The Ecology of a Salt-Marsh.

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With 17 Figures in the Text.

CONTENTS.

INTRODUCTION.

IT has long been known that most aquatic animals are sensitive to alterations in their environment, and that relatively small changes in the composition of the surrounding medium will cause serious physiological disturbances.

Earlier workers showed that many marine animals have body fluids which are approximately isotonic with sea water, and that dilution or concentration of the surrounding medium causes corresponding changes in their blood, and swelling or shrinkage of their tissues. Recent work, however, has shown that this is not true for all marine animals, but that certain of them can, to some extent, control the osmotic pressure of their body fluids. Those which can do so are able to survive in water of varying salinity, a few living as well in fresh water as in salt.

The means by which this is brought about are being investigated by an increasing number of workers, and the parts played in the regulatory mechanism by other factors in the environment, such as oxygen tension, hydrogen ion concentration, calcium content, are gradually being brought to light.

This tolerance of changes in the external medium is of special importance to animals attempting to colonise brackish-water habitats such as salt-marshes and estuaries, where the conditions of salinity in particular are continually fluctuating. In view of the attention that the problem is receiving at the present time, an investigation into the conditions in one type of brackish-water habitat, a salt-marsh, was begun. Owing to other work a complete record of conditions throughout the year could not be made, but it is hoped that sufficient data have been obtained to give a fairly accurate picture of the range of variation in the pools.

I wish to record my thanks to Professor J. H. Ashworth, F.R.S., in whose department the work was carried out, and particularly to Professor A. D. Hobson of Armstrong College, Newcastle-upon-Tyne, whose constant help and encouragement were of the greatest assistance at every stage of the work. I am also indebted to Dr. K. G. Blair, Dr. W. E. China, Dr. F. W. Edwards and Miss S. Finnegan, of the British Museum of Natural History, for the identification of the Coleoptera, Hemiptera, Diptera and Arachnida, and to Dr. P. Gray, of the Department of Zoology at Edinburgh, for the identification of the Copepods.

Literature.

Papers on the fauna of brackish water are numerous, but few of them are concerned with salt-marshes.

Hickson (1920) describes the occurrence of *Protohydra leuckarti* near Southampton, and mentions a few associated animals from the pools.

Robson (1920) gives details of the distribution of two species of Hydrobia in an Essex marsh.

Lambert (1930) gives a list of the species of animals found in the marsh ditches of the Thames estuary.

Ellis (1932) describes the fauna of a number of brackish ditches and pools in Norfolk. A few isolated observations on the conditions in the pools are given.

Lundbeck (1932) gives a detailed list of the fauna found in an extensive series of shallow lagoons and pools in North Germany.

Sick (1933) describes the distribution of a large number of species in certain brackish-water ditches in North Germany. He gives a few observations on the salinity and hydrogen ion concentration, and discusses the fauna of the ditches in relation to that of the adjacent part of the Baltic. He has also drawn up a table of species found in brackish waters in Northern Europe.

Nicol (1933), in a preliminary account of certain salt-marshes in Northumberland, gives a short list of species found in the pools, along with isolated observations on the hydrogen ion concentration and salinity.

Kevan (1934) describes a salt-marsh at Tynninghame in East Lothian, and gives a list of animals in it associated with a new variety of *Limopontia depressa*.

The following papers contain details of the fauna of larger areas of brackish water and of estuaries.

Johanssen (1918) gives an account of the fauna of the Randers Fjord carefully correlated with the salinity of the different regions.

Redeke (1922), in a monograph on the flora and fauna of the Zuider Zee, gives a short account of the hydrographical conditions and a detailed account of the species found.

Willer (1925 and 1931) compares the hydrography and fauna of the Frische Haff from the point of view of fisheries, with the conditions and fauna of a similar, though salter, body of water—the Kurische Haff—in the same neighbourhood.

Segerstrale (1934) describes the hydrography and changing conditions in several small arms of the Baltic, and correlates the fauna with the conditions.

The following papers are concerned with the fauna of estuaries.

Stammer (1928) gives an account of the fauna of the mouth of the Ryck.

Percival (1928) describes the fauna of the Rivers Lynher and Tamar.

Alexander (1930–31) gives a list of the species found in the estuary of the Tay.

