

NEWS AND VIEWS

PERSPECTIVE

A sea water barrier to coral gene flow

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Land is not the only barrier to dispersal encountered by marine organisms. For sedentary shallow water species, there is an additional, marine barrier, 5000 km of uninterrupted deep-water stretch between the central and the eastern Pacific. This expanse of water, known as the 'Eastern Pacific Barrier', has been separating faunas of the two oceanic regions since the beginning of the Cenozoic. Species with larvae that cannot stay in the plankton for the time it takes to cross between the two sides have been evolving independently. That the eastern Pacific does not share species with the rest of the Pacific was obvious to naturalists two centuries ago (Darwin 1860). Yet, this rule has exceptions. A small minority of species are known to straddle the Eastern Pacific Barrier. One such exception is the scleractinian coral *Porites lobata* (Fig. 1). This species is spread widely throughout the Indo-Pacific, where it is one of the major reef-builders, but it is also encountered in the eastern Pacific. Are eastern and central Pacific populations of this coral connected by gene flow? In this issue of *Molecular Ecology*, Baums *et al.* (2012) use microsatellite data to answer this question. They show that *P. lobata* populations in the eastern Pacific are cut off from genetic influx from the rest of the Pacific. Populations within each of the two oceanic regions are genetically connected (though those in the Hawaiian islands are also isolated). Significantly, the population in the Clipperton Atoll, the westernmost island in the eastern Pacific, genetically groups with populations from the central Pacific, suggesting that crossing the Eastern Pacific Barrier by *P. lobata* propagules does occasionally occur.

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Corals are an ecologically important group. We would like to know more about their phylogeography, but they are difficult material for this kind of work. Their morphology often misleads as to their genetic-specific identity (Ladner & Palumbi 2012). They reproduce asexually through breakage

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of branches or death of tissue in previously continuous colonies, making determination of genetic individuals difficult. Most inconveniently, their mitochondrial DNA, the mainstay of phylogeographic studies, evolves slowly (van Oppen *et al.* 1999), rendering it uninformative for intraspecific comparisons. Baums *et al.* (2012) overcame these problems using 12 microsatellite loci, sampled extensively (1264 colonies, 1173 genetic individuals) both in the central and in the eastern Pacific. Because planulae of *P. lobata* carry symbiotic dinoflagellates, which provide autotrophic energy, they could potentially travel for long distances and even cross the Eastern Pacific Barrier on a regular basis. The extensive analyses by Baums *et al.* (2012) of samples collected from Hawaii to Moorea and from Clipperton to Ecuador indicate that this is not the case. Populations in the central Pacific share few alleles in most loci with those of the eastern Pacific.

Although they cannot provide a definitive answer, the data are relevant to an old – but still unsettled – controversy regarding the origin of modern coral fauna of the eastern Pacific. In 1975, Dana (1975) had suggested that eastern Pacific corals had gone extinct in the Pleistocene, and that modern fauna is the result of colonization from the central Pacific. In the heyday of vicariance biogeography, which disdains scenaria involving dispersal, McCoy & Heck (1976) countered that corals in the eastern Pacific belonged to a relict fauna, isolated from the rest of the world's tropical oceans when the Central American Isthmus was completed 3 million years ago. Fossil evidence provides indications that there may be some truth to both views (Budd 1989). There is also good evidence from reef cores that El Niño events, local upwelling and changes in the movements of the Intertropical Convergence Zone have



Fig. 1 A colony of *Porites lobata* at Wolf Island, Galapagos, surrounded by schools of the creole-fish, *Paranthias colonus*. White scars are the result of grazing by parrotfish. (Photo-credit: Joshua Feingold, NOVA Southeastern University).

caused localized collapses of eastern Pacific coral reef ecosystems within the last four thousand years (Toth *et al.* 2012). Where did the propagules that re-established these reefs come from? The low levels of contemporary gene flow between the central and the eastern Pacific in *P. lobata* documented by Baums *et al.* (2012) may, at first glance, suggest that all recolonization by *P. lobata* must have originated from refugia within the eastern Pacific. It should be kept in mind, however, that contemporary gene flow does not necessarily provide reliable indications of colonization events. Peripheral populations can be established in a single pulse of propagules and – if their number is large enough – persist even if subsequently cut off from the species range. When there is gene flow, it will not necessarily be in the same direction as the initial colonization (Lessios & Robertson 2006). The analyses of Baums *et al.* (2012) revealed one colony that may have been a recent immigrant into the eastern Pacific (although its alleles may have also introgressed from the eastern Pacific *P. evermanni*), but also three colonies in the central Pacific whose recent ancestors originated on the other side of the barrier. Thus, on the basis of the microsatellite data, eastern Pacific areas in which *P. lobata* is extirpated have, as a rule, been recolonized from other eastern Pacific populations, but occasional influx of larvae from the central Pacific (with Clipperton as a potential stepping stone) cannot be ruled out. Whether such influx can occur during the acceleration of the North Equatorial Counter Current during El Niño events (Richmond 1990) remains an open question, considering that the warm water carried by this current is responsible for extensive mortality of the local coral fauna.

Another question that remains open is whether the eastern Pacific populations of *Porites lobata* belong to the same biological species as the central Pacific ones. Is there so little gene flow from the central Pacific because larvae cannot cross the barrier, or do intrinsic reproductive blocks prevent genetic exchange between the two demes? This is a question difficult to answer in allopatric populations. Baums *et al.* (2012) argue that these are not separate species on largely negative evidence. They reason that their microsatellites are species specific, yet they amplify specimens with *P. lobata* morphology from both the eastern and the central Pacific. An additional point to consider is provided by the limited evidence from the inaccessible Clipperton Atoll. Baums *et al.* (2012) were able to obtain only five samples from Clipperton, but one among these had a composite genotype that was an admixture of eastern and central Pacific alleles, suggesting that it is an F_2 or later generation hybrid. If hybridization in areas of sympatry is indeed in the order of 20%, then it is not likely that intrinsic reproductive barriers prevent the two demes from exchanging genes. As the authors point out, a larger sample size from Clipperton would provide more definitive answers, but expeditions to this Atoll are not easy to arrange.

Studies that generate interesting findings also generate new questions. We now know that in *Porites lobata*, one of the two species of hard coral for which gene flow through the Eastern Pacific Barrier has been assessed, there is little

genetic exchange between populations from the two regions. Comparisons between the two oceanic regions in *Pocillopora damicornis*, the other coral species for which data exist, have been made on the basis of multicopy ribosomal internal transcribed spacer fragments (Combosch *et al.* 2008), which are difficult to interpret (Pinzon & LaJeunesse 2011). *P. lobata* joins the group of shallow water species with populations on either side of the Eastern Pacific Barrier that are assigned to the same species, yet show substantial genetic divergence. This is an exclusive group, because most species with conspecific populations in both the central and eastern Pacific also show evidence of fairly high gene flow (Lessios *et al.* 1998; Lessios & Robertson 2006). The only other presumed transpacific species that resemble *P. lobata* in having similar morphologies in the eastern and central Pacific even though they are genetically isolated by the barrier are one snail (Duda & Lessios 2009), one starfish (Vogler *et al.* 2008), a lobster (Chow *et al.* 2011) and two fishes (Lessios & Robertson 2006). That morphology is generally a reliable guide as to gene flow through the Eastern Pacific Barrier suggests that the traditional approach to biogeography, of designating provinces on the basis of the number of morphospecies found in common across a suspected barrier, leads (more often than not) to correct conclusions.

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