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NEW PERSPECTIVES IN BIOGEOGRAPHY OF CORAL REEF FISH IN THE PACIFIC USING PHYLOGEOGRAPHY AND POPULATION GENETICS APPROACHES

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BIOGEOGRAPHY
DIVERSITY
SPECIATION
POPULATION GENETIC
CORAL REEF FISH
INDO-PACIFIC

ABSTRACT. – The Indo-Pacific area has been recognised as the most diverse biogeographic area among marine ecosystems. This diversity shows gradient with higher diversity in the Indonesia-Philippines area and decrease of species richness going East in the Pacific islands. Three major theories (center of origins, center of accumulation, and center of overlap) have proposed mechanisms that lead to higher diversity in the Indonesian-Philippines area. Up to now, classic biogeography based on species richness is unable to distinguish the most likely model among the three. We investigate genetic approach as a new tool that could give evolutionary perspective in biogeography. The rationale of such an approach is that genetic diversity has been found to be correlated to species richness. First results on coral reef fishes, revealed a hierarchy of the factors affecting the genetic diversity and consequently the species richness.

BIOGÉOGRAPHIE
DIVERSITÉ
SPÉCIATION
GÉNÉTIQUE DES POPULATIONS
POISSONS DES RÉCIFS CORALLIENS
INDO-PACIFIQUE

RÉSUMÉ. – La province biogéographique Indo-Pacifique est certainement l'écosystème marin le plus diversifié. Cependant, cette diversité n'est pas homogène; très forte dans la région Indonésie-Philippines, elle diminue plus on s'éloigne en direction des îles situées à l'Est. Trois théories ont été proposées pour expliquer la forte diversité de la région Indonésie-Philippines : centre de dispersion, centre de convergence et centre de recouvrement. Les recherches en biogéographie, uniquement basées sur l'étude de la richesse spécifique, ont été incapables jusqu'à présent de distinguer la plus vraisemblable de ces trois théories. Nous pensons qu'une analyse génétique pourrait fournir les réponses souhaitées, en terme d'évolution. Les fondements d'une telle approche reposent sur le fait que la diversité génétique peut être corrélée à la richesse spécifique. Les premiers résultats obtenus sur les Poissons des récifs coralliens semblent hiérarchiser les facteurs affectant la diversité génétique et, par cela même, la richesse spécifique.

INDO-PACIFIC BIOGEOGRAPHY

The Indo-Pacific area contains thousands of marine species which make of this ecosystem one of the most diverse among marine habitats. Such a high diversity is not uniformly distributed over the Pacific plate but shows gradient of species richness that extends from the highly diverse center of the Indonesian-Philippines area to the surrounding archipelagos laying East (Briggs, 1974). Reasons for the present-day distribution are complex and are the subject of fascinating studies, much of which are fairly recent and ongoing.

Among the several hypotheses that have been proposed to explain biogeographic patterns in the Pacific Ocean (see review in Rosen 1988), three

major theories (center of origins, center of accumulation, and center of overlap) can be distinguished (Palumbi 1996). Basically, they proposed mechanisms that lead to a high diversity in the Indonesian-Philippines area (Fig. 1). The center of origins theory suggests that the Indonesian-Philippines area is the place where speciation takes place and that new species diffuse to peripheral habitats such as Pacific archipelagos (Ekman 1953). As an opposite view, it has been proposed that speciation has more chance to occur in isolated peripheral archipelagos and new species would be transported to the Indonesian-Philippines area via prevailing currents (Ladd 1960). In this case the Indonesian-Philippines area can be viewed as a center of accumulation, consequence of migrations of new species from peripheral archipelagos. Fi-

