

The Role of Passive Dispersal in the Distribution of Hemipelagic Invertebrates, With Examples from the Tropical Pacific Ocean

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(3 Text figures)

INTRODUCTION

THE FOSSIL RECORD contains numerous examples of anomalous biogeographic distributions. In the past, the classic approach in explaining these anomalies has been to invoke largely nonbiological mechanisms, such as physical land or sea barriers. More recently, VALENTINE (1973) and others have attempted to relate the distribution of marine faunas to seafloor spreading and to the changing position of the continents through the Phanerozoic. However, the causes of many of these biogeographic anomalies can be more adequately explained by determining the effects of biological mechanisms on dispersal. Unfortunately, the use of the biological approach in solving faunal anomalies in the fossil record has been generally ignored by the paleontologist.

The distribution of Recent molluscan faunas in the northcentral Pacific around Hawaii and along the west coast of Central America is characterized by a number of anomalous associations. It is our contention that these faunal anomalies largely reflect the distributional patterns resulting from dispersal by currents rather than the biogeographic end products necessitated by the long-term effects of plate tectonics. Because many of these anomalies can be explained by the existing oceanic circulation phenomena, it is the focus of this review to examine the role of larval dispersal across broad expanses of deep water as a biological vehicle that contributes to the occurrences of

faunal anomalies. The recognition of these biogeographic relationships provides the framework for a potential model to explain similar faunal associations in the fossil record.

DISPERSAL OF HEMIPELAGIC INVERTEBRATES

The distributional patterns of major components of the marine biota are reflections of oceanic circulation operating temporally as a dispersal mechanism. An understanding of how different organisms are dispersed by currents is essential to the understanding of marine biogeography. Dispersal of marine life may be divided into 2 broad categories (passive and active). Passive dispersal may be defined as: dispersal of planktic organisms by ocean currents during the larval stage of development or by rafting on floating debris. Planktic organisms, in turn, may be divided into 2 groups: those organisms which are totally pelagic spending their entire lives in the plankton and the larvae of benthic species which spend only a portion of their life cycle in the plankton. This is in contrast to the mode of active dispersal of nektonic animals which have the capability to control their movements. In most cases, these nektonic species remain within a particular water mass or current. The major difference between nektonic and planktic organisms in terms of dispersal is that nektonic species have the poten-

tial to control largely their movements and can swim against the flow or leave a given current.

The direction of dispersal is unidirectional and linear, owing to the inability of larvae to swim actively and to move against the flow of the current. Thus, currents may be viewed as distinct one-way corridors of dispersal and at the same time as barriers to dispersal (ZINSMEISTER, 1974b). The importance of distance as a barrier to dispersal in the sea is well known (EKMAN, 1953). The greater the distance, the less likely an organism is able to survive transport. In the case of invertebrates with hemipelagic larvae, this is only partly true. Of greater importance is the direction of circulation. No matter how close two points are, if the current is not flowing in the proper direction, the organism will not be able to bridge the gap. The significance of dis-

tance as a barrier depends on the length of the pelagic stage and the velocity of the current.

Until relatively recently, it was commonly believed that transport of larvae over long distances was rare (EKMAN, 1953, and THORSON, 1961). Recent papers (SCHELTEMA, 1966, 1968, 1971, 1972, 1974, 1977, and ROBERTSON, 1964) have shown that many groups of invertebrates have pelagic larvae that can remain in the plankton for as long as a year. SCHELTEMA (1971), in a discussion of trans-Atlantic dispersal of benthic mollusks, proposed the term teleplanic for larvae that are capable of remaining in the plankton for extended periods of time. For teleplanic larvae distance plays a secondary role to the direction of circulation as a barrier to dispersal.

