Island Evolution
IN MARINE LAKES

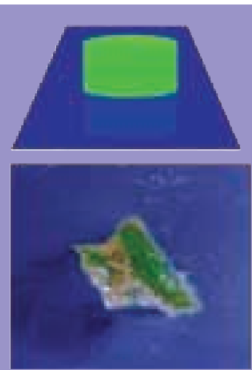
FIGURE 2: Clear Lake, Palau: 30m deep, 39000m²

"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)

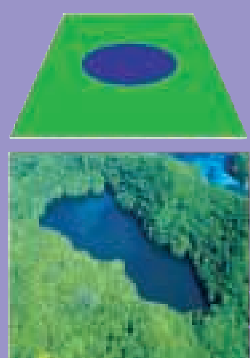
The theory of evolution by natural selection has its origins in the Galapagos Islands and Malay Archipelago (Wallace 1858; Darwin 1859). The discipline of Biogeography began with the study of island life (Wallace 1880). Island biogeography revolutionized perspectives on community structure and biodiversity (MacArthur & Wilson 1967) 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 (e.g. Grant 1998). Studies of island-like reserves and habitat fragments have raised awareness of conservation, invasion, and extinction (Quammen 1996). 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 (Fig. 1). But an island is simply "[s]omething … isolated or surrounded" (OED 2005), as recognized in the description of "habitat" islands, i.e. one environment entirely surrounded by another (MacArthur & Wilson 1967). 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 a piece of seawater surrounded by land (Figs. 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. They were formed when depressions in the fissured karst landscape were flooded by rising sea-level after the last glacial maximum. As such, 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; Fig. 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 (Johnson et al. 2000), the 'Island Rule' (Foster 1964; most recently brought to peoples' attention through the discovery of *Homo floresiensis*), the theory of island biogeography (MacArthur & Wilson 1967), the Unified Neutral Theory of Biodiversity and Biogeography (Hubbell 2001), and look for evidence of peripatric speciation and punctuated equilibrium (Mayr 1963; Eldredge & Gould 1974). Our first study shows that the predicted genetic consequences of island biogeography occur in marine lakes (Dawson & Hamner 2005). 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 (Figs. 6, 7).

FIGURE 3: Uet era Ongael, Palau; 4m deep, 9000m²

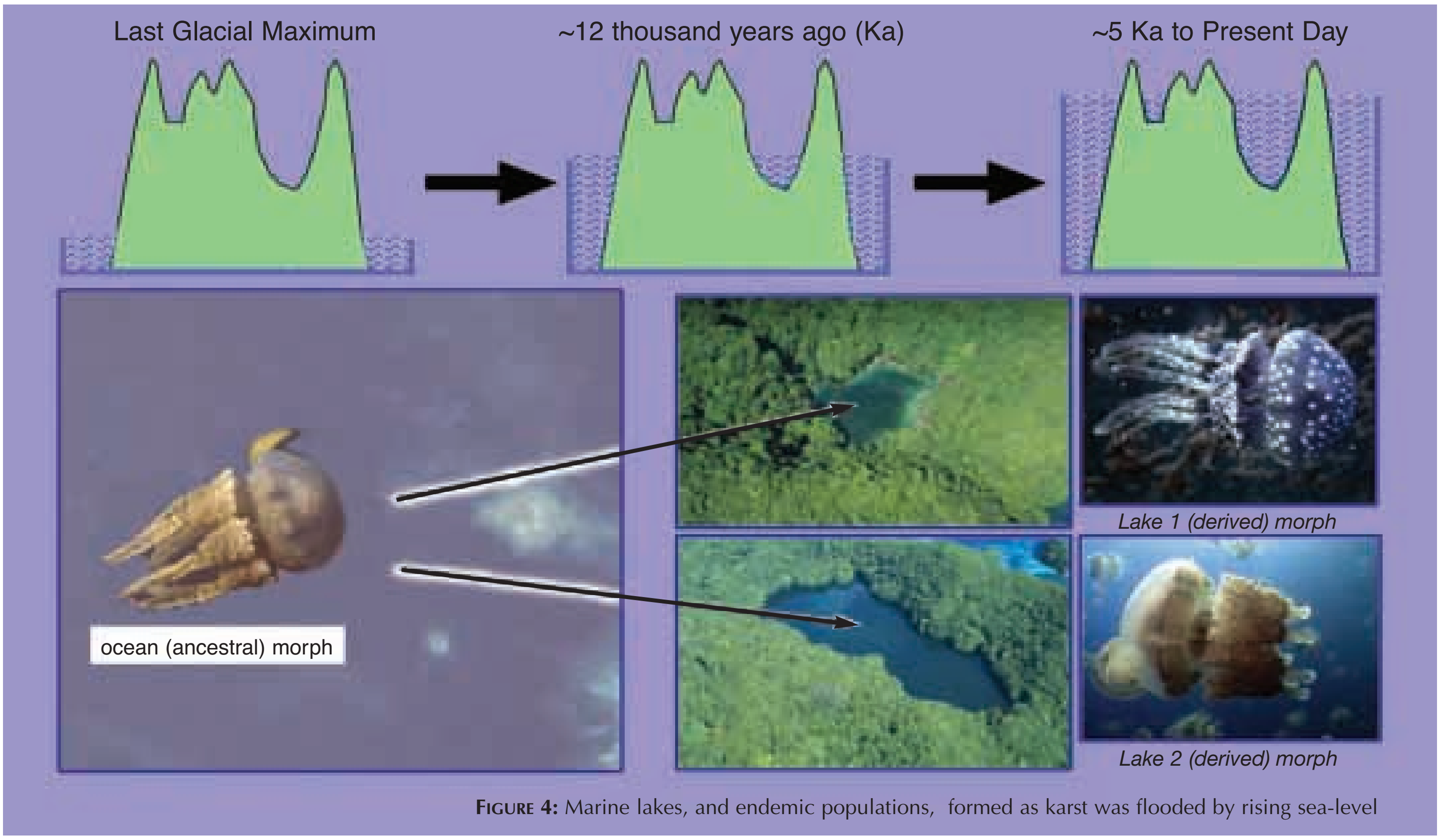


FIGURE 4: Marine lakes, and endemic populations, formed as karst was flooded by rising sea-level

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 1970's were ambiguous and marine scientists have generally found island ideas unconvincing (Knowlton & Jackson, 1994). Many studies still report gene flow over relatively large distances, but evidence of geographic isolation in marine taxa is increasing (e.g. Avise 1992; Turan et al. 1998; Maltagliati et al. 2001; Taylor & Hellberg 2003; Dawson 2005b). Some fish larvae return to, or may never leave, their natal reefs (Jones et al. 1999) and species of marine gastropods can be endemic to individual archipelagoes (Meyer et al. 2005). Distributions of corals and reef fishes are broadly consistent with the predictions of island biogeography (Bellwood & Hughes 2001) and some data seem to support the 'Island Rule' (Robertson 2001). 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 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)

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

IMAGE CREDITS:
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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.

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