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ON THE OCEANIC TRANSPORT OF CRAB LARVAL STAGES*

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ABSTRACT

Evidence from the disciplines of oceanography, marine geology, crustacean physiology, life-history and faunistic studies is marshalled in an attempt to demonstrate the probable manner in which fragile-bodied and short-lived crab zoeae and megalopa have been able to span ocean barriers, following major ocean currents as highways and using remote islands as stepping-stones to continental shores. While the concept has been developed in connection with distribution studies of crabs of western America and its offshore islands in the eastern Pacific, it is believed applicable with suitable refinement to other continents and their outlying islands in other seas.

INTRODUCTION

IT is nearly 20 years since the writer postulated, in connection with studies on Galapagos Brachyura, that "the system of oceanic circulation observed in the Galapagos Islands, *plus* that known to exist in the greater Pacific area, are together capable of accounting for the recognized distribution of brachyuran species within the archipelago on the basis of oceanic transportation of larval stages alone" (Garth, 1946, p. 617). In that study the California, Niño, Peru, and Equatorial Counter currents were designated, either singly or in combination, as the agencies responsible for the transporting of larval stages to the archipelago from the Baja California-Gulf of California region, the Bay of Panama, the South American west coast, and trans-Pacific islands. As a corollary the role of intervening islands as way-stations was recognized: "The fact that other Galapagos species are common to the intermediate outposts of Clarion and Socorro....suggests that these islands, along with those of Cocos and perhaps Clipperton, may have served as stepping-stones for current-borne larval stages" (*Ibid.*, p. 609).

As stated by Hamilton (1956, p. 51), "The chief objection to over-water migrations of shallow-water animals has been the tremendous distances these animals must travel over deep water before finding shallow water of the right temperature in which to find lodgment". In the past twenty years, and particularly within the last ten, considerable progress has been made toward overcoming this objection, and the once unanswerable question of how a fragile and short-lived crab zoea or megalopa can be transported by powerful but torpid ocean currents over distances seemingly too great to be encompassed within its assumed life-span and at their known speeds is well on the way toward solution. The answers are partial and come from six different disciplines, three physical and three biological: oceanography, marine geology, glaciology, crustacean physiology, life-history studies, and faunistic studies. Together they present a more convincing argument, if not an actual proof, in support of the type of transportation postulated than could be given when evidence was largely conjectural and factual information was scanty.

EVIDENCE FROM OCEANOGRAPHY

The nature of ocean currents is better understood now than a few years ago. The late H. U. Sverdrup in a personal interview likened the North and South Equatorial currents to massive

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Mississippis, westwardly directed, piling up water against the Asiatic coast to a height of eight feet, then turning to the north and south to begin their gigantic gyrals, clockwise in the North Pacific and counter-clockwise in the South Pacific, while between them the narrow but swift Equatorial Counter Current flowed eastward, downhill, all the way to the American coast. While there is nothing basically wrong with this concept, it fails to account for the presence in the Galapagos Islands of crabs of Indo-west Pacific origin, for this narrow current passes hundreds of miles north of the Galapagos, and in order for the larval crabs to get there it is necessary that they be carried back from the Bay of Panama by the Niño Current, a southwesterly directed current that periodically or intermittently bathes Galapagan shores.

To clarify his understanding of the situation the writer addressed the following letter to the Woods Hole Oceanographic Institution (May 19, 1948):

"In my research, which is concerned with the distribution of brachyuran Crustacea in the eastern tropical Pacific, it is necessary to account for the presence of identical intertidal forms on islands separated by hundreds of miles and sometimes by thousands of miles of open ocean. To do this I have postulated the transport of larvae by ocean currents; but to attain these distances at the known speed of the currents involved, it is necessary to assume a lower metabolic rate and a longer life-span than occurs when the creatures are reared under optimum laboratory conditions."

In replying, Dr. C. O'D. Iselin, the Director, wrote as follows (May 25, 1948): "I believe it is safe to say that the velocity of ocean currents is about twice that shown on current charts. Evidence is rapidly accumulating that the currents are not broad and gradual as all charts showing average conditions indicate. The flow is narrow, streaky, and fluctuating. Especially the more powerful currents meander widely and throw off large, powerful eddies on either side.

