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THE ANIMAL ECOLOGY OF THE COLD SPRING SAND SPIT

THE ANIMAL ECOLOGY OF THE COLD SPRING SAND SPIT, WITH REMARKS ON THE THEORY OF ADAPTATION

C. B. Davenport

Cold Spring sand spit runs from the west shore of Cold Spring Harbor, Long Island, eastward to within 100 or 200 feet of the eastern shore of the harbor. The history of the formation of the spit is briefly this: Cold Spring Harbor (Fig. 1) is a fiord-like re-entrant about ten kilometers long, emptying at its lower or northern end into Long Island Sound about one-fifth of the way from Hell Gate at New York city to "The Race," south of New London. The Sound itself, 175 kilometers long by 35 kilometers broad at its widest point, and having a prevailing depth of about 30 meters, receives large streams of water from the north — the Connecticut, Housatonic, and Quinnipiac rivers, and many minor ones. These give it a low specific gravity, 1.020, and a muddy bottom. Long Island is covered over its northern part with glacial débris, forming hills that rise to a height of over 100 meters. Between these hills streams flowing north have cut valleys and, in the general sinking to which the whole area has been subjected, these valleys have become drowned, forming long, straight but shallow harbors of which Cold Spring Harbor is an excellent type (Shaler, 1902). Into the head of the harbor a small stream flows with a summer discharge of not far from five cubic meters per minute. This stream is dammed thrice along its course of two miles, so that the deposit that it carries into the basin above the beach is only fine mud.

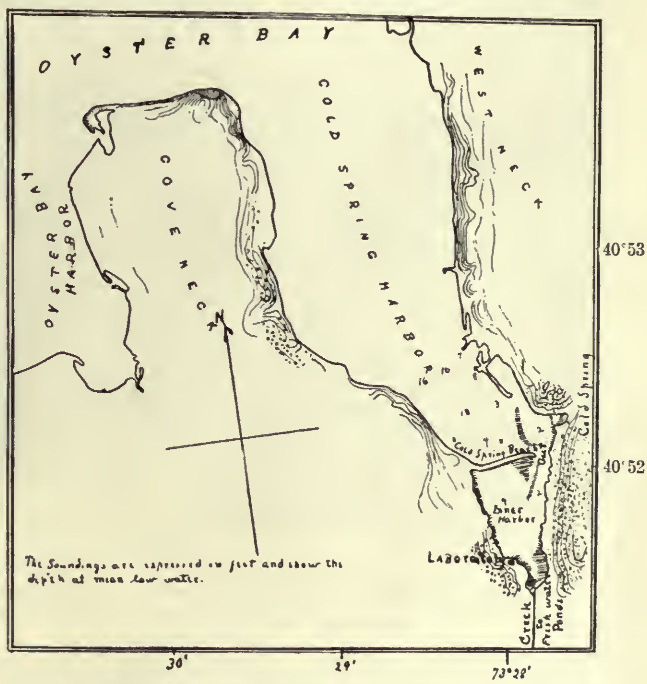

Fig. 1.—Map of Cold Spring Harbor, showing spit (Cold Spring Beach).

The effective winds at Cold Spring Harbor blow from the northeast and, striking with violence upon the bluffs on the west side of the harbor, tend to wear them away. The currents setting southward then carry this eroded material until it is dropped in the shallow and protected waters of the upper end of the harbor, where the sand spit or "beach" is now found. The inner harbor thus cut off is about 800 meters long by 600 wide, and at mean high tide has a prevailing depth of less than 2.5 meters. Its sandy bottom is for the most part covered with half a meter of fine black mud. This is largely exposed at low tide, and supports an abundant growth of "sea cabbage" (Ulva). The specific gravity of the water at high tide varies from 1.018 near the entrance to the inner harbor to 1.005 at the surface near the inlet of the creek. Near the "gut" where the tides rush in and out of the inner harbor the bottom is kept scoured and consists of gravel and stones. Outside the sand spit the water has a pre-

FIG. 2.—View of Cold Spring Harbor at high tide looking north. The inner harbor is in the foreground; between it and the outer harbor is seen the sand spit. Close to the sand spit on the inside is a fringe of Spartina polystachya.

vailing specific gravity of 1.019 and is about 6 to 8 meters deep at high water. A bar (Fig. 2), almost submerged at high tide and consisting largely of hard mud, has formed opposite to the outer entrance to the gut and affords a "shallow sea" fauna.

The sand spit itself (Figs. 2 and 3) is 660 meters long and varies in width from 80 meters at its western end to 15 meters at its eastern end at high water. The prevailing width is about 40 meters. The highest part of the spit is about one meter above mean high tide, and the average height of tide is 2.4 meters. The slope is gradual on the outside (north side), it being 40 meters from high to low water at the western third of the spit. The slope increases to 2.4 meters in 15 at the eastern end. The material of which the spit is built is sand, which at the western end contains much gravel, apparently because of the greater carrying power of the surf, which is highest here. At the gut the sand is very coarse on account of the rushing tide. In the middle stretches of the beach the sand is finer. On the inner face of the spit mud is deposited. On account of the sandy beach and the currents and surf that are washing it all the time, no plants grow on the outside of the sand spit between average tides. On the inside of the spit, on the other hand, the marsh grass, Spartina, finds abundant foothold. All these facts have an important influence on the distribution of the animals of the sand spit. Indeed, for the purposes of this account of the fauna of the spit it will be necessary to treat separately its outer and inner margins and its tip, just because the conditions are so different in the three situations.