The velocity and direction of oceanic currents may vary

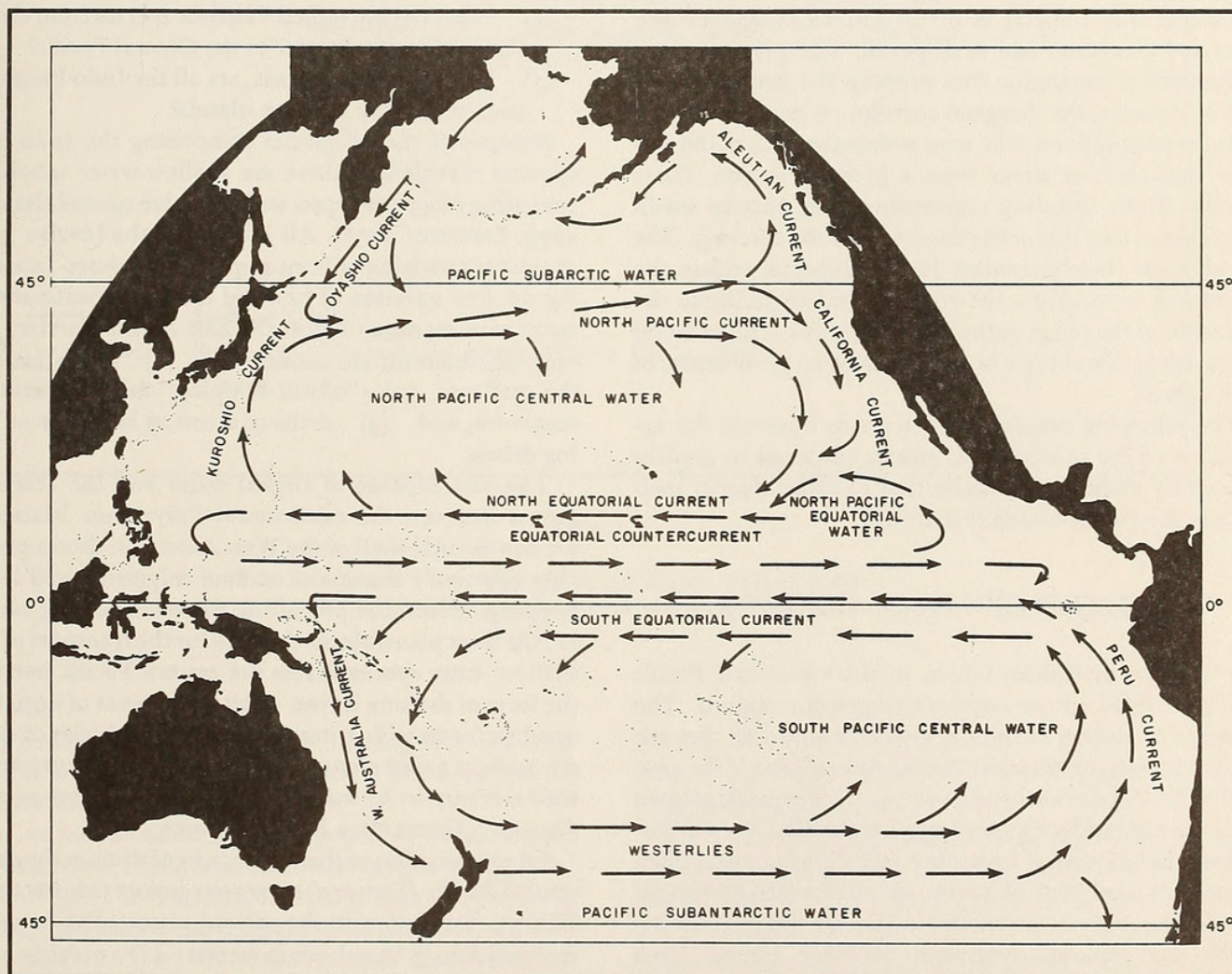


Figure 1

Pacific Ocean Currents (AMERSON & SHELTON, 1976)

considerably over a period of time. The causes of these variations in circulation are not well understood, but are likely to be in response to major short-term climatic fluctuations. These brief periods of atypical circulation play an important role in the distribution of marine life. Such episodes of abnormal transport are here referred to as dispersal pulses and may allow the establishment of a population hundreds of kilometers beyond the taxon's normal range. ZINSMEISTER (1974a) cited several examples of anomalous occurrences of modern Panamic mollusks in southern California well north of their expected normal range. Each of these occurrences could be related to an earlier period of abnormal oceanic circulation off the coast of southern California.