The only detailed work on the conditions in salt-marsh pools is that of Gessner (1932), who made a series of observations at midnight and midday on the oxygen content, hydrogen ion concentration, temperature and "hardness" of the water. He found that at midday oxygen, pH and temperature are at a maximum, while the carbon dioxide and "hardness" are at a minimum, while the reverse is the case at midnight. The pools in which the observations were made were filled with dense masses of *Ranunculus baudottii*.

Methods.

A series of pools was chosen for investigation covering as far as possible the range of conditions which might be expected in the marsh, by reason of their position, nature of the bottom, presence or absence of algæ and diversity of fauna, and a record of conditions was kept for considerable periods of time, under widely different weather conditions. The marsh was visited at least twice a week, and the following factors investigated.

(*a*) Salinity.
(*b*) Oxygen content.
(*c*) Alkali reserve.
(*d*) Hydrogen ion concentration.
(*e*) Temperature.

The hydrogen ion concentration and the temperature were recorded in the field. For the other determinations two sets of water samples were taken, one from the surface and one from immediately above the mud at the bottom of the pool. The water intended for oxygen determinations was pipetted slowly from the pool and run into bottles of about 100 c.c. capacity. At all stages of the process the water was isolated from the air by a layer of liquid paraffin. At the same time a second set of samples was taken for salinity and alkali reserve determinations. The oxygen content was measured by Winkler's method, the alkali reserve by titration with hydrochloric acid after boiling off the carbon dioxide, and the salinity by titrating with silver nitrate.

Samples of mud from the bottoms of pools for estimating the chlorine content of the contained water were obtained by forcing a brass tube of one square inch in cross section into the mud to the required depth, corking the upper end and withdrawing the tube with a column of mud. This was then pushed out, cut up into lengths and placed in separate containers for transport. Each sample was weighed, dried, re-weighed to get the volume of contained water, and washed free from salt with distilled water. The chlorine content of the washing water was then determined, and from it that of the original volume of water calculated.

The meteorological records were obtained from the Meteorological Office of the Air Ministry, to whom my thanks are due for their kindness in supplying them. It was not possible to obtain figures for Aberlady itself, but those recorded for the rainfall at Dirleton, and for sunshine at North Berwick, three and eight miles to the east respectively, are probably sufficiently accurate.

THE MARSH.

The salt-marsh under investigation fringes the sands of Aberlady Bay on the south shore of the Firth of Forth, fifteen miles east of Edinburgh.

Owing to the flatness of the coast, when the tide recedes, two square miles of sand are left exposed for eight or nine hours at a stretch. The bay is intersected by the estuary of the Peffer Burn, which enters it at the south-east corner, and which flows, during the period of low tide, in a channel following the south shore (Fig. 1).

The saltings run as a narrow fringe round the edge of the bay. They vary in character in different parts. On the east shore the sand is clean and unmixed with mud, and the saltings are hardly raised above the level of the bay. Hollows and channels are numerous, but, because of the

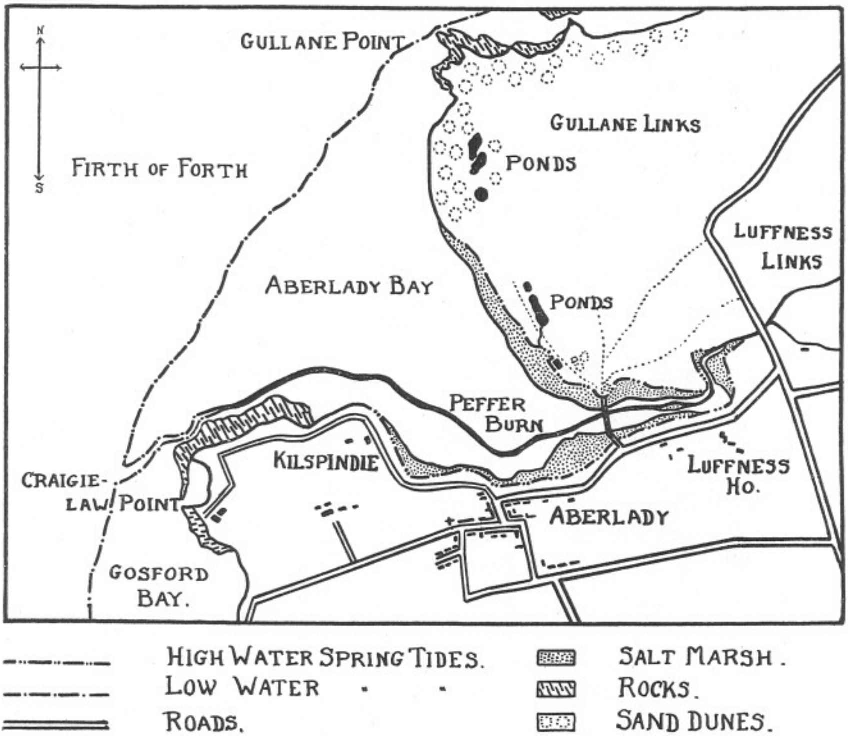


FIG. 1.—Sketch map of Aberlady Bay to show the position of the salt-marsh.