FIG. 3.—View of sand spit taken near western end looking east. Terrestrial border zone with Ammophyla in the foreground. The outer beach with the storm bluff, wreckage-strewn upper beach, and lower beach. At the right the inner beach, passing into mud flats at the edge of which Spartina polystachya is growing.

A. ANIMALS OF THE OUTER BEACH

The outer beach may, for our purposes, be divided into three zones which we may herein designate as : (1) the submerged zone; (2) the lower beach; and (3) the upper beach. The submerged zone includes all that portion of the beach that lies below mean low tide, but which may be exposed by the lowest spring tides combined with southerly winds (Fig. 4). It is a region that is normally covered with water; it is the very margin of the shallow sea. The lower beach is that zone which lies between mean low tide and mean high tide. It is the zone that is twice each day exposed to the air and submerged. It passes without any sharp break into the submerged zone (Figs. 4 and 5). The upper beach is limited on the one hand by the line of débris that marks the average high tide, and on the other by a bluff, half a meter high, that has been cut by storms (Fig. 5).

I. FAUNA OF THE SUBMERGED ZONE

The animals that live below the high-tide line may be considered under four heads: (*a*) sessile species, (*b*) crawling species, (*c*) burrowing species, and (*d*) swimming species.

a. The sessile species of animals, inhabiting the lower beach, include certain molluscs, especially bivalves, or Lamellibranchiata. All the lamellibranchs feed on minute particles of organic matter: Algæ, Infusoria, and decaying bits of organisms.

FIG. 4.—Photograph of lower beach, north side of sand spit, near the eastern end, at very low tide. The gut is seen in the background. At the water's edge (submerged zone) is a dense growth of the alga Enteromorpha. The naked lower beach is thickly peopled with the mud snail, Nassa obsoleta, visible as dots in the photograph.

The silt brought down by the creek is rich in such material and the algæ thrive on the mud flats, consequently these flats and the shallow sea around the flats are especially favorable feeding-grounds for these molluscs. Here occur oysters (Ostrea virginiana) in a semi-domesticated state. They normally attach themselves to some solid object while still young, but those of Cold Spring Harbor have been mostly transplanted and lie loose in the shallow waters, but altogether incapable of movement or of any other defense than that provided by their two thick valves. Here also occurs the scallop (Pecten irradians), which attaches itself while yet less than two weeks old, in the middle of August. The attachment is chiefly to eel-grass or to small stones. About the middle of September the scallops migrate into the inner harbor to live on the mud-flats like the oyster, but they never lose their power of free migration. The jingle shells (Anomia simplex) are permanently attached to stones or larger shells, such as Pecten, from early life. On the lower beach one also finds two species of Arca (Arca transversa and Arca pexata); the hen-clams, Mactra solidissima and Mactra lateralis; the hard clam, Venus mercenaria; and Liocardium mortoni—all lying on or imbedded in the muddy bottom. Here also are found certain species of lamellibranchs that burrow in the mud or sand and, to facilitate that burrowing, have become elongated; namely, the soft-shelled clam, Mya arenaria; the razor clam, Ensis americana, and Solenomya velum. This great group of bivalves represents then a society of animals that are fairly common because of favorable food conditions, but very helpless and much exposed to predaceous animals, were it not for their hard shell or their habit of burrowing into the mud.

b. The crawling species belong chiefly to the three groups of Mollusca, Echinoderma, and Crustacea. The crawling molluscs are slow-moving snails (Gastropoda) which are there partly to feed on decaying animal and vegetable matter, partly to feed on the growing Ulva, and partly to prey upon such living animals, chiefly bivalves, as have no means of escape. The chief omnivorous and carrion snail is the mud snail, Nassa obsoleta (Fig 4), which is abundant everywhere and even remains exposed on the middle beach at low tide, if busy feeding on a dead oyster. The little snails, Anachis avara and Astyris lunata, feed on the Ulva, or sea lettuce. The carnivorous species are of larger size and include two Muricidæ, Eupleura caudata and Urosalpinx cinerea ("oyster-drill"), and the great whelks, Fulgur caniculatum and Fulgur carica. All these feed upon oysters, scallops, and other surface bivalves by drilling holes through the shell. Two species of Naticidæ, Neverita duplicata and Lunatia heros, seek out the burrowing lamellibranchs, and so we find them burrowing into the sand. Then, too, they find in the sand of the beach the proper material for their egg cases, which are made out of agglutinated sand molded in the shape of a spiral collar. The crawling echinoderms are chiefly the starfishes, which are here because of the oysters and other bivalves upon which they prey. They cannot bore through the oyster's shell, and so they smother it until it is forced to open its valves for fresh water. The crawling Crustacea, finally, feed on organic débris of all sorts. Here belong the crabs, such as the three spider crabs, Libinia canaliculata, Libinia emarginata, and Libinia dubia, of which the latter comes farthest in-shore. Here, too, are the three mud crabs, Panopeus depresus, Panopeus herbstii, and Panopeus sayi, of which three the latter is found nearest the sand spit. On the very edge of the submerged zone are found also the two hermit crabs; the small one, Eupagurus longicarpus, finds protection for its abdomen in the cast-off shells of the small gastropods Nassa and Anachis. The large species, Eupagurus pollicaris, occupies such large shells as those of Lunatia heros and Fulgur carica. These scavengers, carrying their borrowed shells behind them, travel quickly along, but just below, the edge of the water, seeking for dead fish and other organic matter that may be resting there. Finally, the horseshoe crab, Limulus polyphemus, the largest and most aberrant of our Crustacea, will be seen, especially during June, traveling over the shallow water and occasionally coming to land to lay its eggs in the sand.