Consideration of the source of pelagic larvae is also important in the discussion of dispersal corridors. Basically, the source of larvae may be divided into 2 categories: primary and secondary loci of dispersal. The primary locus of dispersal is the region that supplies the major proportion of larvae to the dispersal corridor. A secondary locus of dispersal is defined as an area within the path of the corridor that receives larvae from a primary source. These regions, where breeding populations have become established, act as new loci of dispersal within the corridor. The net effect of these secondary loci of dispersal within the corridor is to lengthen the corridor and to facilitate the extension of the range of those organisms with short larval stages, which would not be able to cross large distances of open ocean.

The following examples will serve to illustrate the application of the principles of passive dispersal to explain apparently anomalous distribution of some Recent mollusks in the Pacific Ocean (Figure 1).

WESTERN CENTRAL AMERICA

The modern molluscan faunas of the equatorial Pacific may be divided into 2 large zoogeographic regions. The Indo-Pacific region encompasses the central and western Pacific. It is separated from the Panamic region of the eastern Pacific by 5000 km of open ocean. This expanse of open sea is referred to by EKMAN (1953) as the East Pacific Barrier and has existed at least since late Pliocene time when the eastern-most central Pacific islands essentially had attained their position in the basin (DANA, 1975; VERMEIJ, 1978). The Panamic molluscan province extends from near the head of the Gulf of California southward to Ecuador. KEEN (1971) listed a fauna of approximately 3300 species of mollusks from the Panamic Province. Within this large faunal assemblage a small Indo-Pacific element (less

than 1%) has been recorded (BERTSCH, 1973; EMERSON, 1978; VERMEIJ, 1978). Significantly, these Indo-Pacific species, except for rare occurrences on the continental shelf from Mexico to Ecuador, are restricted to the offshore islands. Furthermore, the presence of an Indo-Pacific element in the Panamic Province is in sharp contrast to the absence of Panamic species in the Indo-Pacific Province (EMERSON, 1967).

This seemingly anomalous occurrence of Indo-Pacific species on the islands off the west coast of Mexico and Central America raises several interesting questions concerning the biogeographic distribution of marine life in the equatorial eastern Pacific.

- (1) How did these shallow-water mollusks manage to cross 5000 km of open ocean of the East Pacific Barrier?
- (2) What has prevented Panamic species from crossing the East Pacific Barrier to the Central Pacific?
- (3) Why, for the most part, are all the Indo-Pacific taxa restricted to the offshore islands?

Analysis of the 52 species comprising the Indo-Pacific element reveals that these are shallow-water inhabitants consisting of 45 gastropod and 7 bivalve species (BERTSCH, 1973; EMERSON, 1978). All but one of the bivalve species are either attaching or boring epifaunal species. In answering the first question of how did the Indo-Pacific shallow-water taxa manage to cross the East Pacific Barrier, 3 primary mechanisms are considered: (1) migration along the seafloor, (2) "island hopping" from seamount to seamount, and (3) drifting across as larvae or on floating debris.

The vast expanse of abyssal water and the absence of guyots between the easternmost Polynesian Islands and the continental shelf of the West American shores presumably effectively eliminates seafloor migration and "island hopping." Thus, the prevailing eastward flowing currents are the most plausible mechanism for the transport of these shallow-water species across the eastern Pacific barrier in the form of drifting larvae, or by attachment of eggs, larval or adult forms to floating debris. Other vehicles of dispersal, such as attachment to birds and nektic organisms, as well as transport by man, may serve as secondary agents of dispersal (HERTLEIN & EMERSON, 1953).

An examination of the oceanic circulation in the eastern central Pacific (Figure 2) serves to support this assessment. Oceanic circulation in the central eastern Pacific may be resolved into 3 broad components: (1) a fairly strong eastward flowing system of currents carrying warm tropical water along and slightly north of the equator, (2) two less well-defined but broader westward flowing cool water currents on either side of warm east-flowing currents, and