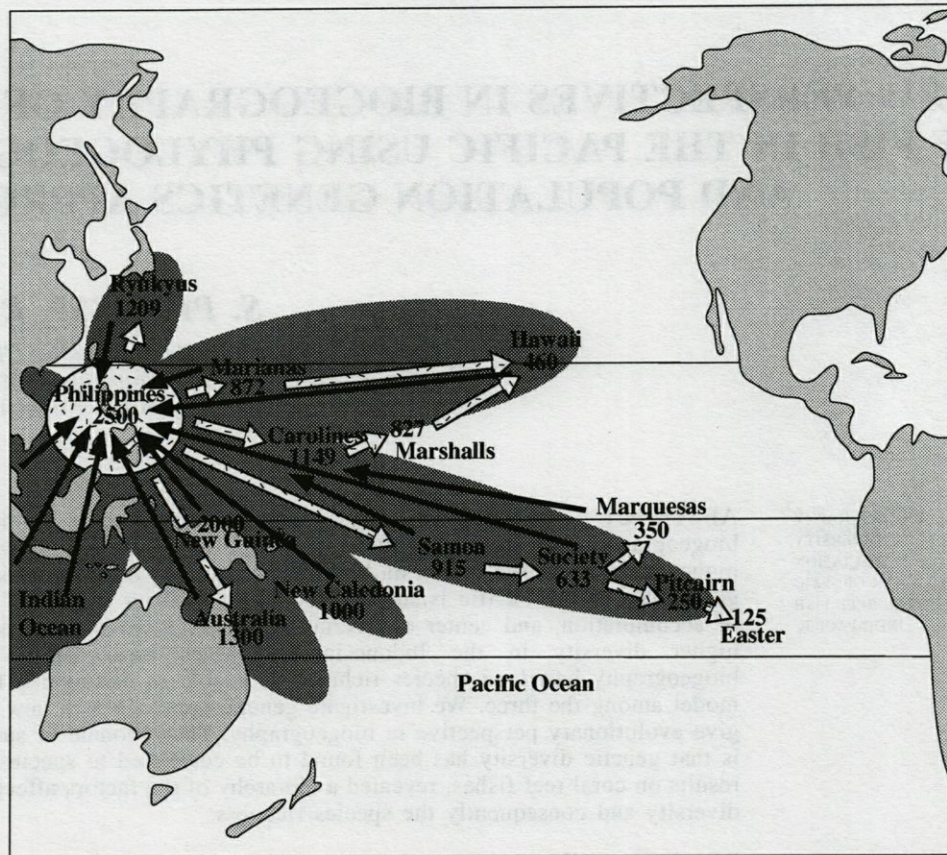


Fig. 1. – Map of the Pacific Ocean area indicating species richness of shorefish. The three major theories proposed to explain the species distribution and more specially the high diversity in the Indonesia-Philippines area are also represented : center of origins with white arrows, center of accumulation with black arrows, and center of overlap with grey ellipses.

nally, the third theory describes a center of overlap where the high diversity of the Indonesian-Philippines area corresponds to a cross-road of several biogeographic provinces. These biogeographic provinces could result from past geological events or present environmental conditions and overlap in the Indonesian-Philippines area where they create high species diversity. Many studies on corals, sea-grasses, molluscs and fishes (Salvat 1971; Springer 1982; Vermeij 1987; Rosen 1988; Kay 1990; Wallace *et al.* 1989; Jokiel and Martinielli 1992; Mukai 1992; Pandolfi 1992; Stoddart 1992; Veron 1995) have investigated species distribution and support one or the other of the theory. However, up to now, it appears that there is no consensus on which model may be more generally suitable.

INTEREST OF THE POPULATION GENETICS APPROACH

Population genetics can contribute in this debate, in the sense that using intra-specific markers, such as allozymes, gives a new opportunity to

distinguish diversity of different islands and/or archipelagos. Up to recent years biogeographic surveys were restricted to compare the number of species or taxa between areas. The population genetics approach gives a new view in biogeographic research because it reveals the structure of genetic variability of marine species. Allelic variation within a species can be used to track patterns of migration. Concordance of species-level and allele-level biogeography have already been demonstrated in some places in the sense that processes determining species distribution are similar to those controlling gene flows (Avice 1994). Consequently, patterns of gene flow, computed from allelic variations within a species, can contribute to explain the origin of species in an evolutionary perspective. In addition, the analysis of genetic markers can help : (1) to distinguish sibling species (Knowlton, 1993) and to provide new data on species diversity; (2) to determine divergence time between species or populations once appropriate calibration is made (Martin *et al.* 1992); (3) and finally to calibrate relationships between species (phylogenies) and to identify derived species.

Such approaches were already developed for giant clam using allozymes (Benzie 1994) and for sea urchin using mitochondrial DNA (Palumbi 1996). Both surveys showed differentiation between populations despite the dispersal capacities inferred from the pelagic larval phase of both species. The giant clam study showed that gene flows were favoured along latitudinal gradient in the Indo-West Pacific. In fact, populations appeared genetically homogeneous within similar latitudes while major differences occurred between samples located on different latitudes. Such a pattern is opposite to diversity clines in the entire fauna which show a decreasing gradient going East along the same latitudes. Research on sea urchin revealed a pattern opposite to giant clams one. Clines of mtDNA variation within species were similar to the total species diversity ones. However, these results are both based on the analysis of single species, while a multi-species analysis would be necessary to average variation in genetic patterns between species.