c. *The burrowing animals* of the submerged zone constitute a remarkable fauna of, for the most part, elongated animals. We have already seen that many molluscs burrow. So do a few sea anemones, such as the white-armed sea anemone, Sagartia leucolena, and the flesh-colored or white Halocampa producta. These sea anemones seem to feed on bits of organic remains, of which the sand is full. The other burrowers are here for a similar purpose; the circumpolar sea cucumber, Synapta inhærens; the worm that shows affinities with vertebrates, Balanoglossus Kowalevskii; two nemertines, Cerebratulus leidyi and Cerebratulus lacteus; and some seventeen different kinds of jointed worms, Annelida. All these find shelter, moisture, and food in the sand and mud beneath the sea bottom. But their immunity from attack is not complete, for as the moles have followed the earthworms and insect larvæ into the subaerial ground, so have several predaceous Crustacea followed the annelids into the mud. These are: the mantis shrimp, Squilla empusa, which is only a little smaller than the lobster, and Callianassa stimpsoni and Gebia affinis, that are somewhat smaller than a large crayfish.

d. *The swimming animals* are partly scavengers and partly predaceous. To the first class belong the prawn Palæmonetes vulgaris, which scours the edge of the tide for floating débris; and also the swimming crabs, the blue crab, Callinectes hastatus, and the commoner "lady crab," Platyonichus ocellatus. Here, too, we may place the little killifishes, Fundulus, although these pick up many live shore snails. The majority of the fishes are predaceous, feeding on the crawling and even the burrowing species that I have enumerated. The "skates" that lie close to the bottom catch burrowing worms and molluscs and also the snail Lunatia heros. The sand sharks and dogfish (Carcharias littoralis and Mustelus canis) gather in the spider crabs, squillas, and hermit crabs. The flounders, likewise, living close to the bottom, get Gebia and the prawns. The toad-fish, which lays its eggs in old shoes or in tin cans or under stones, feeds on the mud snail, Nassa, on crabs, and on prawns. Thus we see that in the shallow sea each species that occurs is present on account of particular relations that it bears to other species or to the non-living environment. The presence of the sharks is determined by that of the squillas, the squillas by the worms, the worms by the decaying vegetation, this by the living vegetation, and this by the salts and the nitrogenous food brought down by the creek from the valley above. This microcosm of the submerged zone affects in turn the lower and the upper beaches.

II. THE FAUNA OF THE LOWER BEACH

As already stated, the lower beach is a zone where aquatic and terrestrial conditions alternate every day. On this account, and on account of the sand, it is an area devoid of all living vegetation excepting the unicellular algæ that grow upon the stones (Fig. 4). It is also a region where oxygenation is combined with abundant moisture, so that conditions peculiarly favorable for respiration would seem to be afforded.

A fine layer of silt is dropped over the whole surface with each flood tide, affording thus abundant but microscopic food. But, on the other hand, it is a region of great exposure to terrestrial animals; so that only the stratum a little below the surface offers great safety. Also the lower beach is a region of wave action which makes it difficult for animals to secure a permanent place on it. Finally, and most important of all, the waves and currents cause the sands to shift, and this adds to the difficulty of maintaining a foothold. Consequently there are but few animals living on the lower beach, and such as there are live a curious and very strenuous life.

All over the lower beach will be found, upon careful examination, large numbers of extremely minute and active insects belonging to the group of Thysanura. These are arctic forms of Collembola of the species Xenylla humicola, O. Fabr. and Isotoma besselsii, Pack., together with an occasional Anurida maritima, Guer.[1] These Collembola are feeding on the rich microscopic débris which has been dropped on the lower beach. Being insects, they are air breathers; and the question arises: What do they do when the tide comes in? To answer this question I made measurements of the area occupied by the Collembola at different stages of tide. At tides lower than one-half tide the upper limit of the Collombolan zone is about nineteen meters north of the storm-cut bluff, or about ten meters north (*i. e.*, seaward) of the mean high-tide line. The lower limit is about two meters from the momentary tide-line. As the tide retreats the lower limit follows, while the upper limit remains constant. Thus, on September 10, 1901, with falling tide, the following determinations were made:

Hour	Distance from Storm Bluff	
	Upper Limit of Collembola	Lower Limit of Collembola
3:10 P. M.	17.7 m.	28.4 m.
3:30 P. M.	17.7 m.	29.5 m.
4:50 P. M. (low-tide)	17.7 m.	31.1 m.

Note that the lower limit of the Collembola travels down *pari passu* with the tide.

As the tide rises, the Collembola tend to retreat before the edge of the water, so that they are even crowded together there. Thus, on September 10, at 7 A. M. (one-third tide, rising), the lower edge of the Collembolan zone was about three meters away from the water's edge. As the tide rises still higher they crawl into the sand, until, at high tide, most of the Collembola are under the sea. But not all of the Collembola are there. At high tide one finds some of them floating on the quiet water out

[1] For the determination of these species I am indebted to my friend, Dr. J. W. Folsom, of the University of Illinois. (*Cf.* Wahlgren, 1899; Folsom, 1901.)

at a distance of ten meters or more, and moving hither and thither upon the surface. We conclude then that the rising tide has caught up with certain of the little insects. They rest upon the surface of the water by virtue of numberless fine hairs with which they are covered, in which the air is entangled so that the bodies of the insects are prevented from getting wet These are chiefly Anurida.