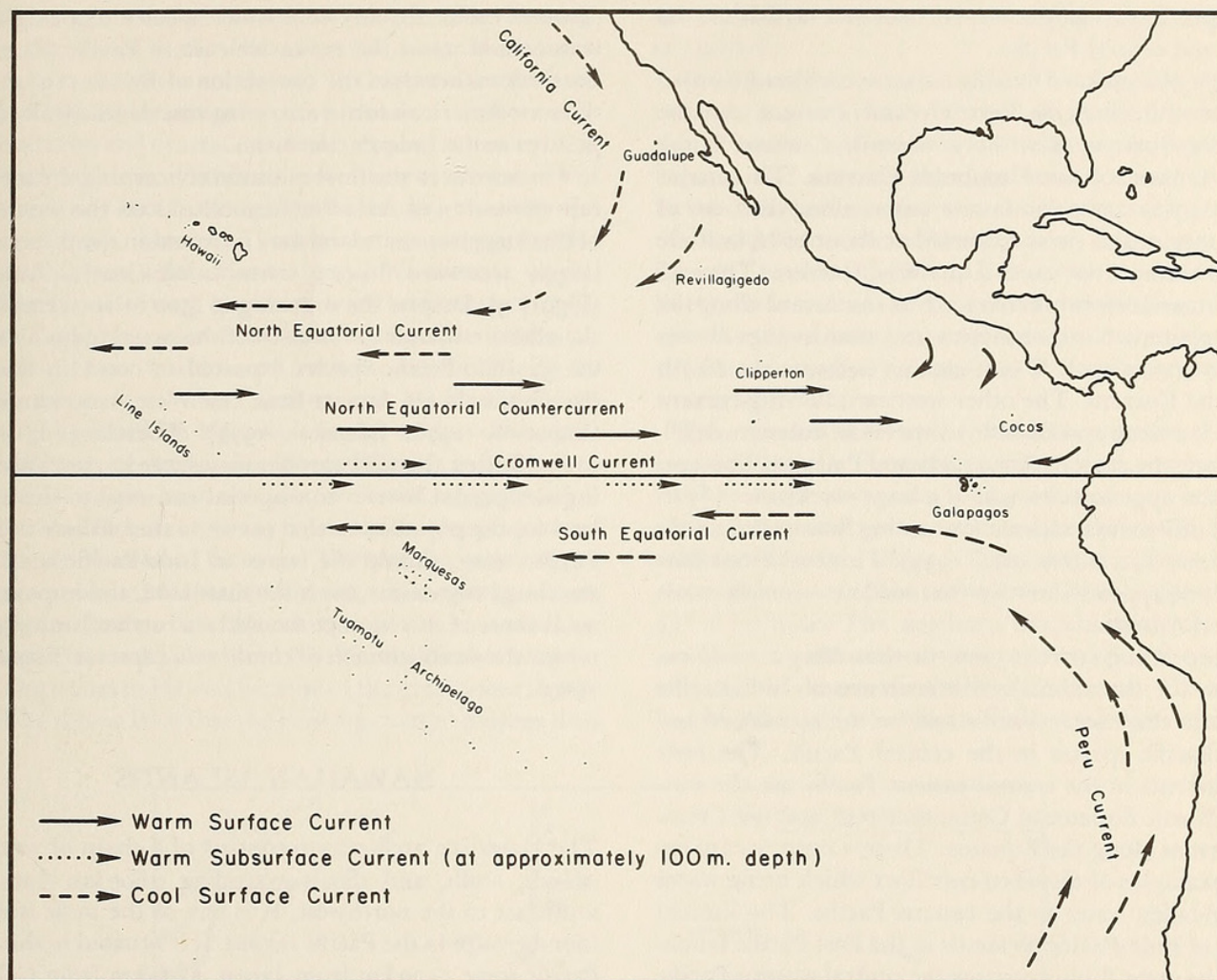


Figure 2

Major Ocean Currents in the Eastern Central Pacific
(modified from AMERSON & SHELTON, 1976)

(3) a smaller region of westward flowing currents originating near the coast of Central America and disappearing about 800 km off the coast.

The warm east-flowing water consists of 2 well-defined currents: North Equatorial Countercurrent and the Cromwell Current. The North Equatorial Countercurrent originates in the western and central Pacific and flows eastward approximately 5° to 7° N of the equator. The strength of the North Equatorial Countercurrent varies considerably during the year. Particularly during the summer months (actually July through November) it is especially well-developed and may have velocities up to 2 km per hour. This warm surface current brings plankton-laden water from

the central Pacific to approximately 1100 km or 1300 km off the coast of Central America. In this region, it becomes ill-defined and disappears.

