temporarily high species numbers), and may take time to reach their new equilibrium. The terms "lag effect" (duration of delay) and "extinction debt" (magnitude of the losses) are each used to describe the delay in species losses following fragmentation of habitat. Rather more controversially, the theory of island biogeography has also been invoked in the design of protected areas networks. It has been proposed that, in general, the theory favors deploying resources to protect fewer large reserves rather than many smaller ones (the "SLOSS Debate"), short rather than long inter-reserve distances, circular rather than elongated reserves (to minimize edge effects), and the use of corridors, when ever possible, to connect reserves and facilitate dispersal between them.

SEE ALSO THE FOLLOWING ARTICLES

Extinction / Fragmentation / Relaxation / Species–Area Relationship

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ISLAND FORMATION

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To understand how islands form, continental islands must be distinguished from oceanic islands, the former being pieces of continents with the connection submerged, the latter being younger islands that originated exclusively within the ocean basins. However they appear today—low or high, limestone or volcanic—all oceanic islands began life as ocean-floor volcanoes. Those that have not yet reached the ocean surface (and many never do so) are referred to as seamounts, whereas those that were once emergent but have since been submerged are often distinctively flat-topped and are called guyots.

OCEAN-FLOOR VOLCANOES: ORIGINS AND GROWTH

It comes as no surprise to learn that we are not very knowledgeable about ocean-floor volcanism because of the difficulties in actually observing it. Most ocean-floor volcanism occurs in the dark beneath 4 km of ocean water. It is not that the technological difficulties are insurmountable, just that it is difficult to be sure that researchers are getting an accurate picture of what is going on. In this regard, places where the ocean floor actually rises above the ocean surface are extremely valuable as observation sites. Second best are places where seamounts have been thrust up above sea level and have their insides exposed for scientists to see how they were built up.

The finest example of the first situation—where the ocean floor actually rises above the ocean surface—is the island of Iceland in the northern Atlantic Ocean. Iceland is part of the Mid-Atlantic Ridge (a divergent plate boundary) that lies at a plate triple junction and where eruptive activity has been unusually voluminous over the past few million years. The mid-ocean ridge—a common site of ocean-floor volcanism—actually passes through the center of Iceland. From studies of this, we learn that the earliest type of ocean-floor volcanism is commonly along fissures. As fissure eruptions continue, some parts of the fissure become blocked, and eruptions begin to occur at points. Point volcanism results in the build-up of the earliest types of seamounts.

Studies of emerged seamounts—which rise from ocean floor that has been thrust upward by tectonic forces—have also given us a lot of information about the undersea development of oceanic islands. In particular, it is clear that intrusion of igneous rocks is at least as important as extrusion is in building seamounts in many parts of the ocean basins.

Another important issue is the depth of overlying ocean water in places where seamount eruption occurs. In most places below about 600 m the weight of overlying water is so great that, however powerful the volcanic eruption, it will not be explosive, and the material produced will generally be pillow lava. At depths shallower than 600 m (the hydroexplosive zone), on the other hand, the weight of overlying water is not always sufficient to subdue explosive eruptions, and there is a reaction between the cold ocean water and the hot magma (liquid rock) that causes the latter to solidify rapidly as numerous small fragments. Some of this fragmental (clastic) material may reach the ocean surface, where it floats as pumice, but most of it sinks and becomes draped over the sides of the more solid seamount as a sediment apron. Given the fragmented nature of the eruptive products produced in the hydroexplosive zone, a growing seamount often takes far longer to build itself up through this part of the ocean than through deeper areas.

HOW ISLANDS RISE ABOVE SEA LEVEL

The three main ways in which a seamount can grow above the ocean surface are extrusion, intrusion, and uplift; each is discussed separately below. These categories should not be regarded as exclusive, for it is often a combination of these processes that actually leads to emergence.

Island Emergence by Extrusion

Underwater volcanoes that erupt within the hydroexplosive zone sometimes cause islands to form. These are often referred to as "jack-in-the-box" islands because they alternately appear (during eruptions) and then disappear (between eruptions because of wave erosion). Examples are comparatively common in southwestern Pacific island groups such as Tonga and Vanuatu, located close to convergent plate boundaries. The reason that these islands do not endure long above the ocean surface is because they are composed entirely of unconsolidated and uncemented rock fragments and are promptly destroyed by wave erosion after the island-forming eruption comes to an end.

For such an island to endure above the ocean surface, clearly it needs to be made of more resistant material. The way this happens has been recorded only once, with the exceptionally voluminous and lengthy eruption of an underwater volcano off the south coast of Iceland from 1964 to 1967, which produced the island Surtsey. In the case of this eruption, the amount of volcaniclastic (fragmented volcanic) material erupted created such a large island that at one point it isolated the volcano's vent from ocean water. Once this happened, there was no longer any explosive reaction between ocean water and magma, and as a result, volcaniclastic rocks were replaced by lava. The lava flowed out over the surface of the volcaniclastic island, armoring it against erosion and leading to the establishment of a permanently emerged island.

Island Emergence by Intrusion

One of the big unknowns in the emergence of oceanic islands is the precise role of intrusion—the emplacement and solidification of igneous rocks within (not outside) an existing island edifice. Studies of former oceanic islands, now uplifted far above sea level and partly denuded to allow glimpses of their anatomy, show that intrusions can comprise as much as 70–80% of the total mass of such islands. Whether or not this is typical is uncertain, but it does underline the importance of intrusion.

Intrusion begins to affect island growth from almost its beginnings, but it appears to be generally less important when an island is significantly emergent. Intrusion in early stages of island growth may be mostly through sill formation, although later, when the island edifice is sufficiently large to accommodate them, large intrusive bodies (batholiths, stocks) may come to dominate.