A second species that occurs on the middle beach in great numbers during the latter part of June is the horseshoe crab, Limulus polyphemus. This occurs here because it lays its eggs in the sand of the beach, thereby reaping the advantage of the superior oxygenation afforded by this situation over sand constantly submerged. The eggs are laid in nests containing several hundred each. The eggs are oval and about two millimeters in diameter. Each is enveloped in a tough membrane so that the sand cannot injure it. The position of the nest may be detected by a slight depression in the surface over it, and by the absence of pebbles. Not all the middle beach is occupied by these nests, but only those regions where the sand is coarse enough to let water through readily, but not so gravelly as to make hard digging. The east end of the sand spit where the current flows swiftest affords the best conditions, and here the nests are crowded together. In June also one finds many carcasses of female horseshoe crabs that have died in consequence of oviposition; for, as in many other species, oviposition is accompanied by a great mortality. Most of these carcasses are eventually thrown up to the high-tide line, and their fate will be considered in connection with the fauna of the upper beach.

Finally, mention should be made of the great annelid, Nereis limbata, that occurs burrowing in the sand above low-water mark. This again is confined to the tip of the sand spit where oxygenation is best carried on.

III. THE FAUNA OF THE UPPER BEACH

The upper beach I shall define as the zone including the high-tide line and above to the storm bluff (Fig. 3 left, Fig. 5). This region is inhabited by a very few annual plants; its main characteristic, however, is the débris cast up by the sea (Fig. 5). All over the world the upper beach is the graveyard of the shallow sea. In this graveyard two sorts of remains are found: first, such as have been floating on the surface of the sea; and, second, such as have fallen to or were lying on the bottom of the shallow sea. The floating remains are carried in toward the shore by winds from the sea. If the sea is quiet, they are merely dropped at the time the tide begins to fall; consequently they mark the high-water line (Fig. 5). If the sea is heavy, the floating or drowned débris may be thrown against the upper part of the upper beach and even against the storm bluff. This flotsam and jetsam consists, in the first place, of such things as lumber and articles of wood and cork; fruits and seeds; bits of eel grass; stems of last year's marsh grass, Spartina; fronds of Ulva torn from the mud flats; jelly fishes; drowned insects, especially heavy-bodied beetles, which have probably been blown out to sea and been drowned or have fallen in during migration. The second class includes chiefly empty shells, whose inhabitants have perhaps met with a violent death through predaceous animals, or the smothering of a stirred up muddy bottom,[2] also the dead bodies of Crustacea, such as Limulus. This débris is piled up at the lower edge of the middle beach and is renewed twice a day. Especially, however, after a storm is the accumulation large. At such times and at certain seasons of the year one may meet with particular species in large numbers. Thus, early in September, 1901, as the young Pectens were swimming into the inner harbor, a combina-

FIG. 5.—Photograph of north side of sand spit, near the western end, at low tide. In the central foreground is the high-tide line, marked by a mass of débris. On the left is the gravelly lower beach; the middle beach and storm bluff are at the right.

tion of high tide and sea breeze left thousands of them stranded on the upper and even on the lower beach.[3] The drowned insects are largely leaf eaters (Chrysomelidæ, including the Colorado potato beetle) and, especially in the early summer, ladybirds (Coccinellidæ) of various species. All of these constitute a rich, frequently replenished food supply, the only disadvantage connected with it being the dangerous proximity of the sea, with its occasional very high tides and its storm-born breakers. As could have been anticipated, certain animals have come together to make use of this food material. Some are herbivorous, others are scavengers, and others still are predaceous.

[2] In March, 1890, the levee gave way on the left bank of the Mississippi river above New Orleans. The waters pouring through Lake Ponchartrain into western Mississippi Sound so stirred up the muddy bottom that the great beds of oysters of this region were killed. (Smith, 1894.)

[3] During a visit to Santa Rosa island, outside of Pensacola Bay, Florida, in March, 1902, I found the beach covered with thousands of Portuguese men-of-war (Physalia), and the floating gastropod, Janthina fragilis, thrown up by the southerly storms.

Of the herbivorous feeders on the wreckage of the sea may be mentioned, first of all, the Amphipoda, marine Crustacea which are so adapted to a terrestrial life that they are rarely submerged. At Cold Spring Harbor two species are found—the small, dark Orchestia agilis and the large, sand-colored Talorchestia longicornis. Both may be seen in great numbers by turning over some of the cast-up Ulva fronds, under which they live and upon which they feed. Here they dwell in a saturated atmosphere and so need no special modification of the respiratory apparatus to fit them for breathing air. They both burrow, also, forming holes varying from three to five millimeters in diameter in the fine sand under or slightly above the line of wreckage. These holes enable the amphipods to reach moisture, they prevent them from being swept away by the sea, and they may serve as nests for eggs. For some reason the Talorchestia only is found at the tip of the spit. If it be asked why these Amphipods have left the water thus to assume a half-terrestrial life, I think it is a sufficient answer to say, first, that they find here abundant food; second, that they are here comparatively immune from the attacks of their greatest enemies—the fish; and, third, that their organization permits them readily to assume a semi-terrestrial life, as is shown by the fact that some of their allies have become even more terrestrial than they. (Compare Talitrus platycheles, and Talitrus saltator, Semper, 1881, p. 188.) That the Talorchestia is no longer an aquatic animal is shown by the way it retreats before the tide, especially if abnormally high.