The Cromwell Current is a narrow, well-defined tongue of easterly flowing water along the equator at a depth of approximately 100 m. This rapidly moving current may attain velocities of 5 km an hour (TAFT, *et al.*, 1974). SCHELTEMA (1968) discussed an analogous current in the Atlantic and noted large numbers of larvae were transported by it eastward across the Atlantic and he also pointed out its possible significance to biogeography. There are not data available about plankton distribution by the Cromwell Current in the Pacific, but presumably it

is an important conveyor of plankton eastward from the western and central Pacific.

The major westward flowing currents consist of 2 broad cool water currents: the Peru Oceanic Current and the California Current. The Peru Oceanic Current is the north extension of the Humboldt Current. This major current carries cool subantarctic waters along the coast of South America and turns westward at about 10° S latitude and then becomes the South Equatorial Current. The cool temperature California Current flows southward along the coast of western North America and then swings almost due west at about 10° N latitude and becomes the North Equatorial Current. The other westward flowing current consists of a weak and ill-defined system of currents developing along the coast of Guatemala and Panama. This current system appears to consist of a large clockwise eddy in the Gulf of Panama with the prevailing flow to the southwest (CROMWELL & BENNETT, 1959). This southwest flow gradually disappears about 800 to 1000 km west of the coast of Central America.

The prevailing current patterns thus offer a ready explanation for the anomalous occurrence of Indo-Pacific mollusks in the eastern Pacific and for the absence of any eastern Pacific species in the central Pacific. The only warm currents in the central eastern Pacific are the east-flowing North Equatorial Countercurrent and the Cromwell Current along the Equator. These 2 currents are excellent examples of dispersal corridors which bring warm plankton-laden water to the eastern Pacific. The limited number of Indo-Pacific elements in the East Pacific faunas reflects the great distance across the central-eastern Pacific Ocean. Only those benthic species with extremely long pelagic larval stages are able to cross this vast expanse of open water. The absence of more Indo-Pacific species on these offshore islands is probably related to the lack of suitable habitats with available ecological niches and specific food sources, and to competitive pressures (*cf.* DEICHMANN, 1959; EMERSON, 1967; BACKUS, 1968; DANA, 1975; VERMEIJ, 1978).

The absence of warm westward flowing currents has prevented Panamic species with long pelagic stages from reaching the Central Pacific. The only westward flowing currents across the East-Central Pacific are the cool temperate California and Peru Oceanic currents. Any cool water species with a long distance larval stage would be unable to find suitable cool temperate habitats if it reaches the nearest land or shallow-water areas (Marquesas or Line Islands) in the central Pacific. Therefore, the absence of eastern Pacific faunal elements in the central Pacific seems to reflect: (1) no warm westward flowing current for tropical Panamic species and (2) an absence of suitable habitats, including the lack of non-coral, hard substrates

(BACKUS, 1968), for any cool water species that might be transported across the expansive eastern Pacific (Ekman's Barrier), rather than the contention of BRIGGS (1974) that the west American forms are not as interfaunistically competitive as the Indo-Pacific forms.

The answer to the final question concerning the meager representation of Indo-Pacific mollusks on the west coast of the American mainland may be found in the presence of largely westward flowing currents off Central America (Figure 3). Despite the narrow gap (500 to 1000 km) from the offshore islands to the coast of the mainland only 16 of the 52 Indo-Pacific species reported to occur in Eastern Pacific waters are known from the West American coast (EMERSON, 1978; BERTSCH, 1973). Therefore, it seems probable that the westward flowing shore currents are acting as a partial barrier to dispersal eastward to the mainland for the populations that occur on the offshore islands. Furthermore, should the larvae of Indo-Pacific coral-reef associated organisms reach the mainland, the impoverishment there of this biotope would be a further limiting factor for the establishment of coral-loving species (EMERSON, 1967).

HAWAIIAN ISLANDS

The Hawaiian archipelago consists of a chain of volcanic islands, atolls, and shoals extending 2600 km from the southeast to the northwest. It is one of the most isolated island groups in the Pacific region. It is situated in the mid-Pacific some 5400 km from Japan, 3200 km from California and 700 km from the nearest island.

