

Dispersal of Tropical Marine Shore Animals : Coriolis Parameters or Competition ?

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Contrary to recent supposition, species gradients cannot be relied on to indicate the direction of successful migrations by tropical shore animals or the direction of the principal ocean currents.

In the low latitude regions of both the Atlantic and Pacific Oceans, the North and South Equatorial Currents move the surface waters in a westerly direction. By comparison, the equatorial countercurrents are weakly developed and move only small amounts of water. The question is whether the predominantly westward movement of tropical waters means that a successful dispersal of shelf animals takes place in the same direction. Theoretically, it may seem logical, and this is the assumption made by Professor H. B. Fell in his article¹ relating both present and fossil distributions to Coriolis (major oceanic current) effects.

As support for his assumption, Fell noted that the molluscan genus *Voluta* and other groups demonstrated speciation gradients in which the number of species gradually diminished around the world in a westward direction. For the purpose of comparison, I shall examine the distribution of the tropical shore fish genus *Entomacrodus*. Here, there is also a diminution in the number of species in the same direction: the western Pacific has sixteen or seventeen species; the Indian Ocean has six or seven; the eastern Atlantic has two; the western Atlantic has two, and the eastern Pacific has one. *Entomacrodus*, however, has just been subjected to a careful systematic study². The relationship of the species indicated that the genus originated in the western Pacific but migrated from there eastward across the Pacific to the New World and then eastward across the Atlantic to West Africa.

Is there any other evidence of successful eastward migrations across the Atlantic and Pacific? Studies on the shore fish fauna in general³ have shown that the East Pacific Barrier, the extensive deep-water area that lies between Polynesia and America, has been successfully crossed (migration followed by apparent colonization) by about sixty-two species. Circumstantial evidence was given to show that this was entirely an eastward colonization movement. Apparently, species belonging to typical New World genera have been completely unable to colonize the opposite direction. At least some of the shore invertebrate groups apparently behave in the same way.

The Mid-Atlantic Barrier is the deep-water area separating the western Atlantic tropics from those of the West African coast. Apart from a group of about twenty-four shore fishes which apparently make their way from the Indian Ocean around the Cape of Good Hope and then westward across the Atlantic, the predominant migratory movement seems to be from west to east⁴. Many of the transatlantic species range broadly along the western Atlantic shelf but have attained only limited purchase in the east. Others that have achieved broad distributions in the east are clearly representatives of American genera. None of the transatlantic species belongs to genera which are typically eastern Atlantic. There are about one hundred and eighteen such species and they comprise about 30 per cent of the shore fish fauna of tropical West Africa. Recent works on West African invertebrate groups also show that an appreciable percentage of the species is transatlantic.

It may be concluded, on the basis of strong evidence for the shore fishes and at least some similar indications for the shore invertebrates, that successful migrations across the Atlantic and Pacific Oceans usually take place in an eastward direction opposite to the flow of the North and South Equatorial Currents. How can this apparently anomalous occurrence be explained? It has been observed

that the region of the Indian and West Pacific oceans has served as the evolutionary and distributional centre for the entire marine tropics⁵. It seems clear that the unusually stable ecosystems and high level of competition provide the proper environment for the evolution of dominant species that can successfully invade the other regions⁶.

From the Indo-West Pacific, dominant species migrate across the open ocean to America, westward around the Cape of Good Hope into the Atlantic, and northward through the Suez Canal into the Mediterranean. Successful reciprocal migrations are, at least, very rare and may be completely lacking. To judge from the general indications of relationship among the four great tropical marine faunas (Indo-West Pacific, eastern Pacific, eastern Atlantic, western Atlantic), this process has been going on for many millions of years. In the shore fishes, for example, virtually all of the tropical families and most of the genera are probably of Indo-West Pacific origin. Some of the dominant species are so successful that they have been able to establish and maintain circumtropical distributions.

The western Atlantic tropics may be considered a secondary centre of evolutionary radiation. Many species produced in this area have proved capable of migrating eastward to colonize the eastern Atlantic region. Species originating in the eastern Atlantic, however, are apparently incapable of successfully invading the western side. Again, the advantage seems to lie with the area that possesses the richer fauna and higher level of competition. Such movements seem to illustrate well a basic zoogeographic concept which received its modern emphasis from Matthew⁶—that dominant species arise in certain important centres and gradually become dispersed into the peripheral areas.

The existence of gradients in numbers of species (or genera) across the major barriers may mean only that certain areas have offered more opportunity for evolutionary radiation than others. In the tropical Atlantic and Pacific there is certainly not a positive correlation between the direction of the major currents and the successful migration of shore species across the mid-oceanic barriers. The Indian Ocean is not separated from the western Pacific by a major zoogeographic barrier and the fauna of the East African coast may be considered an attenuation from that of the Indo-Australian Archipelago. For most groups, there is a decreasing species gradient extending from the latter area westward across the Indian Ocean as well as eastward into the island groups of Polynesia.

In conclusion, I wish to observe that in the tropical oceans the degree of biological competition is probably a more important factor in the dispersal of shore animals than the direction of the major currents. As the direction of the species gradient in recent, tropical animal groups does not necessarily indicate the direction of successful migrations or major currents, there is no reason to believe that fossil gradients can be relied on to give us such information for past epochs.

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¹ Fell, H. B., *Nature*, **214**, 1192 (1967).

² Springer, V. G., *Proc. US Nat. Mus.*, **122**, 1 (1967).

³ Briggs, J. C., *Evolution*, **15**, 545 (1961); *Copeia*, 706 (1964).

⁴ Briggs, J. C., *Studies Trop. Oceanography*, **5** (in the press).

⁵ Briggs, J. C., *Evolution*, **20**, 282 (1966).

⁶ Matthew, W. D., *Ann. NY Acad. Sci.*, **24**, 171 (1915).