Secondly, rove-beetles (Staphylinidæ) of the genus Bledius are found in the débris. This terrestrial insect is here found side by side with the marine Talorchestia, even burrowing into the sand. It feeds upon decaying vegetable matter. A third organism found under the débris is a minute white earthworm of world-wide distribution. This is Enchytræus albidus Henle (Halodrilus littoralis of Verrill, 1873).

As the plant débris is being devoured by the amphipods, staphylinids, and Enchytræus, so the animal remains are being carried off by a number of scavengers. Among these the ants are the most important; there are two species of them. The first, Formica rufa var. obscuriventris Mayr, is reddish brown and about four millimeters long (see Emery, 1893). It digs holes in the sand in the upper part of the upper beach, the grains of sand being brought individually to the surface and deposited in a ring around the hole. This ant also occurs under the shelter of boards and logs. Immediately after the tide has begun to fall and dropped its burden of carcasses these ants sally forth in paths that run perpendicularly to the high-tide line and begin to seize and carry to their nests the drowned insects that have been left there stranded. A second species of ant has its home somewhat farther out of reach of the tide; but its habits are quite similar.

There is, however, a larger carrion fauna to be utilized. I have already referred to the dead horseshoe crabs and the dead molluscs that are left on the shore. These soon attract great numbers of the flesh flies (Sarcophaga carnaria) which lay their eggs in the carrion. A second fly with bronze abdomen (undetermined) is also found here. To test the quickness with which these flies accumulate I took a recently drowned turtle from the water at 3 P. M. July 7, and left it at the edge of the retreating tide. At 4:15 P. M. (wind south) I counted over thirty of the bronze flies upon it. It remains to be determined whether it is chiefly sight or smell that attracts them.

Underneath the carcasses of the horseshoe crabs one will find also large numbers of the carrion beetle, Necrophorus, and larvæ of the museum pests (Dermestidæ).

The rich fauna of carrion feeders and herbivorous and omnivorous species determines still another fauna, namely, a predaceous one. Thus, running spiders, almost as white as the sand, frequent the upper beach and sometimes pass down to the upper part of the lower beach. These belong to the species Lycosa cinerea — a species that occurs commonly in Europe also, and is by no means confined to the sand of *beaches*. I have seen them carrying off Orchestia toward the storm bluff. More powerful still are the robber flies (Asilidæ) which pounce upon carrion flies. Their path of flight is curved, and at the moment of alighting an offset is taken several centimeters to one side. Altogether the irregular flight seems well adapted to the end of putting the victim off its guard, like the curve in the path of the ball thrown by an expert baseball player. Tiger beetles also occur abundantly on the beach in the bright sunlight, especially in August and September. They are chiefly of the species Cicindela repanda Dej. They are the most rapid fliers among beetles and feed upon the other insects of the beach. Finally, all these insects must fall victim to the swift and powerful swallows which course up and down the beach, especially in the latter part of the afternoon.

On the upper part of the upper beach there occur also a few stragglers from the vegetation-grown top of the sand spit. Here one finds grasshoppers almost as white as the sand. The white color of this species seems partly determined by the color of the background, for placed in a cage on grass these spiders become darker, as experiments at the Biological Laboratory have repeatedly shown. Whether the grasshoppers feed upon the dead vegetation of the tide-line was not ascertained. Crickets, Gryllus abbreviatus, quite as black as those living in the grass, occur scatteringly on the upper beach; and under the waste lumber the sow-bug, Oniscus, which is only half adjusted to a terrestrial existence, finds a living on the water-soaked wood.

B. THE BEACH ON THE TIP OF THE SAND SPIT

The tip of the spit is transitional between the inner and the outer sides. Here the sandy beaches of the north side gradually pass over into the mud-flats of the south side with their thick growth of marsh grass, Spartina. Indeed, at the tip of the spit there is a constant struggle going on between the upbuilding tendencies of the Spartina, which tends not only to hold the mud in which it grows together, but also to accumulate additional silt, and the scouring away tendencies of the tide that rushes through the gut. Wherever a weak spot appears in the mass of Spartina there a channel becomes gradually worn through (Fig. 6). These channels gradually widen and may anastomose, and thus the Spartina be left on elevated hummocks, which would seem destined to become smaller and smaller until entirely washed away. But from this fate they are preserved by an interesting association. The current that rushes through the channels carries with it an abundant supply of microscopic food, such as lamellibranchs can make use of. This food is taken advantage of by the mussels which come to line the muddy banks on the channels, and form so close a wall that erosion is almost completely stopped (Fig. 6). Thus the mussels assist the Spartina in their constructive work. The mussels that line the banks are Modiola plicatula, Modiola

FIG. 6.—Photograph taken at the inside of the hook of the sand spit, looking north, at low tide, through one of the passages scoured out by the tidal currents. At the base of the Spartina patches, on the right, are seen some of the beds of mussels which protect the roots from exposure.

modiolus, and Mytilus edulis, the first-named being the most abundant. The channels have irregular bottoms in which shallow pools of water stand when the tide is out. Here the mud snails, Nassa obsoleta, aggregate, scarcely submerged. High up on the stems of the Spartinas, exposed to the air during perhaps half the day, are found clinging the Littorinas, whose lack of a siphon makes it necessary for them to keep out of the mud. Littorina rudis and Littorina palliata were still the prevailing species in 1898 (see Balch, 1899), but in 1901 Littorina littorea, which is rapidly advancing up the harbor, had gained a marked predominance.[4] The independence of the sea water that is exhibited at the tip of the sand spit is also illustrated in the marsh at the head of the harbor through which Cold Spring creek runs. On this marsh Littorina occurs