The Hawaiian molluscan fauna is characterized by a number of anomalous features. The composition of the Indo-Pacific faunal province within the Pacific Basin may be divided into 2 major elements, the Western Pacific and Central Pacific elements. Normally, the farther east an island group is located, the smaller is the percentage of Western Indo-Pacific species (KAY, 1967). The Hawaiian islands, although the most eastward located island group, have an anomalously high percentage of Western Pacific species. KAY (1967) further points out that the Hawaiian fauna is relatively small, consisting of only about 900 species. Faunas from insular groups in the western Pacific at approximately the same longitude normally have 2 to 3 times as many species. The ratio of gastropods to bivalves in the Hawaiian Islands conforms to Kay's observation that the farther east an island group is, the higher the ratio of gastropods to bivalves becomes. Lastly, the percentage of endemic species in the Hawaiian fauna is significantly large, approaching 20%, for insular faunas in the Indo-Pacific.

Following the classical approach to insular biogeography, the origin of the Hawaiian fauna would be interpreted to be from the southwest. Immigrants would have reached Hawaii by using the many islands or seamounts in the southwest and central Pacific as stepping stones in their eastward radiation. This is the most likely case for much of the terrestrial biota, though aerial immigration by the agency of birds, insects and cyclonic winds is suggested for the smaller land snails (SOLEM, 1974; VAGVOLGYI, 1976), but these vehicles were largely rejected by CROIZAT (1978). CLARK (1949) expressed the opinion that the Hawaiian ophiuroid fauna was derived from the central Pacific by insular hopping via the Caroline and Marshall Islands. KAY (1967), based on MENARD'S (1964) studies of the geological history of the Pacific, adopted Clark's hypothesis of a center of origin from the southwest and suggested that the Marcus-Necker ridge may have acted as stepping stones for introduction from the west. The present water depth of the crest of the Marcus-Necker ridge is an average depth of 1463 to 1828 m. It is difficult to conceive that shallow-water species could have used the Marcus-Necker ridge as stepping stones to Hawaii because of the great water depth. It will be shown later that the existing current pattern does

not support the thesis for larval drifting from the southwest to Hawaii.

Insular marine communities are less dependent than terrestrial communities on chance dispersal. The composition of insular marine communities depends largely on the location and distance from the nearest source of pelagic larvae. Since oceanic currents constantly transport larvae, the composition of an island marine fauna can be predicted. The closer the island is to the source area, the more likely the faunas of the 2 areas will be the same. The farther the island is from source area the more depauperate the fauna is and its composition is dominated by species with teleplanic larvae.

Examination of oceanic circulation patterns (Figure 3) suggests that the Hawaiian marine fauna was largely derived from the west across the 5400 km of open ocean. The warm Kuroshio Current is the major current in the western North Pacific, where it flows northeast from Formosa along Japan and splits into 2 branches at approximately 35° N latitude. The northern branch continues flowing northward, gradually turning southward in the north Pacific, and it becomes the California Current. The southern branch (Kuroshio Southern Extension) flows almost due

