

## Speciation extinction dynamics and the topography of diversity on Indo-West Pacific coral reefs

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**Abstract.** Profiles of diversity for reef mantis shrimps (Stomatopoda, Crustacea) demonstrate both latitudinal and longitudinal gradients across the Indo-West Pacific (IWP). The diversity summit in the equatorial Indo-Australian Archipelago (IAA) is 2-10 times higher than diversity to the west, east, north and south. From the IAA, diversity declines in the Indian Ocean (IO) but rises toward the African coast (IOC) and declines into the Central Pacific (CP). Endemism is highest in the IAA, high in the western IO and CP, but low in the mid-IO and western Pacific. Small-sized species in the IAA and IOC have restricted dispersal and higher rates of diversification than extinction, producing diversity centers with high endemism. IAA and IOC assemblages also include large species that produce enormous numbers of dispersive larvae, swamping divergence and preventing extinction in IO and western Pacific populations. In the CP, species become increasingly isolated and dwarfed; speciation is high but extinction even higher, yielding low diversity but high endemism. This model explains (1) why diversity gradients occur, (2) why “hotspots” (concentrations of diversity *and* endemism) occur in some but not other taxa (with different life history and dispersal constraints); and (3) why concentrations of endemism do not always coincide with diversity centers.

**Key Words:** Stomatopod, geographic range, endemism, body size, hotspots

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### Introduction

Gradients of diversity (species richness) on IWP coral reefs have been explained by the following 9 hypotheses, which range from historical and ecological to artifactual explanations. (1) Present centers of diversity are influenced by faunal carry-over and migration from an older Tethys sea-way center of diversity in Europe (Mesozoic onward; Briggs 2000, 2003a, 2007). (2) Plate tectonics carried antecedent biota and created complex topographic and oceanographic environments that fostered high rates of diversification in the IAA from the Miocene onward (Barber and Bellwood 2005, Barber et al. 2006). (3) Oscillating sea level changes, interacting with a complex topographic and oceanographic environment, changed land mass sizes and circulation patterns, especially during the Pleistocene, and affected marine speciation/extinction dynamics (Potts 1985, Paulay 1990). (4) Currents, originally coupled with the idea of high peripheral origination (Ladd 1960), caused accumulation of species (implying low extinction) in diversity centers (Jokiel and Martinelli 1991, Briggs 1995, Connolly et al. 2003, Reaka et al. 2008). (5) The IAA diversity center results from conditions that foster high rates of origination (Center of Origin hypothesis, Briggs 1995, 1999a, 2000, 2003a, 2007). (6) The energy/productivity hypothesis (Rosenzweig 1995) proposes that, over evolutionary time, higher rates of energy flow through an

ecosystem allow more species to co-exist (implying lower extinction rates). Viewed as a surrogate of energy input, temperature correlates with rates of speciation across latitudinal gradients (Allen et al. 2006, Allen and Gillooly 2006), but does not explain longitudinal diversity gradients in reef corals and fishes (Bellwood et al. 2005). Higher phytoplankton abundance generally corresponds with greater diversity and species body size in reef-dwelling stomatopods (Reaka 2000, Reaka et al. 2008). However, the rate of energy flow through an ecosystem may be best viewed as predation intensity across a trophic web. (7) Probably acting via species interactions such as predation and competition, species diversity itself correlates with rates of diversification (Emerson and Kolm 2005, Allen and Gillooly 2006). (8) Increased area is often associated with elevated diversity, probably because larger area increases habitat complexity, reducing extinction and allowing more species to coexist (MacArthur and Wilson 1967, Rosenzweig 1995, Losos and Schluter 2000, Bellwood and Hughes 2001, Hubbell 2001, Barber and Bellwood 2005, Bellwood et al. 2005). (9) The mid-domain effect (MDE) posits that random overlap of species ranges which are constrained by geography artificially generates centers of diversity (Woodland 1983; Colwell and Lees 2000; Colwell et al. 2004, 2005; Connolly 2005; McClain et al. 2007).

Although it explains some of the variance, the MDE does not play a major role in forming diversity gradients in IWP fishes and corals (Connolly et al. 2003, Mora et al. 2003, Barber and Bellwood 2005, Bellwood et al. 2005).

