

MIXING OCEANS AND SPECIES

By

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The Central American region has long been of interest to biologists because of the presence of extremely similar populations of marine organisms along the Atlantic and Pacific coasts. In some cases, these Atlantic and Pacific populations are completely indistinguishable, although others have evolved minor differences and a few have changed profoundly since they became isolated by the rise of the Central American isthmus. The Isthmus of Panama, while acting as a landbridge for the exchange of North and South American terrestrial fauna, is a barrier to marine organisms--a barrier that has remained impenetrable to all species but the few that are able to transgress the fresh-water canal completed in 1913. The precise date at which an uninterrupted isthmian landbridge emerged is not known. Most scientists agree that the water gap was finally closed during the latter part of the Pliocene. This would mean that the marine populations have remained separated for more than five million years.

This relatively recent interruption of the continuity between faunas of the Atlantic and Pacific has resulted in parallelism between many of the forms on the two coasts. These closely related allopatric species (those that do not have overlapping geographic ranges) have been referred to by a number of designations: "geminate species," "species pairs," "analogous species," and "amphi-American species." The parallelisms have been reflected in both the vertebrate and invertebrate faunas.

The degree of morphological similarity between fishes varies among species. Among the grunts, Haemulon steindachneri is considered to be identical in both oceans. Other grunt species pairs, such as Anisotremus surinamensis in the Atlantic and A. interruptus in the Pacific, are difficult to separate. Other Atlantic and Pacific species can be separated with relative ease, although they are obviously closely related. Similar examples are also found in shallow-water groups of echinoderms, crustaceans, mollusks, and even parasitic trematodes.

The fact that there are so many similar species is somewhat surprising in view of the vastly different habitats the two coasts offer. The Pacific coastal waters of Central America have a higher tidal amplitude and in general are more silty than the waters off the Atlantic coast. Also, some Pacific areas are subject to upwellings of cold water not found

in adjacent areas of the Atlantic. These factors contribute to limiting the growth of coral reefs along the Pacific mainland coast, while such reefs are abundant on the Atlantic side.

Problems of Access

Now that a sea-level canal across Central America is contemplated, some interesting biological problems are posed. No one, of course, can tell what the effects of such a canal will be. Certainly, the construction would represent an artificial removal of a geographical barrier that would undoubtedly result in the mixing of the two faunas with unpredictable effects. What will happen when the closely related species on either side of the isthmus are allowed to mingle? Will one or the other be exterminated? Will they hybridize? If so, with what consequences? Theoretically, the results of the sudden intermixing of two formerly isolated populations can be predicted according to certain ecological and genetic principles.

Ecological problems are those concerning competition for food, and space to live and breed. Interference may be direct--by the activities of one species against another--or indirect--through the influence of parasites or diseases of one species upon the others. These complex, competitive factors are frequently difficult to interpret. An example of this is the interaction between the introduced American gray squirrel (*Sciurus carolinensis*) and the native red squirrel (*S. vulgaris*) in England (NATURAL HISTORY, December, 1964). In some parts of that country the gray squirrels have posed serious threats to the native red squirrels, while in other areas the red squirrels are still holding on.

The potential for interbreeding between the newly intermixing populations will depend upon whether or not they have diverged genetically during their isolation in ways that have made them reproductively incompatible. Such changes, referred to as isolating mechanisms, can be inherent in populations that have no corresponding externally correlated features. Two isolated populations, although morphologically identical, may be incapable of gene exchange.

Not every allopatric population has necessarily completed speciation, and it is expected that some populations might successfully fuse with their related allopatric populations if the geographical barrier were removed. Depending upon the level of reproductive isolation and the ecological, behavioral, and genetic adaptations that have been achieved in isolation, the effects of allopatric populations coming into contact with one another may be classified into the following, not necessarily exclusive, categories:

- (1) If during the period of allopatry no isolating mechanisms were

developed, the populations may freely interbreed, producing a viable hybrid swarm. This swarm may eventually include the complete range of variability of both parental populations or it may be limited to a narrow hybrid belt. The extent of such a hybrid belt will be determined by the ability of the hybrids to adapt ecologically to the geographic ranges of both parental populations.

(2) The newly sympatric populations (those with overlapping geographical ranges) may freely interbreed, but if their gene pools are not sufficiently similar, then adaptively inferior hybrid swarms may result, and these could lead to the extinction of both populations.

