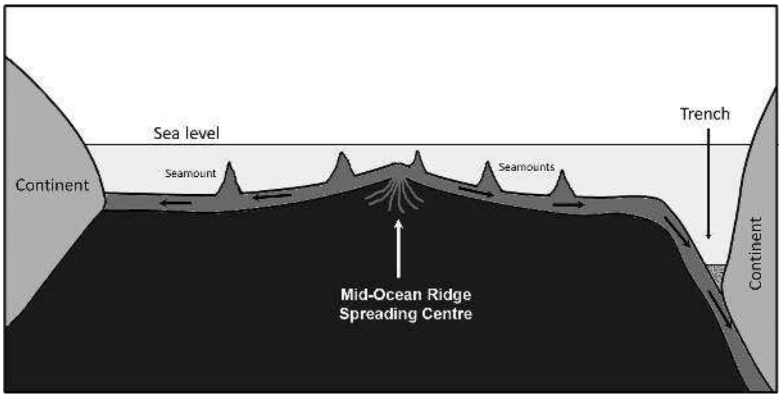

Figure 1.5 Continental Drift. Schematic cross-section of an ocean basin showing motion of oceanic crust away from the mid-ocean ridge spreading centre. Where oceanic crust moves beneath the continent a deep-sea trench is formed (right).

chain, including the Hawaiian Islands, has more than 80 summits extending over 5,800 km. The rate of seafloor spreading varies between 1 and 10 cm per year. At a passive ocean margin there is no relative motion between the oceanic crust and the continental crust; the continent moves away from the mid ocean at the same rate as the seafloor spreads. At the junction between the oceanic and the continental crust the slope of the passive margin tends to become filled with sediments eroded from the continental land mass, creating a zone of sedimentary rocks, which often harbours hydrocarbon deposits (Fig. 1.6a). This type of margin is characteristic of the Atlantic Ocean, where North and South America are moving away from Europe and Africa, respectively. The deepest parts of the Atlantic Ocean are generally in the abyssal plains on either side of the mid-ocean ridge. The mid-ocean ridge axis does not form a continuous straight line; the rate of spreading varies in different parts and because the earth is spherical, a strict linear geometry is not possible. Discontinuities in the ridge appear as transverse fracture zones where the axis of the ridge is often displaced laterally. The fracture zone may also include one or more transverse canyons crossing from one side of the ridge to the other. These are important as areas of exchanges of deep water between the two sides of the mid-ocean ridge and also provide possibilities for deep-sea species to move across what might otherwise be a barrier to dispersal.

Continuous production of new oceanic crust at mid-ocean spreading centres requires equivalent consumption of an equal area of seafloor elsewhere in the ocean. This occurs by subduction at active ocean margins where the oceanic crust moves either directly beneath the continental crust (Fig. 1.6b) or under an offshore volcanic island arc (Fig. 1.6c). The area of subduction is marked by a depression in the seafloor, a trench parallel to the coast. Between the island arc and the continent, a back arc basin may be formed by a distinctive kind of seafloor spreading. Tension is created in the seafloor, either by movement of the continent entrained by the subducting oceanic crust (Van Dover, 2000) or by movement of the island arc towards the ocean by a process known as trench roll-back (Becker and Faccenna, 2009). The resulting tension in the intervening seafloor results in faulting that enables the ascent of magma from the mantle, which then creates a subsidiary seafloor spreading centre and expansion of the back arc basin. This process is most prevalent in the western Pacific Ocean, a notable example being the Sea of Japan (mean depth 1752 m, maximum depth 3742 m). Owing to differences in the process of formation and density of rocks, back arc basins are shallower than the ~4000 m equilibrium depth of oceanic basins (Schopf, 1980) but nonetheless provide significant areas of deep-sea floor. Between the trench and continent or island arc there may be a fore arc basin formed as part of the accretionary wedge of material