"The current charts have been constructed by averaging a large number of observations from ships which were sometimes in the strong part of the current and sometimes not. Thus this type of statistical information is bound to end up with weak, diffuse currents.

"Some of the evidence on which these ideas are based is given in an unpublished report available at Scripps. This is entitled: "Technical Report No. 9 on the Hydrography of the western Atlantic: Meanders and Velocities of the Gulf Stream," by Frederick C. Fuglister and Valentine Worthington, October, 1947. Fuglister and I have also prepared a paper on the same subject which will appear before the end of the year in the *Journal of Marine Research* (*see* Iselin and Fuglister, 1948, p. 324, in which velocities of four and five knots for the Gulf Stream and of three knots for its eddies are given).

"My picture of your crabs is that from time to time they can get a fast ride from one island to the next, the current being something like a snake on the floor."

This newer "snake-on-the-floor" concept explains how offshoot currents from the main Equatorial Counter Current, if directed to the south-east, might transport larval crab stages from Palmyra directly to the Galapagos without the necessity of return by the Niño Current, while if directed to the north-east, might transport them directly to Clipperton. The increased speed, in the case of the Equatorial Counter Current from 2 to 4 knots, or from 48 to 96 nautical miles per day, if maintained would halve the time required in transit from Palmyra to Galapagos, bringing the 2,000-mile journey within the four-week period required by most crabs to reach the first adult stage. That this period may, under unfavourable conditions, be extended will be considered later on.

The currents heretofore mentioned are superficial currents, at most a few hundred feet deep. In 1952 a submerged current was discovered flowing in an easterly direction beneath the westerly directed South Equatorial Current (Cromwell *et al.*, 1954). Named the Cromwell Current for its discoverer, it has since been traced for 3,500 miles from the longitude of the Marquesas, where its core is at 100 meters, to the Galapagos, where it ascends to 40 meters. Its volume equals that of the Florida Current and its speed is three knots, as compared to the one-knot speed of the opposite surface stream. At the equator the depth of the change from west to east flow is at about 20 meters (Knauss, 1960). While little is known of the vertical migration of crab larvae in the mid-Pacific, it is reasonable to suppose that not all individuals remain at the surface in view of the marked turbulence that exists, particularly at the edges of currents moving in opposite directions. It is therefore apparent that any plankter descending below this comparatively shallow depth (of 20 meters) would be captured by the Cromwell Current and be carried hundreds or thousands of miles eastward at speeds up to 72 nautical miles per day.

Evidence from Marine Geology

With the perfection of echo-sounding has come the practicability of mapping the ocean floor with an exactitude never envisioned by those who used the older method. A byproduct of echo-sounding has been the discovery, within the last 20-year period, of hundreds of submerged mountain tops, the so-called *guyots* of the central Pacific (Hess, 1946). These submarine features exhibit a remarkable uniformity in that all rise to about the same height with respect to the sea surface, and all are flat-topped or planed off at that level. They are thought to represent truncated volcanoes with flat platforms eroded by wave action (Hamilton, 1956). While reef-building corals were at one time established upon them, these failed to maintain sufficient growth to keep above water as the block on which they were situated slowly sank, so that they never became fully developed atolls. At their present level of from 700 to 900 fathoms they support a fauna not unlike that of the shelf surrounding the Hawaiian Islands, but separated from it, and from the continental shelves, by oceanic depths. When at sea-level or above, they formed island groups as extensive as existing ones, thereby providing additional stepping-stones for land-bound animals of all sorts, including marine forms restricted to the littoral.