(3) If the development of reproductive isolating mechanisms between two populations was begun but not completed in isolation, then occasional matings between individuals of the populations may be expected. These matings may be sterile, or the progeny may be inviable or sterile. In this case, those individuals whose behavior insures their mating only with others of their kind will be reproductively more successful, and isolating mechanisms will become more prevalent throughout the populations. Selection will act to improve the efficiency of some of the isolating mechanisms so that the two populations continue to remain separate. If, on the other hand, the occasional crossings between two populations does not produce adaptively inferior progeny, the populations may react as in the first category, but somewhat more slowly.

(4) If the isolated populations have completed speciation before they mingle, they may coexist without interbreeding for part or all of their ranges, or if their isolating mechanisms do not include ecological factors, competition between the two forms may cause replacement or extinction of one species by another.

From the various degrees of morphological divergence exhibited by the amphi-American species of shore fishes I have studied, one should be able to predict that different groups will react in almost all the ways enumerated above.

Study Proposals

Several sorts of studies should precede the construction of a sea-level canal if we are to have any hope of predicting the effects of faunal mixing. First, we must understand the levels of reproductive isolation that have been achieved by populations living on the opposite coasts. Ordinarily, reproductive isolation is a criterion that is readily established only in sympatric populations, where one can easily see if two populations interbreed. In Central America, however, the problem is much more difficult, because the populations in question are kept separated by a natural barrier. We can assay the potential for interbreeding between the Atlantic and Pacific populations in two ways:

directly, by experiments attempting to interbreed related species from both coasts; or indirectly, by associating the degree of reproductive isolation with the number of morphological, ecological, and behavioral differences exhibited. Allopatric species that are morphologically very similar are considered to be more likely to interbreed than those with greater differences. By rating the populations on some kind of similarity index, a measure of the potential for gene exchange between related populations could be obtained. However, the levels of genetic and morphological divergence are usually, but not always, closely correlated, so an indirect method based on such an index is of limited reliability. Our current knowledge of marine fishes and invertebrates is too inadequate to allow an interpretation of the evolutionary history of most species or a prediction of their future.

If the barrier is removed, some ubiquitous species certainly will expand into new areas. These may successfully exploit these areas to the point of causing the extinction of less adaptable species. Many of the species that become extinct may be part of the relatively large portion of the Central American fauna that is either undescribed or extremely rare in collections. Their extinction would be a great loss to scientific knowledge.

Even if more information on the results of population mixing were available, there would still be one serious limitation to the reliability of predictions based on such information. The construction of a sea-level canal will change the physical and biotic environments on the respective coasts. These changes will require the resident populations and the newly immigrating populations to make rapid adaptations. The influx of new organisms could upset the balance of populations, and certainly would change the nature of the selection to which the organisms are subjected. The physical changes in the environment probably will be of a more local influence, their extent depending largely on the volume of interocean flow and on the accompanying differences in temperature, salinity, and silt. It is in such "disturbed habitats" that the breakdown of previously existing isolating mechanisms often permits the hybridization of numerous terrestrial species.

Even if isolating mechanisms have evolved in most of the amphio-American species, considerable study must be undertaken before we can hope to predict the ecological effects of the sudden coexistence of two closely related and previously separated species. If the two forms inhabited similar niches on their respective coasts, they would be expected to compete for available habitats. Under such circumstances, the species already resident and established in a region would be expected to resist the intrusion of immigrants from other regions. However, if the environment is changed, as it well may be, then the small populations of immigrants conceivably could be in a better position to adapt to the changed environment, and consequently might multiply and eventually exclude the

previously extant species.

Migration Deterrents

What can be learned by studying the history of the man-made connections of great bodies of water? The situation of the sea-level canal connecting the Mediterranean Sea and the Red Sea is not similar to that which is planned for a Central American site. The Suez Canal contains the Bitter Lakes and other bodies of water of very high salinity and high temperature. In spite of these harsh conditions, some marine organisms have succeeded in transversing the Suez Canal since 1869. Many Indo-Pacific species from the Red Sea have now penetrated through the canal into the eastern Mediterranean (a total of thirty species of fishes comprising approximately 5 1/2 per cent of the total Mediterranean fauna, according to a recent compilation). Many of these species are showing measurable changes as a result of their adaptations to new environmental conditions. Some, such as the commercially important goatfish (Mulloidichthys auriflamma) and the rabbitfish (Siganus rivulatus), are moving west and are now found in the Aegean Sea.