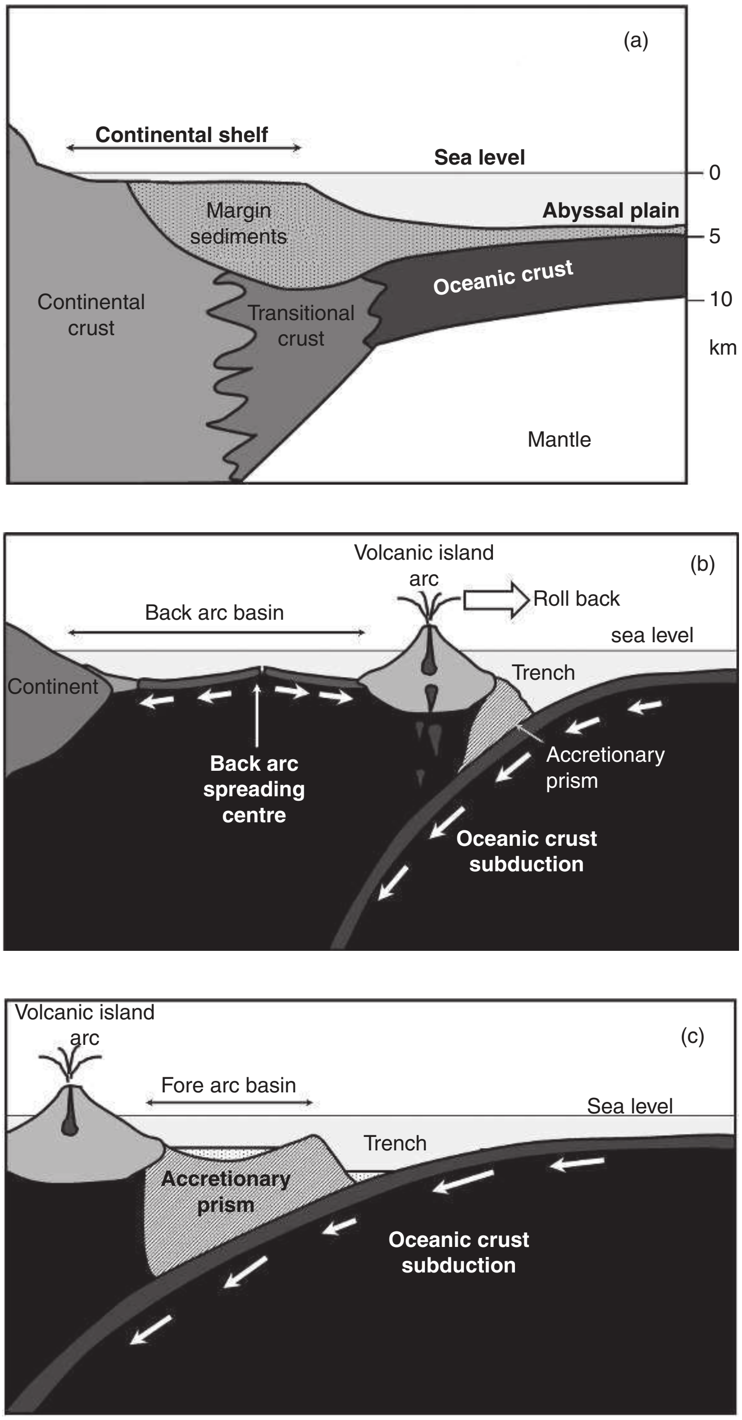

Figure 1.6 Types of Ocean Margin.

(a) Passive Margin, where there is no relative motion between continental and oceanic crust sedimentary deposits accumulate forming layered structures extending out to the abyssal plains.

(b) Active margin with a back arc deep-sea basin. Subducting oceanic crust melts and molten magma ascends to form a volcanic island arc parallel to the trench axis. Movement of the islands towards the trench axis creates a back arc spreading centre with a new sea area bounded by the continent and offshore string of islands.

(c) Active margin with a fore arc deep-sea basin. Folding of the accretionary prism of material trapped as oceanic crust subducts creates a fore arc basin inshore of the trench axis.

accumulating adjacent to the subducting ocean crust. On the Pacific coast of Japan such basins lie between the coast and the trenches further offshore (Fig. 1.6c).