While flat-topped seamounts, although not uncommon in the Gulf of Alaska (Menard, 1955), are of rare occurrence in the eastern Pacific at mid-latitudes, several are known between Hawaii and the North American mainland. Of these may be mentioned Erben and Fieberling guyots, located 800 and 600 miles west of San Diego, and with tops at 400 and 280 fathoms, respectively (Carsola and Dietz, 1952). Two shallow banks also deserve mention: Ranger Bank, located 6 miles north of East San Benito Island, with a minimum depth of 67 fathoms (Emery, 1948), and Stranger Bank, also known as Hurricane Bank, located 200 miles south-west of Clarion Island, with a minimum depth of only 15 fathoms (Hubbs, 1959). The question of how long ago these may have been at the surface, and thus available for larval crab dispersal, is best left until after the next paragraph.

Evidence from Glaciology

It is a well-known fact that much of the earth's water is tied up in its continental glaciers, and that as glaciers wax and wane, so fluctuates the level of the sea. The 7 million cubic miles of Antarctic ice, if melted, would raise the sea-level throughout the world by 200 feet or more, while the abrupt melting of both the Greenland and Antarctic icecaps would raise the present world-wide sea-level by as much as 300 feet (Haag, 1962, p. 115). One of the periods of greatest glacial advance and retreat, and hence of the greatest rise and fall in sea-level, was the Pleistocene; indeed, it is by no means certain that we are not still in one of its interglacial phases. Should severe glaciation ensue, the sea-level might drop to the point that the shallower banks, those under 100 fathoms, would again be exposed, serving once more, as in the past, as island havens. Since it is only about 18,000 years since the last severe glaciation, the Wisconsin, left the northern tier of states, and since at its maximum about 36,000 years ago the sea-level was lowered by as much as 460 feet (*Ibid.*, p. 120), it can be seen that as many as three times within the last 200,000 years islands now hundreds of feet below the surface may have been exposed as Clipperton and other Pacific atolls are today. And 200,000 years is but a fraction of the time that has been available to existing species for trans-Pacific migration.

It is by now apparent that the shallow banks on the one hand and the submerged seamounts or guyots on the other are phenomena of different magnitudes and ages. The shallow banks, being less than 100 fathoms deep, have been exposed repeatedly by inter-glacial fluctuations in sea-level occurring as recently as late Pleistocene. The guyots are the result of subsidence that has been continuous since Cretaceous times and has reached a depth of several hundred fathoms. They are too deep by far to have been exposed by the comparatively superficial changes in sea-level of the late Tertiary and early Quaternary periods. If stepping-stones are sought for recent migrations responsible for species now common to western and eastern Pacific localities, the search must be restricted to existing islands and banks of less than 100 fathoms. If, however, stepping-stones are sought for past migrations responsible for genera now common to the two areas, their common genera being more numerous than common species, it may be assumed that the guyots, as exposed islands or submerged banks of an earlier era, played an important, if not a predominant role.

Evidence from Life-History Studies

The rearing of a crab through all its life stages from egg to adult has been accomplished numerous times in the laboratory: for *Lophopanopeus bellus bellus*, *Pinnotheres taylori*, *Hemigrapsus nudus*, and *H. oregonensis* by Hart (1935); for *Pinnotheres ostreum* by Sandoz and Hopkins (1947); for *Neopanope texana sayi* by Chamberlin (1957); for *Pagurus samuelis* by Coffin (1958, 1960); for *Lophopanopeus leucomanus*, *L. bellus diegensis*, and *Paraxanthias taylori* by Knudsen (1958, 1959 *a*, 1959 *b*); and for *Sesarma cinereum* by Costlow and Bookhout (1960). Length of larval life has been shown to be for *Pinnotheres taylori* 4 weeks; for *Hemigrapsus oregonensis* 4–5 weeks; for *Pinnotheres ostreum* 25 days (at 23° C.); for *Neopanope texana sayi* from 20–25 days (at 24° C.); for *Pagurus samuelis* from 23–32 days (at temperatures ranging from 28–17° C.); for *Lophopanopeus leucomanus* from 5–7 weeks; for *L. bellus diegensis* about 5 weeks; for *Paraxanthias taylori* from 5–6 weeks; and for *Sesarma cinereum* from 20–39 days (at temperatures ranging from 30–20° C.). Thus it may be seen that the pre-adult life of a number of anomuran and brachyuran crabs is from 25–50 per cent. longer than the usual four weeks expected, and that cooler temperatures prolong the larval period.

