Interoceanic Sea-Level Canal: Effects on the Fish Faunas

Past and present zoogeography helps us predict the effects of a forthcoming interoceanic connection.

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Although construction of an interoceanic sea-level canal through the Central American isthmus has been earnestly contemplated for nearly a century, the biological consequences of a man-made "Strait of Panama" have received serious consideration only during the past decade. I wish to add another opinion to the growing body of speculation on possible biological outcomes of this venture: that while the respective characters of the western Atlantic and eastern Pacific ichthyofaunas will not be drastically altered by ingress of species from the opposite coasts, there exist opportunities for faunal enrichment, especially in the Caribbean, by transpacific species of Indo-West-Pacific origin. My conclusions are based on a consideration of the paleogeography of Central America and other areas, and of present ichthyofaunal complexes and their respective environments.

In the past, the gargantuan task of digging a suitable channel by conventional means discouraged all but the most ambitious planners, but now, with nuclear energy available as a tool of excavation, interest in the scheme is at high pitch. Although there is little doubt about the physical possibility of excavating a channel with atomic charges (*1*), the dominant problems at present are problems of politics rather than of engineering (*2*). In any case, surveys by the agents of the Atlantic-Pacific Interoceanic Canal Study Commission are being completed for two alternate sites, the Sasardi-Morti route in Panama and the Atrato-Truando route in Colombia (*3*).

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The existing Panama Canal, with its intervening 40 miles (64 kilometers) of fresh water, Gatun Lake, has thus far served as an effective barrier to all but a few euryhaline fish species. Only one, *Lophogobius cyprinoides*, is known to have established breeding populations on the opposite coast (*4*). A sea-level canal, however, would constitute an unobstructed two-way transport system for dispersal of free-swimming, shallow-water stenohaline marine fishes, and at least a one-way system for planktonic stages. In effect, a deterrent to marine exchange will no longer exist unless positive steps are taken to preserve the barrier.

Possible biological consequences of allopatric populations coming into contact have been listed by Rubinoff (*5*, *6*); these are, briefly, (i) formation of viable hybrid swarms; (ii) production of inferior hybrid swarms, leading to possible extinction of both species; (iii) limited hybridization, with maintenance of discrete populations; and (iv) replacement or extinction of one species by another. Rubinoff concluded, partly on the basis of experimental evidence, that any of these consequences may occur among the Central American shore fishes, depending upon the species involved. Briggs (*7*) has expressed the more general view that most of the western Atlantic species would be competitively superior to their eastern Pacific relatives, basing his supposition on the disproportionate richness and stability of the respective ecosystems. A dissimilar view, expressed by several workers who have compared the two faunas and their environments, is that Pacific fishes, living under more rigorous environmental conditions, would have the adaptive flexibility to compete successfully with, and ultimately displace, most of their Atlantic relatives. Finally, a recent statement by Cole (*8*), based on an incorrect estimate of differences in mean sea level, has suggested an array of frightening eventualities.

Mediterranean–Red Sea Relationships

It has been suggested that faunal changes in the Mediterranean and Red Sea since the completion of the Suez Canal may be instructive in predicting the amphi-American events (events on either side of the isthmus) that would follow excavation of the canal. Many geographical similarities exist, to be sure, there being in both cases two great north-south landmasses narrowing to a width of less than 100 miles at a point some 4800 miles north of the southern end of the landmasses, and both separating two large compartments of water (*9*). The differences stemming from historical events, however, greatly overbalance these superficial similarities when zoogeographical comparisons are made.

As early as the Cambrian, a considerable part of the Middle East was covered by a shallow tropical sea, the Tethys. In the early Tertiary this same sea was broadly continuous from the West Indies through the Mediterranean, with corridors extending to the East Indies. The rich fossil beds of Lebanon and Monte Bolca (Italy) indicate that the Tethys of this period was truly tropical and distinctly Indo-West-Pacific in character, with rich assemblages of coral and other tropical invertebrates, as well as tropical littoral fishes. In the Mediterranean region itself there were some 65 genera of reef corals, and the fossil record indicates that as far north as Belgium the Paleocene fish fauna was tropical or perhaps subtropical, and the Eocene fauna was mainly tropical (*10*).

