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TROPICAL SHELF ZOOGEOGRAPHY

By

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INTRODUCTION

The richest marine fauna is found in the shallow waters of the tropical oceans at depths generally less than 200 meters. Zoogeographically, four great regions may be identified, the Indo-West Pacific, the Eastern Pacific, the Western Altantic, and the Eastern Atlantic. Each region may, in turn, be subdivided into provinces, but these will not be discussed at this time. To the north and south, the tropics are bounded by the 20°C. isotherm for the coldest month in the year. Longitudinally, the tropical regions are separated from one another by barriers that are very effective since each region possesses, at the species level, a fauna that is highly endemic. By studying the operation of these longitudinal barriers, one can learn something about the interrelationship of the regions and can also obtain information leading to a better understanding of zoogeography and evolution.

THE EAST PACIFIC BARRIER

The Indo-West Pacific and Eastern Pacific regions are separated by the East Pacific Barrier, the vast stretch of deep-water that lies between Polynesia and America. In regard to the shore fishes, it was concluded that an eastward colonization movement was taking place across the Barrier and that successful reciprocal migrations were, at least, very rare and might be completely lacking

(Briggs, 1961, 1964, 1966). When the general relationship of the tropical shelf regions was first discussed (Briggs, 1967a), comparable information on the major groups of the shallow-water invertebrates was not available.

Emerson (1967) published a revealing analysis of the distribution of those Indo-West Pacific species of mollusks that have succeeded in penetrating across the Barrier into the Eastern Pacific. He found that such trans-Pacific species were largely restricted, in the Eastern Pacific, to the oceanic islands, the greatest numbers being found at Clipperton (33 species) and at the Galápagos (25 species). It was noted that the gastropods, which greatly outnumbered the bivalves, belonged to groups that were known to have relatively long larval stages. Most important of all, Emerson pointed out that no molluscan species of apparent Eastern Pacific origin were known to occur in Polynesia.

Data on the other invertebrate groups are not as complete, but it is significant that some of the littoral echinoderms (Ekman, 1946), holothurians (Deichmann, 1963), decapod crustaceans (Chace, 1962; Garth, 1965), and hermatypic corals (Emerson, 1967) found in the Eastern Pacific (especially around the offshore islands) are trans-Pacific species of apparent Indo-West Pacific origin. Therefore, it may now be said that for the tropical marine shore fauna in general, including both fishes and invertebrates, it seems likely that successful migration across the East Pacific Barrier takes place in one direction only—from west to east.

THE NEW WORLD LAND BARRIER

The New World Land Barrier, with the Isthmus of Panama forming its narrowest part, is virtually a complete block to the movement of tropical marine species between the Eastern Pacific and Western Atlantic. This state of affairs has existed since about the latest Pliocene or earliest Pleistocene (Simpson, 1965; Patterson and Pascual, 1968) so that, at the species level, the two faunas are well separated. The present Panama Canal has not notably altered this relationship since, for most of its length, it is a freshwater passage forming an effective barrier for all but a few euryhaline species.

The New World Land Barrier is the most effective of the four zoogeographic barriers that separate the tropical faunal regions. It has stood for approximately three million years, but it now appears that man is about to breach this barrier by excavating a sea-level canal somewhere in the vicinity of the Isthmus of Panama. If such a canal is constructed, it would present ample opportunities for marine animals to migrate in either direction. This could result in the Eastern Pacific being invaded by over 6000 species of fishes and invertebrates and the Western Atlantic being invaded by over 4000 species. Since the Western Atlantic species would apparently be competitively dominant, it has been predicted that a large scale extinction would take place in the

Eastern Pacific resulting in the irrevocable loss of a huge number (possibly thousands) of species (Briggs, 1968, 1969).

THE MID-ATLANTIC BARRIER

The broad deep-water barrier that separates the Western Atlantic tropics from those of the West African coast functions in a very interesting manner. An impressive number of shore fishes have managed to traverse the Mid-Atlantic Barrier from west to east. It has been estimated (Briggs, 1967a) that about 118 shore fish species have trans-Atlantic distributions but that only about 24 of them came from the Indo-West Pacific via the Cape of Good Hope. The rest probably evolved in the Western Atlantic and successfully performed an eastward colonization journey across the ocean. Trans-Atlantic species comprise about 30 percent of the shore fish fauna of tropical West Africa.

Works on some of the major groups of West African invertebrates also show that an appreciable number of the species are trans-Atlantic: Dekeyser (1961) found that about 25 percent of the ascidians showed this distribution; Burton (1956), 18 percent of the sponges; Monod (1956), 16 percent of the anomuran and brachyuran crabs; Knudsen (1956), 6 percent of the prosobranch mollusks; Ekman (1953), 16 percent of the starfishes, brittle stars, and sea urchins; and Marcus and Marcus (1966), 29 percent of the opisthobranch mollusks. Furthermore, Chesher (1966), who found 8 trans-Atlantic species of sea urchins in the Gulf of Guinea, stated that gene flow appeared to take place from west to east.

