Island Evolution
IN MARINE LAKES

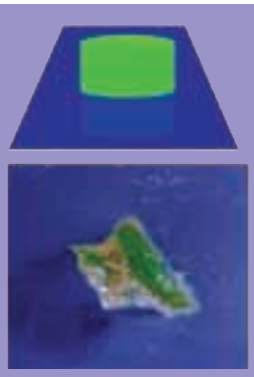
Figure 2. Clear Lake, Palau: 30 m deep, 39000 m²

'An island is … a simpler microcosm of the seemingly infinite complexity of continental and oceanic biogeography … islands provide the necessary replications in natural 'experiments' by which evolutionary hypotheses can be tested.' MacArthur & Wilson (1967)

For over 150 years, islands have played a key role in evolutionary biology and ecology in diverse terrestrial and freshwater settings. The theory of evolution by natural selection has its origins in the Galapagos Islands and Malay Archipelago. The discipline of Biogeography began with the study of island life. Island biogeography revolutionized perspectives on community structure and biodiversity, and our understanding of ecology, evolution, and speciation continue to grow through seminal studies of biotas isolated on islands and mountain-tops, and in lakes, ponds, and valleys. Studies of island-like reserves and habitat fragments have raised awareness of conservation, invasion, and extinction. Yet studies of 'marine' islands are incredibly rare. To understand why, we need to know, what is an island?

WHAT IS AN ISLAND?

Most of us think of a piece of land surrounded by ocean, what island biogeographers call a 'true' island (Figure 1). But an island is simply 'something … isolated or surrounded', as recognized in the description of 'habitat' islands, i.e. one environment entirely surrounded by another. By this broader definition, there clearly are many potential islands in marine systems, including coral heads and the reefs that circumscribe tropical 'true' islands, also atolls, seamounts, hydrothermal vents, estuaries, splash pools, and inland seas. However, it is unclear how many of these really fit the general concept of an island. Coral heads, patch reefs, and atolls, while clearly geographically isolated from others of their kind, are all surrounded by the medium in which eggs, larvae and sometimes adults naturally live and disperse. Inland seas are isolated, but larger than most people's idea of an island. One marine habitat, though, clearly fits the definition of an island—the marine lake.



True Island
Oahu, Hawaii

Habitat Island
Jellyfish Lake, Palau

Figure 1

WHAT IS A MARINE LAKE?

A marine lake is an area of seawater surrounded by land (Figures 1–3). Marine lakes are the last unexplored shallow-water marine habitat. There are tens to hundreds of marine lakes distributed globally, often clustered in karst. In Palau, they were formed when depressions in the fissured karst landscape were flooded by rising sea-level after the last glacial maximum. As such, here, they are all less than 20,000 years old, some as little as c. 5,000 years old (a lake's age is approximately proportional to its depth; Figure 4). They come in a wide variety of sizes, shapes, and depths, with differing communities (e.g. coral or mangrove), and are variously connected to the surrounding ocean.

Marine lakes, like terrestrial islands and freshwater lakes, are extraordinary ecosystems with unique biotas—atypically small, distinct populations of divergent organisms that evolved in unusual, isolated, environments. Such similarities suggest marine lakes could reasonably be considered 'islands'. The key question is: are similarities between marine lakes, freshwater lakes, and terrestrial islands just coincidence, or are they the result of common ecological and evolutionary processes? This question remains almost unexplored, not only in Palau, but also in marine lakes in Indonesia, Vietnam, Papua New Guinea, and the Adriatic (to name a few places where marine lakes occur), let alone other island-like ecosystems around the globe.

ARE MARINE LAKES 'ISLANDS'?

One way to answer this question is to test the predictions of island theories derived in terrestrial studies. For example, we could test the predicted genetic and phylogenetic consequences of island biogeography,

Figure 3. Uet era Ongael, Palau: 4 m deep, 9000 m²

the 'Island Rule' most recently brought to people's attention through the discovery of *Homo floresiensis*), the theory of island biogeography, the Unified Neutral Theory of Biodiversity and Biogeography, and look for evidence of peripatric speciation and punctuated equilibrium. Our first study shows that the predicted genetic consequences of island biogeography occur in marine lakes. Data to test the others are being collected, and preliminary results are exciting. For example, the numbers of species present in a lake are consistent with the predictions of island biogeographic theory, rates of evolution are consistent with peripatric/punctuated evolution, and there are probably many endemic subspecies and species (Figures 6 & 7).