In the late Tertiary two important alterations of the Tethys Sea occurred: (i) in the late Miocene, communication of the Mediterranean with the Red Sea was interrupted by emergence of the Isthmus of Suez (*11*), which divided the uniform zoogeographical province into two compartments, and (ii) during the Pliocene, climatic deterioration that had begun as early as the late Eocene became accelerated (*12*). As the Mediterranean cooled, its tropical fauna was gradually destroyed. This destruction may have been hastened by desalinizations resulting from the temporary

blockage of the Strait of Gibraltar toward the end of the Miocene (*13*). Following these events the impoverished Mediterranean began to accept colonizers through the Strait of Gibraltar, so that the ichthyofauna of the Mediterranean is now more closely related to that of the Atlantic than to any other (*14*).

Since the opening of the Suez Canal in 1869, the Mediterranean has received at least 24 immigrant fish species from the Red Sea (*15*), some of which may be replacing native species (*16*). In view of the geologic history of the area, it is not difficult to understand why the descendants of the preadapted Tethys fauna, with their long-thwarted potentials, are redeploying so rapidly.

As would likewise be expected, there are no reliable records of Mediterranean fish species having penetrated the Red Sea. Although this is partly due to the canal's hydrography, it may also be due to the inability of the Atlanto-Mediterranean fishes to compete with the well-adapted Red Sea ichthyofauna.

Amphi-American Relationships

While the tropical American ichthyofauna has experienced a regime of paleogeographical events similar to that of the Middle East, it has approached a condition of amphi-American parallelism rather than dissimilarity. The reason for this seeming paradox becomes apparent when the history of the area is considered.

The Tethys Sea that influenced Middle East faunal distributions simultaneously maintained continuity with large portions of Middle America. In the middle Cretaceous the broad Central American region was generally submergent and apparently presented no serious obstacles to the dispersal of shallow marine organisms (*17*). Tertiary Central America, according to Whitmore and Stewart (*18*), was characterized by a shifting pattern of island groups and of peninsulas attached to one continent or the other. During this time the equatorial surface currents delivered a steady influx of colonizers westward into what is now the Caribbean province and, in turn, through the Central American seaways into the eastern Pacific (*19*).

From the fossil record we may infer that the Tertiary fauna was distinctly West Tethyan in character, and that the eastern Pacific fauna was quite similar to the fauna of the remainder of the Caribbean province. This continuity of ecological conditions has been recently demonstrated by Woodring (*20*), who found practically identical fossil molluscan faunas along the Caribbean coast of central Panama, in northern Colombia, in the Atrato Trough, and near the Pacific coast of Colombia, Darien, and Chiriquí.

During the Pliocene the Central American isthmus was completed; thus the Americas were connected for the first time in geologic history (*21*). At the same time climatic changes similar to those affecting the Mediterranean were occurring in Central America, destroying a portion of the fauna while displacing the remainder southward and replacing it with cold-water forms. By the time of the continental ice sheets the ocean waters were sufficiently cooled to allow crossing of the equator by organisms that are now "antitropical" in distribution. Such forms now barely reach the existing tropical fauna (*22*).

Up to this point the histories of the Middle East and Central America coincide, both areas having experienced (i) submergence of vast, continuous areas beneath tropical seas; (ii) widespread distribution of tropical shallow-water faunas; (iii) orogenic disturbances interrupting the continuity of the sea by land bridges; (iv) climatic deterioration causing a cooling of the waters; (v) replacement of the tropical faunas by northerly forms; and (vi) rewarming of the seas following the periods of continental glaciation.

At this point, however, the analogies cease. During periods of climatic amelioration the original Mediterranean fishes were denied readmission to their former domain by a barrier which obstructed their northward movement, whereas in Central America this was not the case. When the American fishes were displaced southward during periods of cooling, many took refuge along the coasts of South America. During warmer periods they attained their earlier latitudinal ranges without obstruction from the newly formed isthmus. Northeastern South America, for example, is thought to have been a refuge for much of the western Atlantic fauna during the Pliocene and early Quaternary (*10*). The similarities of the present fauna on the two sides of the isthmus furnish convincing evidence that the former distributions were in large part restored.

These similarities were first noted by Günther (*23*), who postulated the existence of former marine continuities even before this had been demonstrated by geologists. The similarities are most striking at the generic level, where coincidence for amphi-American fishes (45 percent) far exceeds that (19 percent) for fishes on the two sides of the Atlantic (*24*).

At the species level, only about 1 percent of the fishes are judged to be identical amphi-American species-pairs (*25*); this indicates not only the effectiveness of the geographical barrier but the amount of speciation that has occurred during the past 3 or 4 million years of geographical discontinuity.

Much of the ichthyofaunal dissimilarity at the species level undoubtedly reflects the dissimilar environmental conditions which developed on opposite sides of the isthmus as the seaways became disrupted. These differences, summarized by Rubinoff (*6*), include differences in temperature, salinity, transparency, tidal amplitude, and associated biota. On the whole, the Pacific coast now presents a much more rigorous and fluctuating environment than the Atlantic coast does.