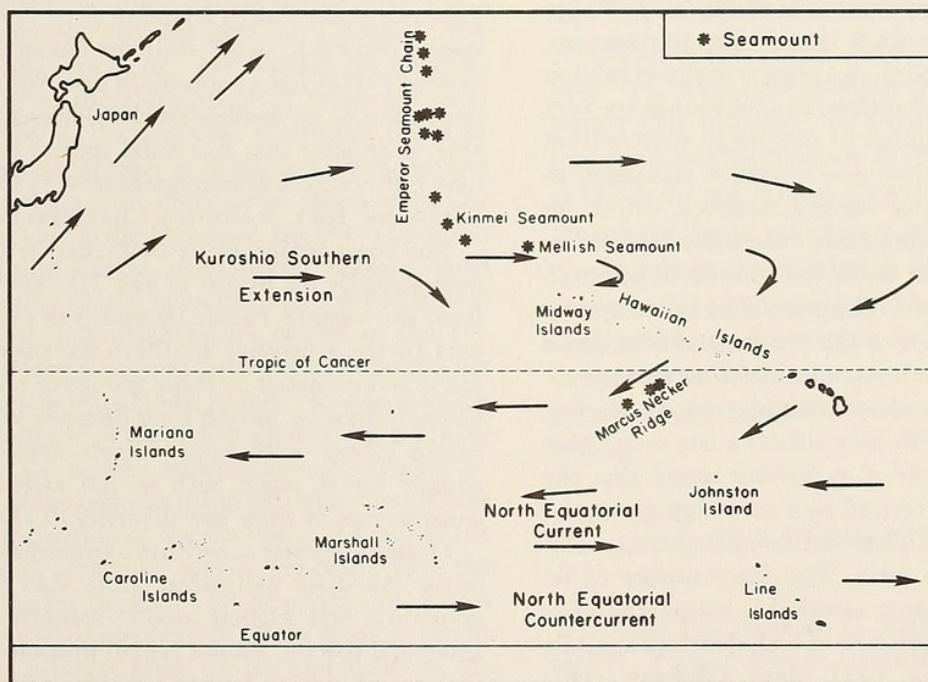


Figure 3

Major Ocean Currents in the Western Central Pacific
(modified from AMERSON & SHELTON, 1976)

east. In the vicinity of longitude 155° to 160° E, a considerable amount of water is deflected southward forming the Kuroshio Countercurrent (SVERDRUP, *et al.*, 1942). By this vehicle a large amount of warm tropical plankton-laden water from the western Pacific is brought to the region around Hawaii.

Johnston Island, located 720 km to the southwest of Hawaii, lies in the westward flowing North Equatorial Current. The northernmost Line Islands lie in the east flowing Equatorial Countercurrent and had attained this position before the end of the Pliocene (DANA, 1975). Any larvae originating from these islands are transported by the prevailing currents away from Hawaii. It therefore seems highly unlikely from oceanographic evidence that the modern Hawaiian molluscan faunas originated from the southwest.

It is interesting to note that the molluscan fauna of Johnston Island is very closely related to Hawaiian faunas (REHDER, *in* AMERSON & SHELTON, 1976). Because of its location down current from Hawaii (Figure 2), it seems likely that instead of acting as a filter bridge for migration to Hawaii (AMERSON & SHELTON, 1976), its fauna was largely derived from the Midway-Hawaiian chain.

A western Indo-Pacific source area for the modern Hawaiian molluscan faunas by means of pelagic larvae is supported by biological evidence as recorded by the composition of the fauna. KAY (1967), in a review of the Hawaiian molluscan faunas, noted that these insular faunas are very attenuated. The total number of molluscan species from Hawaii is slightly more than 900 species as compared to "... New South Wales and western America, which are about the same latitude above and below the Equator as the Hawaiian chain, have molluscan faunas of approximately 2000 species, in the Philippines about 3000 species ... Okinawa which is close to the continental area, has a molluscan fauna of about 1700 species." The most probable cause for this observed attenuation may be the fact that only those species with long distance larvae are able to cross the western Pacific. Kay further noted that the Hawaiian fauna is characterized by a very high gastropod to bivalve ratio (Table 1). There are two possible explanations for this anomalous ratio. The low number of bivalves may reflect the absence of suitable habitats in insular situations, especially the lack of well-developed, sandy substrates (THORSON, 1950; TAKI, 1953). THORSON (1961) stated that the bivalves were "... among all the groups studied ... [the] one most unfit for long-distance transportation." Therefore, if the source of the fauna is from the west, it would be expected that the number of bivalves reaching Hawaii would be low. In addition, the diversity of the intertidal Hawaiian fauna is quite low. This low

Table 1

Composition of modern marine molluscan fauna of Hawaii (modified from Kay, 1967).

Class	No. of Species	Percentage of Hawaiian Marine Mollusca
Cephalopoda	15	2
Amphineura	5	1
Scaphopoda	9	1
Bivalvia	150	16
Gastropoda		
Archaeogastropoda	38	4
Mesogastropoda	262	29
Neogastropoda	254	29
Opisthobranchia	165	18
		80
Total	719	100%

diversity is clearly illustrated by comparing the diversity of the amphineuran fauna of Hawaii (5 species) with that of other warm water regions in the Pacific. The Aupourian Province of the North Island of New Zealand contains 32 species (POWELL, 1958) while the Panamic Province of the eastern Pacific has 51 species (KEEN, 1971). From the limited number of molluscan developmental studies available, it appears that intertidal species in general tend to have either direct development or very short veliger stages (THORSON, 1961; RADWIN & CHAMBERLIN, 1973).