porosity of the soil, they drain dry in a few hours and are not refilled until the next period of spring tides. This region is relatively barren. On the south shore, however, where the mud brought down by the stream accumulates, many permanent pools are formed.

The part chosen for particular investigation lies at the south-east corner of the bay at the point where the Peffer Burn enters the sea at high tide. It is divided into two regions by the stream, the part on the right bank being about a hundred yards square, the part on the left being nearer the open sea and about six times that area (Fig. 2).

On the right bank of the Peffer the greater part of the Gullane Links consists of blown sand, but underlying this are areas of quartz dolerite, which appear on the surface on the higher parts and which dip south-west towards the bay. On the left bank, a few hundred yards inland, rocks of the lower carboniferous series underlie the soil. Immediately behind the marsh are calciferous sandstones dipping west-north-west so that water draining over these rocks might reach the marsh. Farther west, Aberlady village is situated over rocks of the carboniferous limestone series. These, however, dip west-south-west and drainage water from this area cannot affect the marsh. The soil on top of these rocks might be expected to be derived partly from them and partly from blown sand from the bay, and to be fairly limy. Between the carboniferous rocks and the shore is a strip of raised beach, which also appears on the right bank of the burn, consisting of sand and comminuted shells, and it is on this that the marsh is formed.

Besides drainage water from the hinterland, the water of the Peffer Burn affects the conditions in the salt-marsh pools. The stream rises near East Fortune in a patch of alluvial soil. It then flows for two miles over basalt, and crosses a mile of quartz trachites. The last three miles of its course are again across an alluvial plain. One tributary, the Mill Burn, rises near Dirleton, also in a patch of alluvium, and crosses two miles of quartz trachites and a mile of calciferous sandstone before reaching the Peffer Burn as it winds across the alluvial plain on its way to the sea.

On the left bank the soil of the marsh is soft and muddy, and the greater part of the surface is covered with a loose turf of *Armeria vulgaris* mixed with some *Aster tripolium*, *Spergularia marina*, *Plantago maritima* and *Triglochin maritimum*. Here and there round the edges of the lower pools *Pelvetia canaliculata* and *Salicornia herbacea* grow in quantity. *Glycera maritima* does not occur as a definite band along the seaward edge of the marsh as in so many places, but forms here a clearly-marked network in the wetter parts, marking out the old drainage systems now filled up or converted into chains of pools. The higher parts of the marsh are covered with *Festuca ovina* mixed with *Cochlearia officinalis* and *Potentilla anserina*. Round the edges of the pools *Triglochin maritimum* forms numerous tufts, and one or two patches of *Atriplex patula* are also to be found. The Festuca association is not confined to the region round high-water mark, but occurs in isolated patches on hummocks right down to the seaward edge of the marsh. This edge shows erosion by wave action where it is exposed to the north-west; near the bridge and behind the hulks this is absent, but elsewhere the edge of the marsh is undercut, and is raised from three to twelve inches above the level of the mud of the estuary.

On the right bank the vegetation is somewhat different. Little or no erosion is taking place and irregular patches of Glycera and Salicornia are pushing their way out over the surface of the sand and increasing the area of the marsh. In the higher marsh on this side the soil is sandier and drier, and the turf is closer and composed almost entirely of *Armeria maritima*, mixed in the wetter parts with *Salicornia herbacea*. The