Island Emergence by Uplift

Uplift refers to the upward forcing of an island, irrespective of its extrusive or intrusive activity. Island uplift is most common at convergent plate boundaries, where arcs of non-volcanic islands are often found, produced by the movement of the overriding (upper) plate across the top of the downgoing (lower) plate. Examples include the limestone islands of Tonga (South Pacific) and those of the Mentawai group (Indonesia). At convergent plate boundaries, the downgoing plate is commonly flexed (bent) upward before it goes down into the Earth's interior, producing island emergence; examples include the Loyalty Islands (Southwest Pacific).

Island uplift can also occur in the middle of plates, where islands are carried on moving plates across hotspots or other ocean-floor irregularities such as intraplate swells. Some of the Tuamotu Islands (South Pacific) have emerged as a result of such a process.

More complex cases of island emergence result from a variety of causes. For example, there are various islands that are largely composed of pieces of ocean floors (ophiolites) that have been peeled off and pushed upward across a crustal irregularity. Examples include Crete (Mediterranean Sea) and La Grande Terre in New Caledonia (Southwest Pacific).

ROLE OF SEA-LEVEL CHANGE IN ISLAND FORMATION

It may seem paradoxical, but both sea-level rise and sea-level fall can cause islands to form.

Sea-level rise floods dry land and, in doing so, can transform a large island, for example, into a series of smaller islands. This is what happened as sea level rose after the last glacial maximum in the Channel Islands off the coast of California, where people about 12,000 years ago occu-

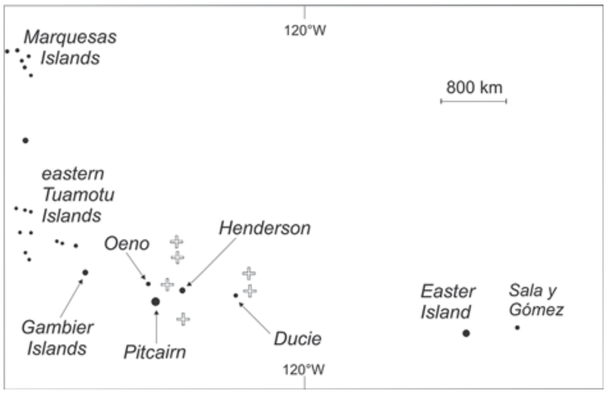

FIGURE 1 Islands of the east central and southeast parts of the Pacific Ocean. The biota of high Pitcairn Island shows affinities with the Gambier and eastern Tuamotu island groups. Henderson Island was uplifted during the late Quaternary (about 200,000 years ago) but was periodically submerged in earlier times. Ducie and Oeno atolls have been regularly submerged during high sea-level stages of the Quaternary; their terrestrial biota is derived from Pitcairn yet is consequently much less diverse. The existence of shallow-water (less than 130 m) submerged islands (marked by crosses on the map) that emerged during glacial low sea-level stages (most recently between 22,000 and 16,000 years ago) has undoubtedly aided the successive recolonization of Ducie and Oeno. The lack of any submerged islands between the Pitcairn group and Easter Island–Sala y Gómez accounts for the marked lack of biotic similarity between these island groups.

pied a large island (named Santarosae), which was subsequently broken up into several smaller ones, something that had discernible effects on societal evolution there. Yet in the same period of sea-level rise, some ten of the 26 islands that existed during the last glacial maximum in the Channel Islands were completely submerged.

A similar situation occurred in East Asia. During Quaternary glaciations, when sea level was low, the main islands of Japan often formed a single land mass (named Hondo), sometimes connected to the Asian mainland. Yet this connection was severed when sea level rose at the end of these glaciations, isolating Japan (and its occupants) from the continent and transforming one large island into a number of smaller ones. When Japan became a land of islands, people's diets changed focus from terrestrial- to marine-dominated.

For almost all of the past 2–3 million years, the ocean surface has lain tens of meters below its present level. Thus, for most of this time, the geography of islands has been quite different from the way it appears today. Many more islands were emergent at times of lower sea level, having emerged solely because of exposure as sea level fell to below their surface level. Many biogeographers have speculated that at such times the dispersal of plants and animals throughout the ocean basins was much easier than it would have been in a drowned world such as we occupy today. A good example is provided by the remote Pitcairn island group in the southeastern Pacific Ocean (Fig. 1).

SEE ALSO THE FOLLOWING ARTICLES

Continental Islands / Earthquakes / Motu / Oceanic Islands / Sea-Level Change / Seamounts, Geology / Surtsey

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ISLAND RULE

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The island rule is a name given for the supposed tendency of small-bodied animals to evolve larger sizes on islands whereas large animals evolve toward relatively smaller body sizes. The evolutionary forces that drive the observed patterns and the circumstances under which the phenomenon is manifest are widely debated but are thought to include changes in resource abundance, lower interspecific competition, elevated levels of intraspecific competition, and reduced predation on islands.

SIZE EXTREMES ON ISLANDS

Anecdotal observation can lead to the conclusion that in many clades, island-dwelling species are characterized by extreme body sizes relative to their mainland counterparts, especially on large oceanic islands. Several animal groups have their largest or smallest representatives on islands. For example, the St. Helena earwig *Labidura herculeana* and the New Zealand wetas (*Deinacrida* spp.) may be the largest representatives of their clades. The world's largest bat is the Philippine-endemic golden-crowned flying fox (*Acerodon jubatus*). Brown bears on Kodiak (*Ursus arctos*