

The Status of Faunistic Studies of Pacific Coral Reef Mollusks: 1974¹

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Introduction

Four themes characterize faunistic studies of coral reef-associated mollusks in the Pacific: that they are representative of the Indo-West-Pacific faunal region, that within the faunal region there are areas of endemism, that there is an attenuation in numbers of species from west to east across the tropical Pacific, and that tropical Pacific mollusks exhibit high species diversity compared with temperate regions. These patterns have emerged from the descriptions and records of 19th century explorer-naturalists who crossed and re-crossed the Pacific. Their observations are summarized in such great molluscan classics as Kiener's (1834-1879) *Coquilles Vivantes*, Reeve's (1843-1878) *Conchologia Iconica*, Sowerby's (1842-1887) *Thesaurus Conchyliorum*, and Tryon's (1879-1898) *Manual of Conchology*. In the 20th century, the descriptive and summary work of Dall, Bartsch, and Rehder (1938), Ladd (1966, 1972), Cernohorsky (1967, 1972), and the ever increasing issues of *Indo-Pacific Mollusca* (edited by R. T. Abbott) provide further documentation for the themes.

Patterns are generalizations of observations, however, not explanatory devices, and we are now in an era of biological thought in which a major concern is that of explaining the patterns of distribution.

Faunal Regions and Endemism

Recognition of the Indo-West-Pacific faunal region with a probable source area in Indonesia has received little criticism since it was proposed in the 19th century, although Ladd (1960) has suggested that the oceanic islands of the Pacific could have been the home of many elements of the Indo-Pacific fauna, with faunal migration favored by winds and currents toward Indonesia rather than from it. Nor has the idea of provinces of peculiar character or endemism received undue criticism, albeit there is some disagreement as to the number of such provinces which should be recognized. Most recently Briggs (1974) finds four provinces, definable

¹ Contrib. No. 485, Hawaii Institute of Marine Biology. Paper presented at a Colloquium on "The need for faunistic information on Pacific coral reefs", International Symposium on Indo-Pacific Tropical Reef Biology, Guam and Palau, June 23-July 5, 1974.

in terms of more than 10 per cent endemism among several faunal groups. Traditionally these areas are explained by "isolation", or barriers to gene flow (see Briggs, 1974). MacArthur and Wilson's (1963) suggestion that ecological events are at least as important as evolutionary phenomena in determining such patterns provides some insights into endemism which isolation alone does not explain.

Some years ago it was suggested that endemism in the Hawaiian marine mollusks is especially noticeable in high intertidal forms (Kay, 1967). Vermeij (1973) substantiates the observation with work in the Atlantic which shows that in Brazil and Ghana species ranging into or restricted to high shorelines are significantly more limited in latitudinal range than those restricted to low shorelines. Vermeij's points can be illustrated on a large scale in the tropical Pacific: of 30 species recorded on reef flats from Yap in the western Pacific to Fanning Island, on the southeastern fringe of the Central Pacific, 83 per cent of the species found at Yap are also present at Fanning and 63 per cent in Hawaii. In contrast, Yap and Fanning share only 20 per cent of the high intertidal mollusks and Hawaii less than 5 per cent (Kay, unpublished).

Endemism, of course, is not restricted to high intertidal species: a suite of six endemic cowries occurs in Hawaii and there are distinctly Polynesian and southern Japanese fasciolarids, muricids, and miters. But at least we have made a beginning in attempting to explain patterns in terms of habits and habitats.

Attenuation and the Problem of Patchy Distribution

That an attenuation of biota in species numbers occurs from west to east across the tropical Pacific is almost a rule of thumb in any discussion of Pacific biogeography (Zimmerman, 1948; Carlquist, 1965). Hedley (1899) recognized the phenomenon in marine mollusks, explaining the absence of such species as *Melo*, *Voluta*, and *Nautilus* from oceanic islands in terms of egg size; mollusks with large eggs and no larval stages are restricted to continental areas. With the accumulation of additional records it becomes increasingly evident that there is also a host of species with direct development which are widely distributed among oceanic islands of the Pacific, notably *Tricolia variabilis*, several muricids, nassarids, and turrids. The observations that juvenile *Tricolia* occur in the plankton, utilizing a mucous net in traversing the water column (Taylor, personal communication), and that some cypraeids can produce viable fertilized eggs up to six weeks after fertilization (Kay, unpublished) provide alternative dispersal mechanisms to that of larval transport.