Evidence from Crustacean Physiology

These averages were achieved with abundant food present. It is well known that starvation retards ecdysis (inhibits molting, Passano, 1960, p. 583). It is therefore possible that the life-span of an emaciated zoea or megalops might be extended until such time as sufficient food could be procured with which to fuel the next metamorphosis. The observations of Hahn (1948, p. 103) regarding the semi-starved condition of the pelagic population of the Sargasso Sea during an investigation by the *Atlantis* are pertinent in this connection. Wilson (1952, p. 120) found that the larvae of *Ophelia bicornis* have a period of at least several days during which they are able to metamorphose, and concluded (*op. cit.*, p. 56) that the ability to postpone metamorphosis until a suitable environment for adult life is reached is undoubtedly widespread.

Evidence from Faunistic Studies

As long as knowledge of the littoral marine faunas of remote islands and island groups was based upon incomplete collections, randomly made, and often by persons not overly familiar with the animals collected, it was difficult to discern patterns of distribution. Now that the Galapagos Islands have been investigated by the Hancock Expeditions and Clipperton Island by the Scripps Oceanographic Institution Expeditions, each with a staff of scientists, and with faunal lists reasonably complete, it can be seen that the occurrence of Indo-west Pacific species in the eastern Pacific is not an isolated phenomenon, but one that occurs regularly and predictably in all groups having larvae suited to transport by ocean currents. (This is independent of, but not unrelated to, the occurrence at these same islands of western Pacific species of *Plagusia*, *Planes*, and *Pachygrapsus*, whose members are habitually transported on drifting logs or on sea turtles as adults.) It has been reported for mollusks by Hertlein (1937), and by Hertlein and Emerson (1953, 1957), and for fishes by Briggs (1961), and by Rosenblatt and Walker (1963). In fact, it is so prevalent that the Central Pacific Oceanic Barrier may either no longer be considered the absolute obstacle to east-west distribution that it once was (Ekman, 1953), or its line of demarcation must be moved eastward to include Clipperton Island at least (Garth, 1965). The new point for conjecture is no longer how western Pacific littoral species may have reached the outliers of the American continent; it is why, having reached Clarion, Clipperton, or Culpepper (an outpost of the Galapagos group), they have not made it to the mainland coast.

Summary

Thus, while no one has followed the passage of a larval brachyuran or anomuran crab from one Pacific island to another by radioactive tracer or otherwise, it is almost a foregone conclusion that this is the way in which their dispersal occurs, following the highways of the seas, the ocean currents. Factors unknown or only surmised twenty years ago that increase this certainty are (1) a new concept of ocean currents as faster, narrower, and more highly irregular than was formerly believed; (2) the discovery of flat-topped seamounts or guyots representing submerged truncated volcanoes that as islands provided additional resting places in the distant past, and of shallow banks that similarly served more recently; (3) the knowledge that sea-levels have fluctuated widely in response to advances and retreats of continental glaciers, and will continue to do so, making islands where none presently exist, as well as obliterating existing islands; (4) the fact that crustaceans control, within limits, the time of molting, and hence, presumably, of metamorphosis, waiting until conditions are propitious before advancing to the next life stage; and finally (5), that crabs reared under laboratory conditions, and with an abundant food supply, require from a month to six weeks to reach adulthood, while in the absence of food or of a suitable substrate this period may be indefinitely extended. In the absence of evidence to the contrary, it may be assumed that random dispersal of ocean current-borne larval stages operating over long periods of time and great distances is responsible for the present assemblage of species of brachyuran and anomuran crustaceans found at Clarion, Socorro, San Benedicto, Clipperton, Cocos, Malpelo, and the Galapagos Islands. And, with the possible exception of the guyots, which until recently have been regarded as an exclusively mid-Pacific phenomenon, the same factors that have assured the distribution of crustacean species in the eastern Pacific would appear to have operated in similar manner in other oceans and their seas.

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