The standing crop of diversity at any one place ultimately results from the rate at which species immigrate and either persist, diverge into new species or go extinct. This is essentially the thesis of classical Island Biogeographic Theory (MacArthur and Wilson 1967) and the Unified Neutral Theory of Biodiversity and Biogeography (Hubbell 2001), although the assumptions of these 2 approaches (evolutionary equilibrium under deterministic conditions vs. random ecological drift among species) differ. Except for Jablonski et al (2006), the concept of immigration and speciation/extinction dynamics, however, has not usually been applied to latitudinal and longitudinal diversity gradients, and that is what we explore here.

### Materials and Methods

All available IWP distributional records and individual body sizes for species of coral reef stomatopods (Alainosquillidae, Gonodactylidae, Odontodactylidae, Protosquillidae, Takuidae [but not Pseudosquillidae because of their very different reproductive, larval and life history patterns]) were collated, using current taxonomy, from our own and US National Museum collections and the published literature. These data were mapped to determine endemism and diversity. Typical body sizes of species from each region were analyzed according to both maximum and median body sizes of individuals in the population or species assemblage. The 6 biogeographic/habitat regions were chosen on the basis of habitat type (influenced by continents vs. open ocean) and biogeography (cohesiveness of faunas, relative geographic position from the western margin of the IO to the CP).

### Results

#### *The Topography of IWP Stomatopod Diversity*

We present the first longitudinal transects of species diversity for coral reef stomatopods at 3 latitudes across the IWP (fig. 1). Stomatopod diversity in the IWP is strikingly monolithic—the summit of diversity in the equatorial IAA towers above that of the rest of the IWP in every direction. Less than half as many species are found in the western IO, western Pacific and higher latitudinal regions of the IAA (20°N, 20°S) as in the center of diversity around Indonesia, Malaysia and western New Guinea. Another much lower peak of diversity along the equatorial western margin of the IO climbs higher toward the south around Madagascar. In the IOC,

diversities at the equator and 20°S are approximately double those at 20°N. At the West Pacific margin, diversities of the southern and equatorial transects are higher than (but not double) those at 20°N, but in the West Central Pacific, diversities are high only at 20°S in comparison to transects on the equator and 20°N. In the eastern IO (70-90°E) and especially the CP (170-140°W), diversity is strongly attenuated, declining to only 10-20% of that in the equatorial IAA.

#### *Life Histories and Evolution in Stomatopods*

Reef stomatopods are limited by the availability of bioeroded holes in the substrate due to intense fish predation (Reaka 1985, Dominguez and Reaka 1987, Steger 1987). Because small holes in the reef are vastly more abundant than large holes (Moran and Reaka 1988), territorial fighting and the possibility of not having a refuge increase—life becomes ever more risky—as species become larger in size. Yet increased body size confers behavioral (mating, fighting) and reproductive benefits.

Within lineages, large species of mantis shrimps grow faster, produce larger and exponentially more eggs with longer dispersal stages, reproduce more frequently, have broader geographic ranges, saturate a higher % of available habitat within their range, compete more intensely for refuges, exhibit more complex fighting and reproductive behavior and are more brightly colored than smaller species (Reaka 1979a,b; 1980, 1985, 1986, 1991; Reaka and Manning 1981, 1987a; Reaka et al. 2008).