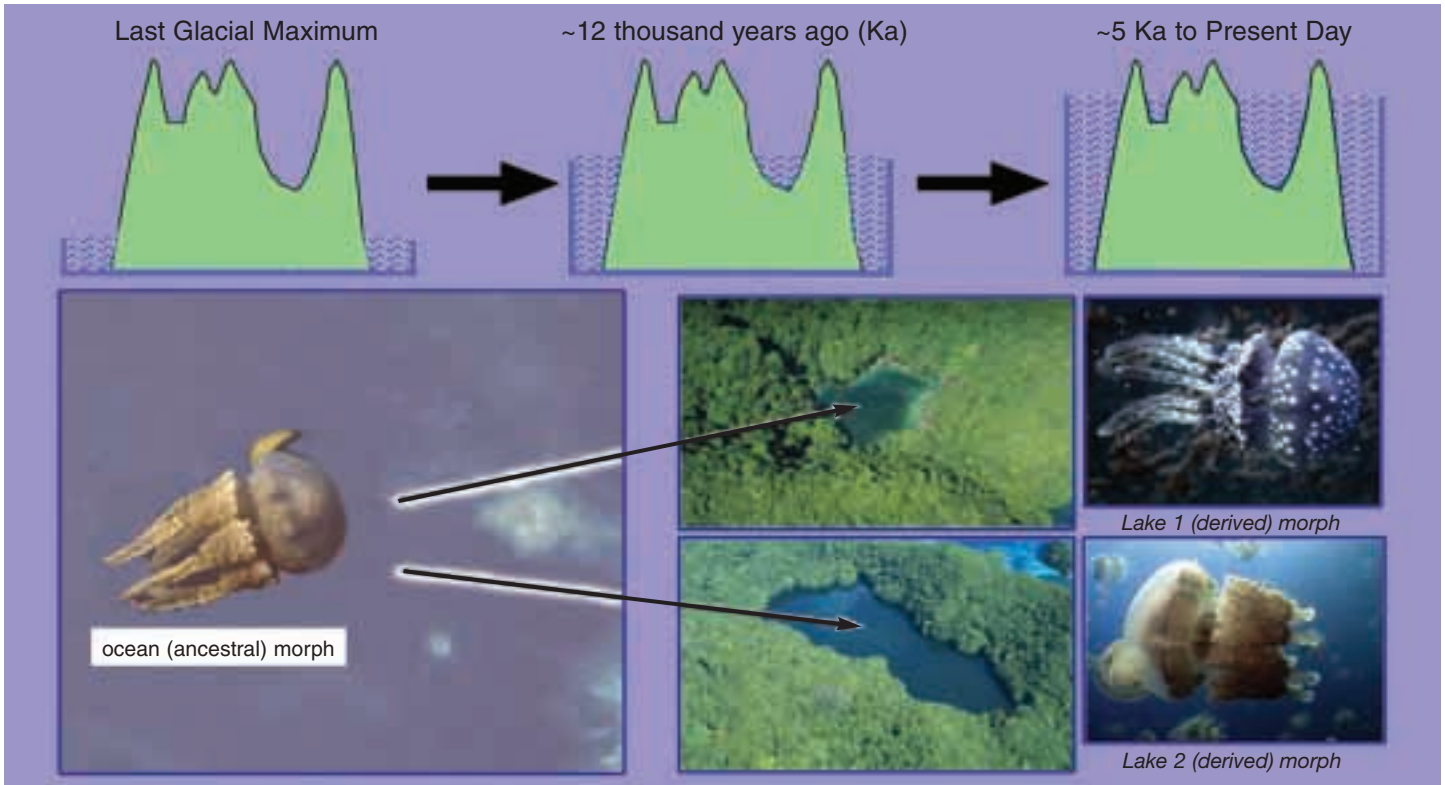


Figure 4: Marine lakes, and endemic populations, formed as karst was flooded by rising sea-level

Figure 5. A view across 'Jellyfish Lake', called Ongeim'l Tketau , in Palau. The lake is 30m deep, 50,000m^2

ARE OTHER MARINE SYSTEMS ISLANDS?

This idea is largely untested. Some studies in the 1970s were ambiguous and marine scientists have generally found island ideas unconvincing. Many studies still report gene flow over relatively large distances, but evidence of geographic isolation in marine taxa is increasing. Some fish larvae return to, or may never leave, their natal reefs and species of marine gastropods can be endemic to individual archipelagoes. Distributions of corals and reef fish are broadly consistent with the predictions of island biogeography and some data seem to support the 'Island Rule'. As such, it may be time to revisit the question of whether island studies might benefit marine science. This would be particularly timely because modern approaches to marine conservation draw heavily on ideas from terrestrial systems including island-like protected areas (surrounded by unprotected areas) and networks thereof.

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"Evolutionary biologists have ... concentrated on denizens of the dry land … islands have been viewed as tidy, self-contained systems in which ecological processes and their evolutionary consequences become transparent in the way that island air is clear without the obfuscation of continental haze ... But islands are, quite literally, tidy places for seashore life as well ... however, few marine-oriented biologists have asked how the marine life on islands differs from that near mainlands, and even fewer have thought about how islands as seen from the perspective of sea creatures differ from islands as we humans and other land-adapted species might perceive them." Vermeij (2004).

Figure 6. Endemic jellyfish, *Mastigias* cf. *papua etpisoni*, in Ongeim'l Tketau (OTM; Dawson, 2005)

Image credits:

Oahu satellite image *NASA, Visible Earth, http://visibleearth.nasa.gov/*

Aerial images of marine lakes *courtesy P.L. Colin, Coral Reef Research Foundation*

Image of Ongael medusa *courtesy L. Sharron, Coral Reef Research Foundation*

All other images and compositions by the author.

Figure 7: An endemic anemone, *Entacmaea medusivora*, in OTM (Fautin & Fitt, 1993)

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