[4] This habit of clinging to rushes is even more exaggerated in the southern Littorina irrorata. For, in a visit to the Lagoon on Ship Island, Mississippi Sound, in March, 1902, I found nearly all of them living on the stems of the short marsh grass twenty to thirty centimeters above the water level and exposed to the sunlight. Cooke (1895, pp. 20, 93, 151, note) cites other cases of Littorina living out of water.

at places where it is submerged for only a short time at high tide and then under water that is nearly fresh. Littorina rudis behaves similarly in other parts of the world. Thus Fischer (1887, p. 182) states that at Trouville (Calvados) on the English Channel he has found L. rudis on rocks two meters above the other marine animals and moistened only by the highest tides. In fact, according to Simroth (1891, p. 84),

FIG. 7.—Photograph taken at half tide from the base of the sand spit, looking east, showing inner harbor, the hook of the spit, and the gut beyond.

species of Littorina pass the winter out of water with their gill chambers full of air. Littorina rudis, then, has evidently progressed far on the road toward adaptation to a terrestrial life—a road that the Pulmonata must have traveled long ago.

C. THE INNER EDGE OF THE SAND SPIT

Along the whole length of the inner beach, not far from the high-tide line, occur the holes of the fiddler crabs. These crabs belong to two species, namely, Gelasimus pugnax and Gelasimus pugilator. A remarkable thing in the distribution of these species is the fact that although their habitats are not markedly different their areas of distribution are so well defined that they hardly overlap. Both species occur at the edge of the Spartina. The pugnax is found all the way from the western, proximal end of the sand spit to about two-thirds of the way toward its eastern point. Then pugilator abruptly comes in. For a distance of a meter or so the two species occupy ground in common, and, so far as I could make out, peacefully. The pugnax alone occurs at the head of the inner harbor. It burrows in the banks at a level that is reached only by the high tides. Walking along the beach at high tide July 7, I found that many of the fiddlers had migrated to above the high-tide level. It is clear, I think, that they do not find submergence altogether agreeable, and it is probable that prolonged submergence would drown them as it does Ocypoda arenaria, the sand crab of the beaches south of Cape May. G. pugnax prefers the marshier ground and the higher water, and it is probably that preference which determines its spacial separation from pugilator on the sand spit.

D. THE TOP OF THE SAND SPIT (TERRESTRIAL BORDER ZONE)

Above the storm bluff on the outer beach, and at a less well-defined line on the inner beach, lies the zone of permanent vegetation in which certain shrubs have gained a foothold. Here the fauna at once assumes a strictly terrestrial aspect. No close ally, even, of a marine form occurs. On the contrary, the animals living on vegetation are precisely those species that occur in the fields, especially the plant feeders: the plant lice (Aphidæ), the leaf beetles (Chrysomelidæ), the bright-colored Buprestidæ, and the various blister beetles. On the sandy ground are sand-colored grasshoppers, sand-colored spiders, Lycosa cinerea, and also small black spiders (Lycosa communis; *cf.* Emerton, 1885), black crickets, and little red ants apparently identical with species that people the upper beach. Over the vegetation wandered, in early July, an abundance of the predaceous dragon-flies, a black wasp (Polistes), and an occasional dusk-flying butterfly (Hesperidæ)—quite the fauna of a meadow not far from water.

SUMMARY ON THE ANIMAL ECOLOGY OF COLD SPRING BEACH

The outer beach is a region of breakers where débris is thrown on the shore. The submerged zone is crowded with marine animals, some of which make their way out of the water and others of which contribute the débris with which the upper beach is strewn. The lower beach is covered with Collembola that feed upon microscopic organic débris and crawl into the sand at high tide. The line of débris is a rich feeding-ground for animals that live on vegetable matter and on carrion. The débris feeders—Amphipoda, staphylinids, earthworms, ants, carrion flies, necrophorous beetles, attract a predaceous fauna of spiders, robber flies, and tiger beetles. These predaceous species are fed upon, in turn, by the swallows.

The tip of the beach, where the marsh grass grows, is a region of swift currents which the lamellibranchs (mussels) find advantageous because of the food that the currents bring. The currents tend to wear away the spit, but the mussels grow so abundantly on the banks of the channels as in turn to protect these banks from further erosion.

The inside of the sand spit is a region of sedimentation. Plants grow here, and here the plant-feeding snails and fiddlers live. The organisms that are found on the beach are not accidentally there, nor is the fauna determined by causes remote and too complex to be unraveled. The fauna is determined by definite proximate causes of a simple sort that act, the world over, in the same way, and so give to a similar sea beach in other parts of the world a similar collection of animals — excepting that each species may be replaced by another.

COMPARISON OF COLD SPRING BEACH WITH THAT OF LAKE MICHIGAN NEAR CHICAGO

The question arises : How far is the fauna of the sea beach determined by the beach conditions of sand, sunlight, and proximity to a body of water with its strand zone of débris? Will beaches in general, whether of a fresh-water lake or of the sea, tend to have the same fauna? To test this question I have examined the fauna of the shore line of Lake Michigan, south of Jackson Park, Chicago. Here one finds a sandy beach essentially like that at Cold Spring Harbor. On one side extends a huge body of water which differs from that of the harbor chiefly in its lower specific gravity and in the absence of marked tides, but resembles it in its waves. We may recognize here a submerged beach and a terrestrial beach.