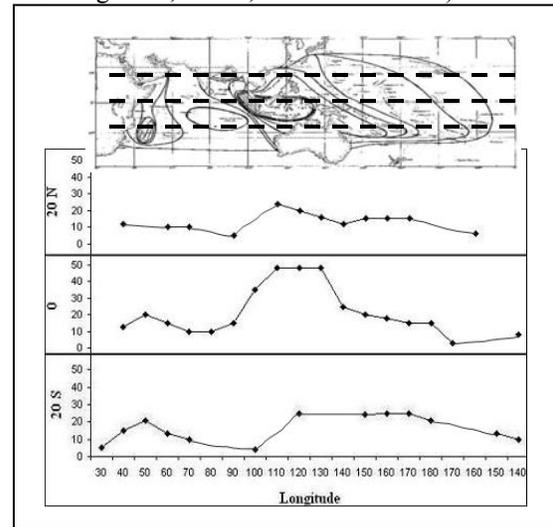


Figure 1. Longitudinal transects of diversity in reef stomatopods at the equator (0°) and at the margins of the tropics (20°N, 20°S). Number of species present at each longitudinal coordinate is indicated on the vertical axis for each transect. Degrees longitude is shown on the horizontal axis. Inset map shows continental masses, contours of diversity across the IWP, and positions of the 3 longitudinal transects (dashed lines).

In contrast, small adult body size is strongly associated with abbreviated larval development and restricted dispersal in marine invertebrates in general (Strathmann and Strathmann 1982; Jablonski and Lutz 1983; Strathmann 1985, 1990; Jablonski 1986a) as well as stomatopods. Small species of stomatopods are characterized by small geographic ranges and high endemism, relative rarity (low abundance, low saturation of available habitat within their range), major ecological innovations and occupation of reefs rather than level bottoms (Reaka 1980, 1986, 1991; Reaka and Manning 1981, 1987a; Reaka et al. 2008).

Because of its close relationship to the life history traits discussed above, body size strongly influences speciation in stomatopods. Large-bodied lineages and those with long-lived larvae remain conspecific or closely related even when separated for several million years by biogeographic barriers (e.g., the Central American Isthmus). In contrast, the % of species without close relatives elsewhere and within locally radiating lineages (more closely related to each other than to any species outside the region) are significantly elevated in small-bodied lineages, those with restricted larval dispersal and those inhabiting reefs. Only taxa of smallest body size within each of the major stomatopod lineages have invaded new types of habitat or adopted new feeding habits (Reaka 1980, Reaka and Manning 1987a).

Similarly, because of its influence upon life history traits and geographic distribution, body size is closely tied to extinction vulnerability in stomatopods. Although adequate fossil data are lacking, apparent extinctions—conspicuous gaps in distributions where extinction is the most parsimonious explanation—are significantly elevated among small-bodied species with restricted larval dispersal. Supporting this interpretation is the fact that, in other groups, species with low dispersal, low abundance and restricted distributions have been repeatedly shown to be more vulnerable to extinction over both ecological and evolutionary time than widespread dispersive taxa (Jablonski 1986a,b, 1987, 1991, 1994, 1995, 2008; Gaston 1994; Gaston and Blackburn 1996; Hubbell 2001; Jablonski et al. 2003; Hunt et al. 2005; Jablonski and Hunt 2006).

#### *Speciation/Extinction Dynamics and Gradients of Species Diversity*

Because of the correlation between body size and patterns of life history and evolution in stomatopods (and in many other marine species), body size can be used as a surrogate for the propensity to diversify and become extinct. Figure 2 depicts typical body sizes of reef stomatopod species across the IWP ( $\chi^2=11.07$ ,  $df=5$ ,  $p=0.02$  for species above/below median body size of the 6 assemblages). Although the range in

body size of each assemblage is large, especially from the IOC to the IAA, *most* species are diminutive in the diversity centers of the IOC and IAA, suggesting that these regions are hotspots of diversification and extinction. They also are hotspots of endemism (48% and 26% in the IAA and IOC).

Given their life history characteristics, large species in the IAA and IOC undoubtedly swamp the adjacent regions with larvae, accounting for the larger median body sizes of assemblages in the mid-IO and western Pacific regions. Populations in these adjacent off-shore regions are unlikely to diverge, and also are insulated from local extinctions, due to regular influx of larvae from ancestral populations and other large-bodied off-shore populations. Only 12% and 8% of IO and WPM species are endemic.