A related problem has received little attention: the patchy distribution of marine mollusks among oceanic islands. In the Marshall Islands, *Turbo setosus* occurs at Majuro but not at Kwajalein. In the Hawaiian Islands *Drupa grossularia* is common at Midway but absent in the windward islands. In the Line Islands *Oliva*, *Planaxis sulcatus*, etc. are present on some atolls but not at Fanning (Kay, 1971). Whereas temperate zone biologists tend to dismiss patchiness in the tropics as an artifact of inadequate exploration or insufficiently understood habitat re-

quirements, patchiness among tropical Pacific oceanic islands would appear to be as recognizable a pattern as that of attenuation.

Explanations for patchiness are temptingly simple: chance dispersal by currents among islands separated by wide expanses of ocean is an obvious hypothesis. More complex explanations may also be useful, however, especially those which involve substrate and/or topography. In the Hawaiian Islands the northern (leeward) islands are atolls with little or no vertical intertidal zone, while the windward islands are volcanic with a tidal range of about a meter and even greater effective wave height. In the leeward islands the occurrence of only one of the two dominant Hawaiian littorines and the absence of patellid limpets (*Cellana*) on calcareous shorelines may be more meaningfully explained by tidal factors and substrate than by chance dispersal. Similarly among the atolls of the Pacific, the type of lagoon (that is, closed or open), the presence or absence of mangroves and beds of sea grass, etc. may also determine the presence or absence of species (Kay, 1971).

Species Diversity

The list of works documenting diversity in tropical Pacific mollusks is legion— as are the hypotheses to account for diversity. An especially useful approach is that which addresses the question by asking what maintains the number of species in a particular situation. How many species can co-exist in a given environment?

Marine mollusks play a central role in this approach, largely through the work of Kohn (1959, 1966, 1967) on *Conus*. In a recent summary, Kohn (1971) suggests that co-occurring species of *Conus* overlap more with respect to microhabitat than in the utilization of prey species, and that adaptive radiation and the existence of co-occurring species among these predators has occurred with respect to food habits. Miller's (1972) work with terebrids points to a similar conclusion.

Another aspect of the diversity problem may be related to patchy distribution. Transects of several reef flats from Palau to Fanning Island, indicate that whereas the biota of the reef flats is remarkably similar in the dominance of relatively large molluscan predators, there is an intriguing variety of dominants (Kay, unpublished). On the windward reef flats at Majuro, Marshall Islands, *Conus* is dominant but at Kwajalein, *Morula* and other thaidids are dominant. A species of *Mitra* is dominant on one reef flat at Yap and on another in American Samoa. On one section of the barrier reef flat at Ponaʻpe, *Engina* is dominant, whereas on another *Vasum* is apparently the top carnivore. Similar patterns have been noted at Fanning Island (Kay, 1971). The implications of these observations are worth pursuing for they may mean that patchy distribution provides yet another mechanism by means of which diversity is maintained on islands in the tropical Pacific.

Micromollusks

Most of our knowledge of Pacific coral reef mollusks is based on species which

are large enough to be seen with the naked eye, and on those habitats which are readily accessible, that is, high shorelines and intertidal reef flats. There remain, however, hundreds of species which have received little attention: those less than about 10 mm in greatest diameter which I term micromollusks. And major portions of reefs are subtidal and unexplored.

Shells of micromollusks are deposited *in situ* in low energy environments and can be obtained quantitatively as are foraminifera and cladocerans, that is by picking them from standard volumes or weights of unconsolidated material. Analysis of unconsolidated sediments samples large numbers of species and allows quantitative inter-area comparisons of biota.

At Fanning Island distinctive patterns of distribution of micromollusks emerged from analysis of samples from the lagoon, seaward reef flats, and the slopes of the seaward reefs (Kay and Switzer, 1974). The reef flat assemblage is dominated by *Tricolia variabilis*, the patch reefs by *Diala flammea*, and the lagoon floor by two species of *Obortio*. All are probably microherbivores, standing crop is high, and species diversity is relatively low. On the seaward reefs and subtidally, the dominants are faunal grazers, sponge and ascidian feeders such as *Triphora*, *Cerithiopsis*, and marginellids; standing crop is low and species diversity is high. Similar patterns appear at Canton Island (Phoenix Islands) and at Funafuti (Ellice Islands) (Kay, unpublished). Reefs and subtidal areas of high islands such as Samoa and Hawaii exhibit quite different assemblages of mollusks than do atolls, with high proportions of trochids, turbinids, *Bittium*, small arks, etc. Micromollusks thus appear to be useful tools for faunistic studies of distribution patterns in the Pacific.

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