The migration of other organisms through the canal has also been more or less limited to one-way traffic. The Cambridge Expedition to the Suez Canal in 1924 reported that only two of the sixteen species of crabs they found in the canal were of Mediterranean origin. The highly saline waters, together with the primarily northerly directed current in the canal, have essentially limited dispersal to a south-to-north direction. Additional factors also operate to prevent Mediterranean fauna from moving into the Red Sea. Biologists consider the higher temperature of the Red Sea and the numbers and diversity of the extant fauna to be important factors in preventing immigrants from taking hold.

The present Panama Canal also represents a potential interocean passageway for marine fishes, as they are free to enter the locks with the ships. However, the fresh waters of Gatun Lake, through which marine fishes must pass in order to transit the canal, have remained an effective barrier to all but the most widely adaptable marine species. The most notable immigration that has occurred in this area is the occasional passage of the Atlantic tarpon (Megalops atlanticus) into Panama Bay on the Pacific coast of Panama.

The proposed Central American sea-level canal would not act as an effective barrier; in fact, the tidal differential between the respective coasts would, under certain conditions, tend to wash populations from one ocean into the other. Under these circumstances, the opportunities for successful immigration and interoceanic dispersal of many species is almost certainly assured.

Dangers of Introductions

The history of man's voluntary and involuntary introductions of animals into areas where they did not previously exist indicates that, as often as not, the results have been disastrous. One need only mention the famous cases of the Dutch elm disease, the house sparrow, the starling, and the gypsy moth in North America; the mongoose in the West Indies; the red deer in New Zealand; and the rabbit in Australia. Some of these unwanted invasions have been controlled or eradicated by expensive human counterefforts. Occasionally the introduction does not become a nuisance for a long time. It took approximately one hundred years for the population explosion of the sea lamprey to occur. When the Welland Ship Canal was opened as a bypass around Niagara Falls it removed the barrier that had previously prevented the sea lamprey from penetrating the western series of Great Lakes. The eventual decimation of the whitefish and lake trout populations that resulted is only just now being controlled. The cost of this control research, as well as the loss to the fisheries of the Great Lakes region, is a vivid example of the economic effects that can result from inadvertent introductions.

Some introductions have the desired results, as illustrated by the establishment of the striped bass (Roccus saxatilis) off the coast of California or the successful introduction of the Gray Partridge (Perdix perdix) and the Ring-necked Pheasant (Phasianus colchicus) into North America. However, attempts to introduce European songbirds into North America have largely failed. These examples illustrate our general ignorance concerning the dynamics of population introductions.

A sea-level canal, however, will not provide every species with a free pass to a new ocean. For example, as a result of the environmental differences between the Atlantic and Pacific coasts, particularly in the abundance of reefs, many organisms more or less dependent upon corals would not be capable of penetrating the Pacific rapidly. We can expect that for species with narrowly restricted ecological niches, the opportunity to extend their ranges may not be exploited. However, for most species the hydrographic conditions on the respective coasts are about equally hospitable, and would not present a severe obstacle to the dispersal of populations.

Finally, we must be concerned not only with the fate of the fish populations but also with the invertebrate, the flora, the movements of parasites into new areas, and the possible effects of silt influxes on Atlantic reefs. We see, then, that there are many parameters to this problem. Without question, the construction of a sea-level canal in Central America represents an important experiment, but its full scientific value can only be realized if it is carefully controlled. A complete and thorough pre-canal survey on the same order of magnitude as those studies conducted in connection with the International Indian

Ocean Expedition could be one important step. This would make it possible to evaluate properly the changes in the physical and biological environment that are produced by the canal. A comprehensive survey of levels of isolation achieved by the respective populations also would help us to determine intelligently what measures, if any, it may be necessary to incorporate into the new canal, either to inhibit or to prevent the interocean exchange of species. Such surveys and studies would contribute immensely to our basic scientific knowledge of a relatively unexplored area. In addition, they could serve to lessen the probability of our inadvertently permitting the interoceanic introduction of species that might have detrimental effects on extant fish and fisheries.