At active continental margins, relative motion of the crust at the edge of the plates creates frequent earthquakes. Volcanic activity is common, bringing material to the surface that creates the offshore island arc or erupts on the edge of the continent. Active margins surround the Pacific Ocean making up the so-called Ring of Fire with active volcanoes, earthquakes and the presence of most of the world's deep trenches with depths in excess of 6000 m (Fig. 1.7). Passive margins are found predominantly around the Atlantic Ocean, the Indian Ocean and the Arctic Ocean (Fig. 1.7). On a passive ocean margin the seafloor generally descends quite steeply beyond the shelf break, reflecting the step down from continental to oceanic crust. This segment is known as the continental slope and extends down to about 2000 m, although subdivisions are often recognised. The continental slope may be bisected by canyons, which add further complexity to the seafloor (Plate 1c). Apart from bare rock in areas of strong currents or where the topography is very steep, the slope is draped with fine sediment of largely terrigenous origin. The gradient then decreases on the continental rise out to the almost flat abyssal plains. In graphic displays the vertical scale is usually exaggerated giving a misleading impression of the true gradient. The average continental slope gradient between 200 and 2000 m depth in the NE Atlantic (Fig. 1.1a) is 3.4 per cent and on the continental rise the gradient decreases to 2.8 per cent. The surface of the continental rise is usually made up of successive layers of sediment that have slumped down from the slopes, been transported through the canyons from the continental shelf or slowly deposited over time. Occasional turbidite flows of suspended sediments triggered by earthquakes or slope failure can be violent events both eroding the sediment surface and depositing new layers on old. The largest such slides deposit material on areas in excess of 100,000 km extending over the continental slope, rise and abyssal plains (Mienert et al., 2003). With increasing distance offshore, the sediment of terrestrial origin gradually disappears and is replaced by oceanic sediment derived from shells of planktonic organisms. Wind-blown dust from human sources, deserts and volcanoes precipitated out of the

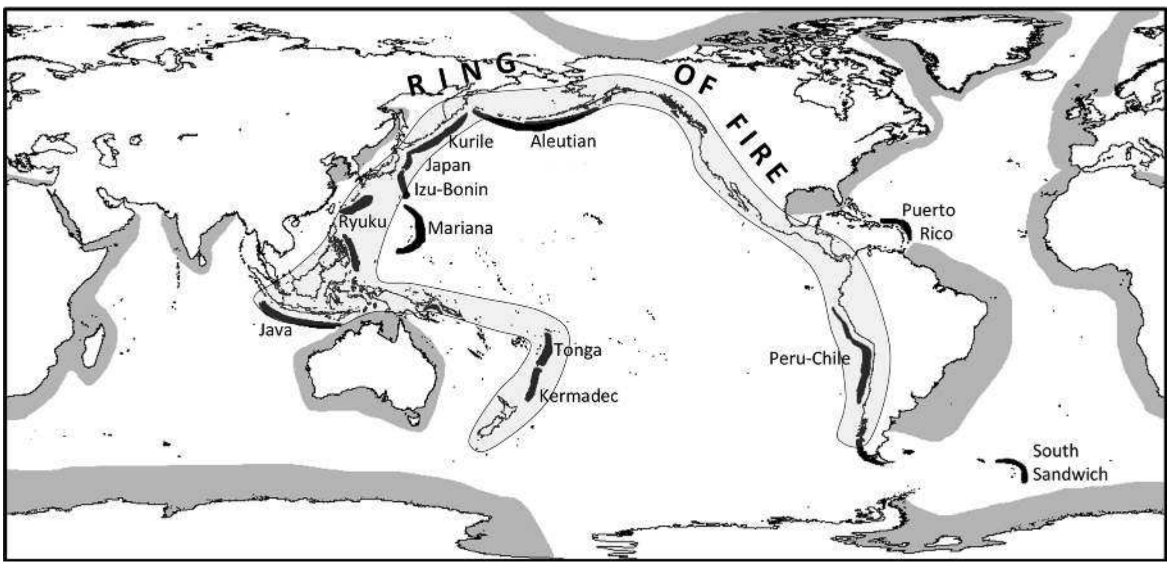

Figure 1.7 Distribution of Active and Passive Margins around the World's Ocean. The Pacific Ocean is surrounded by active ocean margins of the 'Ring of Fire' characterised by seismic activity, major volcanoes and deep trenches (black and labelled with names) created by subduction of oceanic crust. Passive ocean margins (grey shading) occur around most of the rest of the oceans. Based on information from Kious and Tilling (1996) for the active margins and Pinto (2007) for the passive margins.

atmosphere and deposited on the seafloor is an additional source of sediment.