I. FAUNA OF THE SUBMERGED ZONE

This inundated part of the beach supports, as one would expect, a fauna the species of which are quite unlike those of the sea. Yet we may recognize a sessile fauna, a crawling fauna, and a swimming fauna.

a. The sessile fauna includes here, as in the sea, the lamellibranchs. These belong to two families, the Unionidæ and the Spheridæ. These, like their marine allies, feed on minute organic particles, chiefly algæ. The Unionidæ are the large forms and seem to take the place of the marine Mactra, Venus, and Mya. They occur in the streams and lakes of all parts of the northern hemisphere, but the group is best developed in North America. The Spheridæ are small, and take the place of the Nuculas of Cold Spring Harbor and Donax of our southern seashore. They are found in the streams and lakes of all countries.

b. Crawling animals belong chiefly to the groups of gastropod Mollusca and Crustacea — the Echinoderma being wholly absent. The snails are mostly small and seem to replace the Littorinas and the Rissoas of the seacoast. The principal crawling crustacean is the isopod Asellus communis, which lives on the wood and among the roots of the shore line. The group is, indeed, poorly represented here as compared with the sea. Burrowing animals seem to be almost entirely absent, possibly on account of the absence of such predaceous forms as occur in the sea.

c. The swimming animals are here, as in the sea, partly scavengers and partly predaceous. First of all we have in the water above the shore numerous Entomostraca. The prawns of the sea are replaced by a very closely related species, Palæmonetes exilipes, which may have gained the great lakes by the way of the Mississippi river, in which it is abundant. The marine lobster is replaced by the crayfishes (Cambarus propinquus and C. virilis). The predaceous forms are the fishes which feed largely upon the snails and the Crustacea.

II. FAUNA OF THE BEACH

In the tideless lake the lower and upper beaches are hardly to be distinguished. On the lake strand Collembola are found just as on the lower sea beach. In the line of débris that the waves deposit are found the wrecks of all the shallow-water forms of which I have spoken, and, in addition, the carcasses of vast numbers of insects that have fallen into the lake, have drowned, and are cast up by the waves. This wreckage line affords, then, just the feeding-ground for inland species that the marine species find on the coast. What animals do we find here? The burrowing Orchestidæ seem, indeed, to be absent, but there is a closely related species (Allorchestes) that lives in the shallow water. That it is not a beach burrower may be due to just these causes that have eliminated the burrowing habit in general. But under the débris rove-beetles and insect larvæ are to be found feeding on the vegetable matter. And small red ants build nests on the beach and visit the débris for the carcasses of insects. A similar carrion fly and carrion beetle (Necrophorous) occur. Feeding upon this fauna is a running spider (Lycosa cinerea) the same as that of the coast. Here, too, occur robber flies and tiger beetles, and even white grasshoppers. Thus the lake beach, having a similar strand zone of decaying vegetation and plant wreckage with the sea, has, at a distance of nine hundred miles from the sea, excepting certain strictly marine species, practically the same fauna as the sea. The conclusion to be drawn from this fact is the immense importance of habitat (*i. e.*, of environmental details) in determining similarity of fauna, or, in other words, the fauna of a point is, within limits, determined rather by the environmental conditions than by the geographical position of the point.

REMARKS ON THE THEORY OF ADAPTATION

Everyone must admit the fact of adaptation of the structures of animals to their environment. The generally accepted theory to account for this is that of Darwin and Wallace that a species coming into a new habitat gradually acquires a fitness to that habitat by the killing off of the less fit individuals born into the species. There are some cases, as, for instance, that of the leaf insects, that of the fungus beetle, and those of mimicry, that I can see no other explanation for but this, that an external condition existed first and a structure or coloration was acquired by the race that fitted or adjusted it to that external condition.

We must not, in accepting any theory as a true one, try to force it as a universal theory and become blinded to other possible theories. Now there is another and fundamentally different possible theory of adaptation, and this is that the structure existed first and a fitting environment was sought or fallen into by the species having the peculiar bodily condition. Thus the adaptive result is, on this theory, not due to a selection of structure fitting a given environment, but, on the contrary, a selection of an environment fitting a given structure. I shall now consider some special cases that are best explained on this theory. Thus, Eigenmann (1899) shows that the cave fishes, which in many points show an adaptation to the cave environment, are not to be thought of as having accidentally got into caves and as having subsequently gained a structure fitting them for that environment. But, on the contrary, as they all belong to one family, their getting into the caves was evidently not an accident. Moreover, this family includes species that are structurally especially fitted for cave life, even when they occur in regions where there are no caves and never have been any. They shun the light, and live in crevices and under stones. Their bodily conditions fit them for cave life and when, in their constant search for dark holes, some of them succeeded in getting into caves, they naturally thrived there.

Again, in many cases of parasitism among snails the radula is known to be absent altogether, and this has been accounted for by Cooke (1895) on the hypothesis that these snails lost their teeth through disuse. However, it is pointed out as a curious fact that the same absence of a radula occurs in species of Eulima known to be not parasitic. Cooke suggests the hypothesis that in cases like this the form must have derived from parasitic ancestors. It is equally probable that Eulima is a mollusc that will probably soon be driven to parasitism because it has no radula.