INDO-PACIFIC CORAL REEF FISHES MODEL

The Indo-Pacific region, which stretches from the Red Sea to the Polynesian Islands, contains the world's largest shorefish fauna estimated at over 4 000 species (Springer 1982; Myers 1989). As we mentioned previously, the distribution of species richness shows higher diversity in the Indonesian-Phillipines area which decreases further East, in the Pacific islands (Fig. 1). According to species lists, we can observe four major steps in terms of diversity: (1) about 2 500 species in the Indonesian-Phillipines waters; (2) around 1 000 to 1 300 species in Micronesia and Australia; (3) about 600 further East in the Hawaiian and Polynesian island and (4) finally only 200 remain in isolated island such as Pitcairn, Eastern of Johnston islands.

Most coral reef fishes have a pelagic larval stage, resulting in a life history with two distinct phases. Pelagic and benthic stages differ in almost all characteristics from morphology to size, habitat, food and behaviour. Although a few types of larvae complete their pelagic stage in the immediate vicinity of their natal reef, the large majority apparently moves some distance away from the reef to more open water (Leis, 1991). The common idea is that planktonic larvae are dispersed from their spawning sites. This transport is fundamental in maintaining the integrity of species and avoiding speciation that could result from isolation. Evidence to support this broad hypothesis initially came from surveys of marine invertebrates: species with planktonic larvae are re-

ported to be more widely distributed (Shuto 1974; Scheltema and Williams 1983), to have genetically more homogeneous populations (Scheltema 1977) and to persist longer in the fossil records (Hansen 1978; Scheltema 1978). Similarly, it has been hypothesised that species with long larval planktonic stage will tend to have larger distribution than species with shorter ones (Thorson 1961; Scheltema and Williams 1983). Data on fish fauna are far less extensive, only a few studies were devoted to the duration and the distribution of planktonic larvae and results have suggested similar hypothesis (Rosenblatt *et al.* 1972; Leis, 1984; Avise *et al.* 1987; Waples and Rosenblatt 1987). Such initial surveys were limited to the analysis of the relationship between planktonic duration and population structure because of the difficulty of measuring the duration of the planktonic larval stage which was estimated by rearing larvae to metamorphosis. Recent progress in using otoliths to estimate larval stage duration in counting daily rings up to the "settlement mark" give more reliable data to address the relationship between planktonic duration and population structure (Victor 1986). Up to now, studies developed on coral reef fish fauna of the Indo-Pacific (Thresher and Brothers 1985; Brothers and Thresher 1985; Thresher *et al.* 1989) did not show any correlation between either the size of distribution and larval distribution, or between the mean planktonic duration of a genus and either species richness or degree of endemism in that genus. The only significant result indicated that species with mean planktonic stages longer than 45 days were almost invariably broadly distributed across the Pacific, whereas those with shorter planktonic stages varied in the extent of their distributions (Brothers and Thresher 1985). However, Thresher *et al.* (1989) investigating Pomacentridae family did not find any correlation with planktonic larval duration.

EXAMPLES OF POPULATION GENETICS APPROACH ON CORAL REEF FISH

Up to now there is no general survey of coral reef fish realised over the Pacific and all genetic analyses are restricted to regional scales such as the Great Barrier Reef, Polynesian archipelagos, Hawaiian archipelago, etc. In reef fishes of the Pacific, results of genetic surveys ranged from panmixia (genetically homogeneous populations) within an archipelago (Shaklee 1984; Shaklee and Somolow 1984, Planes *et al.* 1993) to regional (Bell *et al.* 1982; Planes 1993; Doherty *et al.* 1995; Lacson and Clark 1995) and local (Planes 1993; Doherty *et al.* 1994; Johnson *et al.* 1993) differentiations. We will present three examples

and their interpretations in terms of mechanism to explain the observed population structures.