Most of the ocean floor (>90 per cent) has never been directly mapped by soundings from ships. Continental slopes and adjacent areas have been surveyed relatively well in recent years to assess resources and to support offshore sovereignty claims by coastal states under the United Nations Convention on the Law of the Sea article 76 (UN, 1982). However, in the open ocean, outside specially surveyed areas, bathymetric maps are based on satellite gravimetry interpolated with available ship-borne data (Smith and Sandwell, 1997). The highest resolution achieved in this way for global mapping is 30 arc second (Becker, 2009; GEBCO, 2014) or approximately 1 km (Wessel et al., 2010). Using such data, Yesson et al. (2011) estimated the global number of seamounts to be 33,452 plus 138,412 knolls. A computer algorithm was used to search for conical features defined as seamounts in which the average height of the summit is >1000 m above the surrounding seafloor (Morato et al., 2008). Small features in which the average height of the summit is between 200 and 1000 m above the surrounding seafloor are termed knolls (Yesson et al., 2011) or small seamounds (Morato et al., 2008). The existence of most of these features has not been directly verified by ship's soundings, and the estimated number of seamounts differs between different studies. There seems to be convergence towards an estimate of *ca*. 15,000 large seamounts with heights >1500 m (Wessel, 2001; Yesson et al., 2011). However, Wessel et al. (2010) speculate that there may be 100,000 uncharted seamounts >1000 m in height and 25 million knolls or small seamounts >100 m in height.

Yesson et al. (2011) define summits with a depth less than 1500 m below the sea surface as 'productive' and identify 9,239 productive seamounts and 10,185 productive knolls worldwide. Whilst 1500 m is beyond the depth at which photosynthesis is normally possible, these are depths at which cold-water corals, sponges and other reef- building organisms are likely to thrive, and these depths are accessible to deep water fishing activity. There are therefore probably about 20,000 submarine summits worldwide that can be considered to be of economic significance (Fig. 1.8).

Seamounts and mid-ocean ridges are made up of basaltic rocks reflecting their volcanic origin, and this hard substrate is usually exposed on summits, cliffs, steep slopes (gradient >45 per cent) or in areas of strong currents. However, intervening flat areas and gentle slopes are generally covered with soft sediment of pelagic origin (Hughes, 1981). Animal tracks or lebenspüren are conspicuous in the soft foraminiferal sand covering of deep seamounts in the Central North Pacific (Kaufman et al., 1989). At lower bathyal

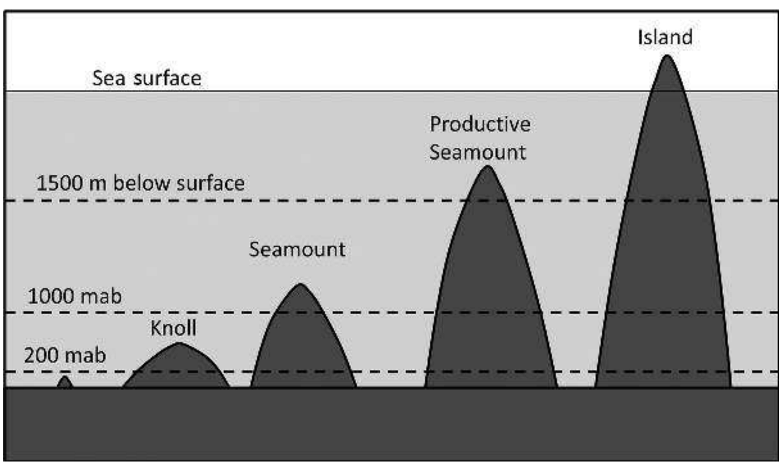

Figure 1.8 Classification of seamount summits according to height above the surrounding seafloor and depth below the sea surface. mab = metres above bottom.