Meek and Hildebrand (*26*), in attempting to explain the differences in fish faunas, speculated as follows:

> . . . before the last passage between the Atlantic and Pacific Oceans was closed to marine fishes, the representatives of certain families had already found that one side of the "divide" was better suited to their particular needs than the other. The result, with respect to such families, was that when at last the passageway was completely closed that most of the species of some of them were on one side of the isthmus, while those of another were on the opposite coast.

Although this may account for certain initial differences, it is unlikely that the faunas had segregated to so great a degree while the sea was still continuous. It is more likely that they diverged after being separated into environments with differing selective pressures.

At this point we can profitably compare the present amphi-American situation with the situation that existed on either side of the Isthmus of Suez before the canal was built. We have seen that in the latter case there was a tremendous imbalance between the two biomes, while in Central America there exist historically well-adapted faunas on both sides of the isthmus that are closely related in many respects but differ as a reflection of the differing

environments. It should, then, be clear that it is unsound—or at least unfair—to make predictions about amphi-American faunal interchanges on the basis of events on both sides of the Isthmus of Suez after excavation of the canal. And, at the same time, we should avoid making emotionally charged analogies to the introduction of various pests (for example, goats or rabbits) into previously pristine habitats. The Suez events involved the reintroduction into an otherwise unsaturated area of a fauna well qualified to live in the new environment. The pest situation involves the introduction and expansion of prolific nuisances without the hindrance of predators or effective competitors.

Conclusions and Prognosis

Finally, we may return to the original question of the effects of unleashing the two Central American ichthyofaunas, one upon the other. Having no valid precedents that approach the magnitude of this forthcoming experiment, we must rely heavily on our general knowledge of zoogeography and evolution, and must temper our predictions by an understanding of the history of the area and its faunal complexes.

The higher taxa are already characterized by a high rate of amphi-American coincidence, and thus can undergo few changes; rearrangements will be primarily at the species level. In Rubinoff's (*6*) list of possible biological effects, three of the four involve some degree of hybridization. The lifelong observations by Carl Hubbs on hybridization and speciation in fishes supply a multiplicity of examples and comment, all of which dissuades me from believing that hybridizations of any significant extent will occur. Even among species that can be readily cross-fertilized in aquaria there is, according to Hubbs (*27*), an extreme infrequency of recognized fish hybrids in nature. Hubbs (*28*) has, moreover, noted that interspecific crossings are least likely to occur in tropical marine waters (as compared to temperate or fresh waters), for "much greater opportunities have existed [in tropical marine waters] for the development and operation of the multitudinous fine adjustments involved in the location, with precise timing, of the proper breeding grounds and the proper mates." Among subspecies—the taxon to which some of the amphi-American "species-pairs" may eventually be relegated—there may be ecological, behavioral, or other blocks to successful interbreeding, so that, even in the absence of genetic isolating mechanisms, fusion is countered by "the effective adaptation of each subspecies to its own habitat, so that a high breeding potential is realized and the appropriate habitats are saturated with their own respective pure stocks" (*27*).

Some gene flow will occur, to be sure, especially when an individual crosses the isthmus and is forced to breed with genetically dissimilar individuals, but here again there is serious question as to whether such introgression will result in an enrichment of the gene pool or in elimination of the genes of the invaders.

As for the more serious possibility of replacement or extinction of fish species by better-fitted groups from the opposite coast, widespread occurrence of such phenomena appears improbable when considered in the light of paleogeography and present faunal adjustments. It is difficult to believe that any great number of fish species will be preadapted to colonize an environment which not only is less hospitable in terms of their own background but is, moreover, occupied by well-adapted related forms.

Of course, it would be folly to assume that no changes at all will occur. Species with generalized ecological requirements, such as the piscivorous-carnivorous grunts (Pomadasyidae) or porgies (Sparidae), may find the canal easy to transit in either direction and may become established on the opposite coast. Another source of potential colonizers, the Indo-West-Pacific fauna, may have a far greater impact on the ultimate composition of the Atlanto-East-Pacific fauna, and particularly on the fauna of the Caribbean.