It seems apparent that, in both the fishes and the invertebrates, the great majority of the trans-Atlantic species originated in the Western Atlantic and then migrated eastward. The westward colonization traffic appears to be restricted to certain dominant species that originated in the Indo-West Pacific and then gained access to the Atlantic by rounding the Cape of Good Hope. So far, there are no indications that species originating in the Eastern Atlantic, and belonging to genera typical of that area, have been successful in becoming established on the western side.

THE OLD WORLD LAND BARRIER

The Eastern Atlantic and the Indo-West Pacific regions are separated by the Old World Land Barrier. It has been estimated that the continental masses of Eurasia and Africa have been linked at least since the beginning of the Pleistocene (Gohar, 1954). The Suez Canal is a sea-level passage that has been open since 1869 but migration of marine animals has been inhibited for two reasons: first, the canal connects two areas that are separated by a temperature barrier, the Red Sea being tropical while the Mediterranean is warm-temperate; second, the Bitter Lakes, which form part of the Suez passageway, have a high salinity (about 45 percent). Despite these difficulties,

the limited migratory movements that have taken place through the Suez Canal do provide some significant information.

The Mediterranean has been invaded by at least 24 species of Red Sea fishes (Ben-Tuvia, 1966), 16 species of decapod crustaceans (Holthuis and Gottlieb, 1958), and several species in other groups such as the tunicates (Pérès, 1958), mollusks (Engel and van Eeken, 1962), and stomatopod crustaceans (Ingle, 1963). So, while there is ample evidence of intrusions into the eastern Mediterranean, there are no reliable data that indicate any successful reciprocal migration. Also, there are some indications that the invaders from the Red Sea (a part of the Indo-West Pacific Region) are replacing rather than coexisting with certain native species (George, 1966).

The various circumtropical shore species have probably been able to preserve their genetic homogeneity by means of migration around the Cape of Good Hope (in addition to crossing the open ocean barriers in the Pacific and Atlantic). Talbot and Penrith (1962) remarked that surface temperatures of 21°C. are often present round the Cape outside a cold upwelling area. There are about 16 known species of circumtropical shore fishes (Briggs, 1960). Besides these, there are about 15 other species that apparently transgress the Old World Land Barrier at the Cape (Briggs, 1967a). Of the total of 31 fish species, eight are monotypic but all the rest represent genera that are best developed in the Indo-West Pacific.

Apparently, only a few tropical invertebrate species have been able to migrate around the Cape of Good Hope. Monod (1956) in his monographic study of the West African decapods showed that 10 out of 176 shore species occurred in the Indo-West Pacific. Ekman (1953) noted that only 2 percent of the tropical Atlantic echinoderms (Asteroidea, Ophiuroidea, and Echinoidea) extended around the Cape. It appears, especially from the ichthyological evidence, that the colonization movement of tropical shore species around the Cape takes place entirely in a westerly direction, from the Indo-West Pacific into the Atlantic.

RELATIONSHIPS OF THE SHELF REGIONS

Evidence now available about the dispersal of the shallow-water marine invertebrates tends to substantiate the general nature of a remarkable distributional phenomenon that was discovered earlier for the shore fishes (Briggs 1961, 1964, 1967a). Successful (colonizing) migrations across the zoogeographic boundaries that delimit the Indo-West Pacific can apparently take place in one direction only, outward into areas where the fauna is poorer and the competition is less. The realization that the East Pacific and Old World Land Barriers operate as one-way filters enables us to understand better how the Indo-West Pacific Region serves as *the* evolutionary and distributional center for the tropical shore animals of the world. We can see that competitively dominant species continue to migrate, as they probably have for mil-

lions of years, from the Indo-West Pacific eastward across the open ocean to America and westward around the Cape of Good Hope into the Atlantic; since 1869, some of them have also been able to pass northward through the Suez Canal into the Mediterranean.

The Western Atlantic Region may be considered a secondary center of evolutionary radiation. Many species evolved in this area have proved capable of migrating eastward to colonize the tropical Eastern Atlantic. However, species originating in the Eastern Atlantic are apparently incapable of successfully invading the western side. Again, the advantage seems to lie with the area that possesses the richer fauna and the higher level of competition.

It can be seen that the completely eastward direction of successful migratory movements across the East Pacific Barrier and the predominantly eastward movements across the Mid-Atlantic Barrier take place in a direction opposite to that of the main flow of the surface waters via the North and South Equatorial Currents. In contrast, the surface and subsurface countercurrents in the tropical Pacific and Atlantic are weakly developed but these smaller currents are obviously the principal means by which successful transport is achieved.

Fell (1967) noted that certain groups of shore species apparently demonstrated speciation gradients in which the number of species gradually diminished around the world in a westward direction. He interpreted this to mean that the direction of successful migrations had also been to the west and that such dispersals had been carried out by the North and South Equatorial currents. Subsequently, it was pointed out that the existence of a gradient in numbers of species (or genera) across a major barrier did not necessarily indicate the direction of the original successful migration (Briggs, 1967b). The fact that colonizations do take place in a direction opposite to that of the major currents is a good indication that biological competition rather than passive transport is probably the most important factor controlling the successful dispersal of tropical marine shore animals.

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