On the other hand, typical body size declines from the western Pacific regions toward the CP, with associated reductions in number of eggs and dispersal capability. This pattern is particularly exaggerated on atolls compared to high islands (Reaka 2000, Reaka et al. 2008), suggesting that Pacific populations are challenged by low productivity. Given enough time, larvae from large-sized dispersive species in the IAA and western Pacific must occasionally reach the CP, but, once there, the dwarfed populations are trapped, unable to produce enough propagules to reach another archipelago. If the population survives, divergence is almost inevitable due to selection and genetic drift. Endemism increases from 8% to 15% from the WPM to the CP. These founding populations also must frequently become extinct, especially in atoll environments that are characterized by low terrestrial input, high predation, smaller body sizes and lower reproductive capacity than high islands. We have directly observed extinction of 1 such population/species after storm disruption of local habitat on a mid-Pacific atoll (Reaka and Manning 1987b).

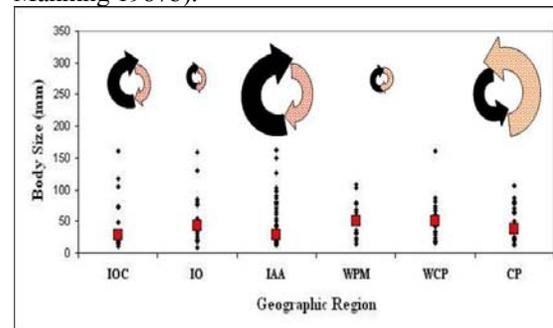


Figure 2. Body sizes of species assemblages of reef stomatopods at each of 6 biogeographic regions in the IWP (IOC=continental margin of the Indian Ocean, IO=open Indian Ocean, IAA=Indo-Australian Archipelago, WPM=western Pacific margin, WCP=West Central Pacific, CP=Central Pacific). Each dot represents maximal size of 1 species, squares represent the median body size of each regional assemblage, size of arrows represents relative strengths of speciation (black) and extinction (stippled).

Therefore, there are 3 centers of diversification in the IWP—in the diversity centers of the IAA and IOC but also in the remote and non-diverse CP. Body size of most species is diminished in all 3 regions, promoting genetic isolation and rapid speciation. However, the causative factors promoting small body size differ in the 3 regions. Biotic interactions (especially competition with other species of stomatopods for bioeroded refuges in the coral) likely are the main factors causing shifts toward predominantly diminutive body sizes (with consequent genetic isolation and rapid divergence) in the productive IAA and IOC. High reef community diversity also may provide more types of minute microenvironments for exploitation by small species in these areas. In contrast, low productivity likely causes dwarfism in the CP. Selection due to low productivity and predation, and especially isolation from western populations, probably are the main factors fostering rapid diversification in the CP.

The processes generating small body sizes and restricted dispersal ability in the IAA, IOC and CP, however, also constrain species to small geographic ranges and render them vulnerable to extinction. High rates of extinction in the IAA and IOC may even fuel higher rates of speciation, given abundant source populations (which is not true in the CP), since extinction continually re-opens niches. This leads to an accelerated cycle of speciation and extinction in the diversity centers. Extinction is especially high, and is likely to overwhelm speciation, however, in the harsh isolated conditions of the CP.

### Discussion

Consequently, the standing crop of diversity—as represented in any diversity gradient across a geographic realm such as the IWP—is necessarily a result of 3 processes: immigration, speciation and extinction. Immigration—dispersal from other ancestral and sibling populations—influences both speciation (or lack of it) and extinction (or lack of it). In reef stomatopods, this cycle is controlled by life history traits, especially the number and dispersal capability of propagules produced—which in turn are controlled by species body size—which in turn is controlled by ecological and environmental factors that may vary in different regions, such as along a longitudinal or latitudinal gradient. The standing crop of diversity at any one place is a result of how fast and in what direction the wheels of speciation and extinction are spinning (arrows in fig. 2). In the IOC and especially the IAA, the wheels of speciation/extinction turn rapidly compared to the adjacent off-shore oceanic regions, and the rate of speciation exceeds that of extinction—yielding high diversity

and endemism. The wheels of speciation/extinction also spin rapidly in the CP, but here in the reverse direction—extinction exceeds speciation, yielding low diversity but high endemism. This is *why* concentrations of endemics do not always coincide with areas of high species diversity, *why* “hotspots” (areas in which *both* endemics and high species diversity are concentrated) are not always congruent among different taxa, and *why* a longitudinal diversity gradient stretches across the IWP.

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