As Ekman (*10*) has demonstrated, the Mesozoic and Eocene fauna of the Atlanto-East-Pacific was not inferior either in quality or in quantity to the fauna of the present-day Malay region. But the Atlanto-East-Pacific is far from having recovered from the impoverishments suffered during the Cenozoic climatic changes. Briggs (*29*), for example, has found that western Pacific fishes are indeed transgressing the East Pacific Barrier to become established in the eastern Pacific. Of the 62 species of shore fishes documented on both sides of the Pacific, most of the eastern Pacific representatives are confined to offshore islands, but they are nevertheless potential colonizers of both the eastern Pacific coast proper and the environmentally more hospitable Caribbean. In this regard, some concern has arisen over the possible spread of the transpacific sea snake, *Pelamis platurus*, into the Caribbean (*30*).

A complicating factor is the change that may occur at lower trophic levels, providing new niches and causing shifts in feeding patterns, with corresponding declines in adaptive levels among the resident fishes and increased competitive advantages for the invaders. Since many of the Central American invertebrate and floral groups are imperfectly known (*31*), it is dangerous to make predictions about other levels of the food chain. But, if my reasoning may be extended in a general way to groups other than fishes, it should follow that widespread extinctions will not occur. There is good evidence that much biotic transfer may, in fact, be already occurring. Fouling animals, for example, may be making regular transits through the present canal on the hulls of ships (*32*, *33*), and planktonic larvae and other microscopic organisms may be transiting in the saltwater ballast which is taken aboard ships to increase their maneuverability through the canal (*33*, *34*). These same agencies in world commerce are recognized as steady and powerful influences in the worldwide spread of marine organisms (*35*).

Another imponderable is the question of parasites, for we may find preadapted species unleashed upon particularly vulnerable hosts which have not had the opportunity to make genetic defensive adjustments. The native sturgeon of Lake Aral, for example, was seriously damaged by a parasitic worm, *Nitzschia sturionis*, carried by an introduced sturgeon (*35*). Studies aimed at assessing such possibilities are clearly in order.

As for hydrographic changes resulting from a sea-level canal, these will certainly be minor, with only local effects. The array of calamitous effects suggested by Cole (*8*), based on an idea that "the Pacific Ocean stands higher than the Atlantic by a disputed amount which I believe to average 6 feet," are unfounded. The Pacific Ocean is higher, but the mean difference is not disputed and stands at 0.77 foot at the present Panama Canal (*36*). The combined effects of tidal oscillation and the mean difference in sea level would cause the water in the channel to move

alternately toward the Atlantic and then toward the Pacific, with a net advance toward the Atlantic of about 5 miles per day (*36*). This rate of advance, applied linearly to channel dimensions of a cut excavated by nuclear charges (*1*), gives an average flow of a little more than 500 cubic meters per second, a value corresponding to the flow of a small river, or less than 1/400 the average discharge of the Amazon River.

Although the transported Pacific water would at times be cooler by a few degrees than the water of the Atlantic, it would be of nearly the same salinity, and changes in the physical environment would be minimal. The greatest contribution of this Pacific water to ichthyofaunal change would be its role in providing a transitional area on the Atlantic side in which Pacific fishes could be harbored, possibly with competitive advantage, and from which propagules could be dispatched.

Under hydrographic conditions similar to those proposed by Meyers and Schultz (*36*), a sea-level canal may remain an effective barrier to weak swimmers or plankton from the Atlantic. Freshwater drainage into the canal would provide a deterrent to strictly stenohaline marine organisms only if it were deliberately and constantly controlled.

The rather general predictions I have made represent only one of several opinions recently advanced, and should in no way detract from the critical and immediate need for preliminary surveys and analytical studies of the sort outlined by Rubinoff (*6*). If my views are incorrect, and if widespread or disastrous biological effects are felt, no amount of hindsight will be of avail. Our only consolation will be that the establishment of a man-made sea-level interoceanic connection may merely have hastened what may well occur by natural means in, say, a few million years.

Summary

Although an interoceanic sea-level canal through Central America will allow easy exchange of stenohaline marine fishes, the characters of the existing ichthyofaunas will not be drastically altered by ingress of species from the opposite coasts. The Suez Canal cannot be taken as a valid precedent in spite of superficial analogies, for, in the case of the Suez Canal, well-qualified Red Sea faunas were reintroduced into the otherwise unsaturated Mediterranean. In Central America, historically similar faunas exist on either side of the isthmus, their differences being only a reflection of their differing environments. It is therefore unlikely that any great number of fish species will be preadapted to colonize an environment which not only is less hospitable in terms of their own background but is occupied by well-adapted related forms.

Opportunities for enrichment exist in the Atlanto-East-Pacific province, and the greatest potential source of Caribbean colonizers may be the western rather than the eastern Pacific. Factors which complicate predictive efforts are changes in lower trophic levels, and parasites. Hydrographic changes will be minor, having only local effects.

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