Now, that which is true for the cave animals, and probably true for edentulate snails, is illustrated time and time again in the animals of the beaches. We have seen that the Anurida are covered with fine hairs, which enable them to float upon the tide and thus keep them from drowning. Are not the fine hairs a remarkable adaptation to the necessities of the situation? They certainly are, but the probability is that the hairs were not developed to meet this situation at all; at least, such a coating of fine hairs is widespread among Collembola, and the hairs subserve a variety of functions. Thus, Schäffer (1898) finds that the long hairs protect the animal against the action of the sun's rays in the case of certain species that live on leaves; and the importance of such protection would seem to be great, for Absolon (1900) finds that certain cave forms of Collembola, which, so far as he describes them, seem to be scantily covered with hairs, are killed by a few minutes of exposure to sunlight. Hairs are, we may then say, common occurrences on the thin-skinned Collembola. The hairs are important to keep the thin skin from desiccation. Because the skin is thin, the Collembola favor damp or wet places; just because they are covered with hairs, they can float on the water; just because they can float on the water, they can live on the lower beach. Also, they find there their appropriate food. Having by some means got to the beach, they remain there, because they find the conditions existing on the beach peculiarly suitable.

This law is illustrated again by an inhabitant of the upper beach, Oniscus. Oniscus seems, on the whole, rather poorly adjusted to a terrestrial life. Its gills lack the well-developed tracheal chambers of the wood louse, Porcellio, and the pill bug, Armidillidium, its close relatives (Stoller, 1899). Correspondingly we find it only in moist situations, under logs, in cellars, in greenhouses, etc. On the other hand, Porcellio ratzburghii, Brandt, is a species in which all five pairs of outer gills possess tracheal chambers. As Stoller (1899) remarks: "This species lives in situations where the air is charged with moisture only in a moderate degree in excess of that of ordinary atmospheric air. Their habitat is under the bark of dead trees, and they may often be found a meter or more above the ground." Now, experiments that I have made show that a water-inhabiting isopod (Asellus), if taken out of the water, will go back into it if free to do so; and Porcellio, if put in water, will leave it for dry land, if free to do so. Similarly we may conclude that Oniscus chooses a situation that affords the requisite moisture. Shall we conclude that the reason why Oniscus has no tracheal chambers is the result of its living in a moist situation, or is it the cause? We find it where it is because it is hydrotactic. Now, is it hydrotactic because it has no lungs, or is it without lungs because it is hydrotactic? Certainly it would be rash to assert the latter, even though we cannot prove the former.

So likewise we find Nassa, which has a siphon to enable it to draw pure water from above the mud, living in the mud; whereas Littorina, which has no such siphon, clings to the stems of the marsh grass above the mud. Can we say that Littorina has no siphon because it clings to the marsh grass, or does it cling to the marsh grass because it has no siphon? I maintain that the latter is no less true than the former.

Let us consider still one other case. We have seen that the mussels cling to the banks of the channels in such numbers as to make a protecting wall. Of the advantageousness of that situation for the mussel as a lamellibranch there can be no doubt; abundant food and oxygen are brought to its doors every day. The wonder is that no other lamellibranchs than the mussel occupy this favorable situation. Why is this? It is because the mussels are the only species living about the sand spit that have a byssus in the adult stage. Lacking a byssus, the other species cannot attach themselves to the banks. Now, does Mytilus have a byssus because it tends to attach itself to banks, or, being provided with a byssus, was it led to take advantage of the favorable position offered? Did the situation or the organ precede? In this case we may see, I think, the necessity of the organ being well developed before the special habit (of attachment) could be exercised. However, it is quite likely that the byssus has been improved in the race by selection, and with every step of improvement the race has been able to take up a more and more advantageous habitat.

This brings us, indeed, to the most reasonable hypothesis of adaptation, namely, the combination of the improvement of the organ to meet the requirements of the environment, through selection, and of improvement of situation to meet the abilities of the organism. There have gone on, hand in hand, a selection of more appropriate organs and of more congenial habitats. Adaptation of organization to environment has been effected by the double process of selection by environment of the most appropriate organization and by the organism of the most congenial environment.

This hypothesis, I think, should be welcomed by those palæontologists who, like Osborn (1897), are led from their phylogenetic studies to conclude "that there are fundamental predispositions to vary in certain directions." They help out, too, I believe, the fundamentally important observations and experiment of DeVries (1901), who finds that race change is a series of steps, of mutations, that may often have no relation to adaptation; the adaptation comes later. For all those theories, in general, that assume that change of specific structure occurs independently of selection of the fittest, the hypothesis here proposed must be considered a welcome complement. It may be well to point out that the selection of a fitting environment is not confined to migratory animals. It is applicable to all organisms that have a means of dispersal. The seed that falls upon good ground—the race that gets into a favorable environment—will survive.

The theory may thus be summarized: The world contains numberless kinds of habitats, or environmental complexes, capable of supporting organisms. The number of kinds of organisms is very great; each lives in a habitat consonant with its structure. Each species is being widely dispersed, and, by chance, some members of a species get into an environment worse fitted for them; others into one better fitted. Those that get into the worse environment cannot compete with the species already present; those that get into a habitat that completely accords with their organization will probably thrive and may make room for themselves, even as the English sparrow has made room for itself in this country. This process may go on until the species is found only in the environment or environments suited to its organization. As Darwinism is called the theory of the survival of the fittest organisms, so this may be called the theory of segregation in the fittest environment.

In conclusion I repeat that the theory of segregation in the fittest environment does not replace that of survival of the fittest organism, but is complementary to it. It has this *raison d'être* that it shows how unadaptive mutations may become adaptive *if only they can find their proper place in nature.*

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