One of the largest study concerned the genetic structure of *Acanthurus triostegus* (Planes 1993) and *Dascyllus aruanus* (Planes *et al.* 1993) within French Polynesia. Each species showed a different genetic structure. *D. aruanus* populations appeared homogeneous overall the Polynesia while *A. triostegus* populations were highly structured with large genetic differences between islands. The genetic structure of populations of *A. triostegus* was directly linked with the major oceanic currents within the area and led authors to propose a "patchy population" model – a atypical metapopulation model – (Planes *et al.* 1996). Comparison of results obtained on *D. aruanus* and *A. triostegus* did not fit with the idea that species with long pelagic larval stages exhibit larger dispersals and consequently show higher gene flows between populations. In fact, *D. aruanus* larvae spend about 25 days in the ocean when *A. triostegus* ones stay about 60 days. Authors proposed that this contradiction was due to historical factors. During the last glaciation that occurred 10 to 8 thousand years B.P. the sea-levels was 120 meters under present sea-level and lagoons of classic Darwinian atolls that are of 50 to 70 meter deep at the maximum were completely dry. Because *D. aruanus* inhabits only lagoons, and such habitats were not available in French Polynesia during the last glaciation, we proposed that at that time the species was absent from the area and that the actual population is a result of a unique and recent recolonisation. Consequently there is not enough time for the appearance of genetic structures as a result of genetic drift. *A. triostegus* is more ubiquitous and inhabits lagoons as well as oceanic slope. Because this fish could be maintained on oceanic slope, *A. triostegus* populations would be older and showing longer evolution with genetic differentiation due to long term genetic drift. This study suggested that oceanic currents as well as historical events affect the population structures between oceanic islands. In these interpretations, historical factors played a more crucial role than pelagic larval duration.

Doherty *et al.* (1995) selected seven species of coral reef fish, to provide a range of pelagic larval duration from 0-55 days, for genetic comparison between two regions of the Great Barrier Reef separated by 1 000 km. Only one species, an anemone fish, did not show significant heterogeneity among reefs within regions indicating chaotic genetic patchiness at local scales, probably arising from recruitment. After pooling regional variation, all but two species also showed significant regional differences. The two exceptions were a lutjanid and a surgeonfish, which had the longest pelagic larval durations. The logarithm of genetic differentiation between regions was correlated

with pelagic larval duration by an inverse linear relationship that explained 85% of the variance among species. On this basis, it was estimated that larval periods longer than one month should result in enough gene flow to homogenize fish populations over half of the Great Barrier Reef. Comparisons with invertebrates taxa sampled over the same sites show that fish populations are more differentiated for a given pelagic larval duration. Such a difference between invertebrate and fish suggests that fish larvae may use their greater mobility to resist to dispersal using either their swimming abilities or favorable currents to limit dispersal. This study clearly demonstrates that within the fishes taxa the pelagic larval duration is a predominant factor explaining larval dispersal and colonisation. At the same time, Doherty *et al.* (1995) compared populations of the Great Barrier Reef with an outgroup (Chesterfield reefs) and confirmed the genetic homogeneity of mainland population but demonstrated that the relationship between pelagic larval duration and genetic differentiation does not apply to island systems. In the Great Barrier Reef, which represent a continuous reef matrix, the pelagic larval duration comes out as the major factor explaining the population structure. The Great Barrier Reef also was affected by sea-level variations but because it makes a geomorphological unit, the evolutions of different species were parallel and in that situation, the biology of each species the key factor of population structures. Evidence that historical events are predominant to biological ones can be found in the population structures observed in the Capricorn and Bunker reefs (located at the extreme south of the Great Barrier Reef where reefs are at their actual limit of extension). They show large genetic differences when compared to populations of the central Great Barrier Reef (Doherty *et al.* 1994)

Finally, population genetic structure of *Stegastes nigricans*, *Epinephelus merra* and *Acanthurus triostegus* was investigated throughout New Caledonia (Planes *et al.* in press). Each species was sampled in three sites all around the lagoon of New Caledonia. Analysis of genetic differentiation between sites showed inconsistent results between species, with limited gene flow in two species (*Acanthurus triostegus* and *Stegastes nigricans*) and homogeneity in one species (*Epinephelus merra*). Survey of hydrological and climatic data from the lagoon which surrounds New Caledonia suggests that the eastern and western sides of the lagoon could be isolated because they lie in water masses of different origin and this may explain the genetic differentiation found at local scale. Homogeneity in *Epinephelus merra* populations is possibly related to its low genetic diversity and the reproductive behaviour of members of this family.

CONCLUSIONS

Considering the three examples described previously, we can divide factors affecting genetic structure of coral reef population in the Pacific ocean into three major groups. (1) Functional factors which are related to the ecology and the biology of each species. This includes parameters such as, reproduction behaviour or pelagic larval duration. (2) Historical factors such as colonisation or extinction consequent to sea-level variation, which will modify directly the population structure. (3) Physical factors including the effect of oceanic currents and/or the geomorphological structure of the reef. We have shown that the patterns observed along the Great Barrier Reef are not similar to those found around isolated island systems. In that case the genetic structures seem to fit an unusual metapopulation model where currents appear as the determining factors. The three major factors acting on the genetic structures are not equivalent: historical factors seem predominant to the other ones. Phylogeography and population genetics will in the future provide data to ascertain such a hierarchy and its biological consequences.

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