The composition of its molluscan fauna seems to support strongly an origin of the Hawaiian marine faunas from the western Pacific by means of pelagic larval transport by the Kuroshio Southern Extension Current. The fauna is dominated by those groups of mollusks which are characterized by having long distance larvae. Those molluscan groups with either direct development or short pelagic larval stages such as the archaeogastropods are conspicuous by their low diversity (Table 1).

Endemic species constitute a prominent element (20%) of the Hawaiian molluscan fauna. KAY (1967) noted that endemism was highest among western Indo-Pacific and intertidal species. BRIGGS (1966) proposed that insular endemism of marine faunas could be related to changes of sea temperatures during the last glacial period. "Those islands that demonstrate the least amount of endemism were probably exposed to the greatest decline in surface temperatures." In those insular regions where significant temperature changes occurred, the fauna were displaced and they have only recently been repopulated. The length

of time since the repopulation presumably has not been sufficient for evolutionary changes to have occurred. Conversely, in insular areas where temperatures have remained constant for long periods, there would supposedly be sufficient time for new taxa to evolve and these areas would be characterized by high endemism. This may have been the cause of the endemism in Hawaii, but this diversity may also be explained by changes in sea level (ZINSMEISTER, 1973).

Eustatic fluctuation in sea level during the Pleistocene approached 200 m. These changes resulted in the shallow water seamounts north of Hawaii becoming islands or shoals. The present depth of the Mellish Seamount at the extreme north end of the Hawaiian archipelago is 117 m and the Kinmei Seamount (southern end of Emperor Seamount chain) has several peaks with water depths of less than 183 m. The presence of islands and shoals in the Pleistocene would have reduced the distance of open sea between the present islands in the western Pacific and the modern Hawaiian Islands. This would have enabled species with relatively short pelagic larval stages to use these islands as filter bridges in their eastward journey. Removal of these stepping stones with the rise of sea level would have effected molluscan dispersal across the western Pacific by widening distances between insular land in either of 2 ways: (1) caused the development of a barrier (distance) to all drifting larvae, or (2) caused the development of a barrier to those species with relatively short pelagic larva stages. In the first case, endemism could be explained by differential rates of evolution. In the second case, only those species with short larval stages would be prevented from reaching the Hawaiian Islands. The result would be that those species with shorter pelagic stages would be effectively isolated from the western Pacific and would follow their own evolutionary course in the Hawaiian Islands. Species with long distance larvae would not be affected by the removal of these islands and would retain their genetic identity with the western Pacific faunas. KAY (1967) noted that the highest endemism occurs in the intertidal species. This would be the group that would show the effect of the formation of the barrier at the end of the Pleistocene because intertidal species generally have the shortest pelagic larval period. The development of this partial filter to eastward dispersal from the western Pacific appears to be the primary cause for the endemism in the Hawaiian molluscan fauna. Although the level of endemism is relatively high (20%), these elements are largely limited to taxa on the specific and sub-specific level, which suggest a relatively recent formation of the barrier.

CONCLUSION

The dynamics of passive dispersal by currents of the larval forms of marine organisms are related to the inability of these larvae to control actively their movements. Larvae may be dispersed by currents only parallel to and with the direction of the flow. Currents may be viewed as one-way corridors of dispersal. The direction of circulation, not spatial distance, is the most critical factor in determining the distribution by currents of these species in the sea. The length of the larval stage and the distance between suitable habitats also serve to limit larval dispersal and to act as a distributional survival factor for species. The biogeographic distribution of benthic invertebrates with pelagic larvae thus may be viewed as a reflection of oceanic circulation patterns operating temporally as a dispersal mechanism. The role of passive dispersal of hemipelagic invertebrates is illustrated by modern and past faunistic distributional patterns occurring in the tropical Pacific Ocean.

The role of passive dispersal as a vehicle for the introduction of faunal elements into existing and past assemblages of organisms must also be interpreted in the light of geologic events within a framework of chronology. Without temporal considerations, the student of biogeography may draw erroneous conclusions owing to the multiplicity of factors that influence distribution. A realization of the significance of the function of currents on the distribution of life in the sea, however, provides an additional tool for the paleontologist to interpret biogeographic history. Based on the present knowledge of the oceanic basins and the position of the continents for the most of the Phanerozoic, it is possible to approximate the general circulations within the basins. Utilization of the principles of passive dispersal should permit a better understanding of paleobiology.

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