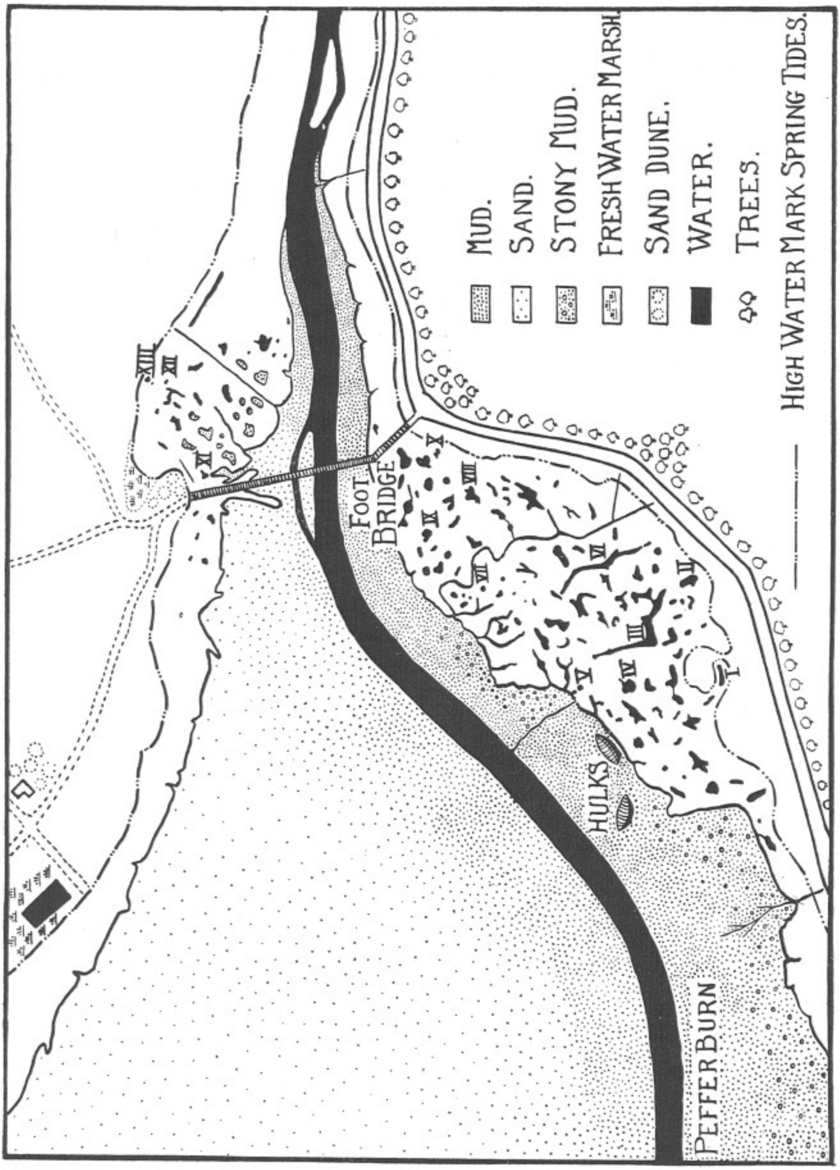


Fig. 2.—Sketch map of Aberlady salt-marsh to show the position of high-water mark and the distribution of the pools.

upper edge of the marsh merges gradually into a fresh-water bog at one place and into a small sand-dune at another.

The pools are formed all over the marsh from high-water mark to the seaward edge. Unfortunately a complete transition series from marine to fresh-water conditions is not found, since both areas of marsh are terminated abruptly by a four-foot bank at their landward edge, marking an old beach level, and, although the land appears to be rising still, none of the pools has yet been completely freed from tidal influence.

The pools differ greatly in shape and size. Some are almost circular, while others are long and narrow, winding about with numerous side branches. They appear to be derived from old drainage channels which have become blocked in places by fallen banks and rubbish brought in by the tide. On the left bank the course of the channels can be clearly traced by means of the *Glycera maritima*. The area of the pools varies greatly. The smallest are not more than a square foot, while the largest are as much as twenty or more square yards in surface area. In depth they vary from three or four up to eighteen inches. As a general rule the pools near the top of the marsh are the shallowest, but there are many exceptions.

On the right bank the soil is sandy and the bottoms of the pools are firm and porous. Consequently the pools are of a less permanent character, many of them draining dry for part of the time between each group of high tides. The effects of drainage water on the conditions in the pools is also more marked on this side. On the left bank there are a few pools with sandy bottoms, but the majority have a thick layer of fine mud to a depth of eight or ten inches on top of the sand. A few pools near the foot-bridge have gravelly bottoms with large stones here and there. In the pools near high-water mark quantities of dead leaves accumulate, which decay and alter considerably the consistency of the mud.

In several places the old drainage channels have been kept open, or new straight ones cut. The water running in these is fresh.

THE FAUNA OF THE MARSH.

The fauna of the marsh can be considered under two main headings: the fauna of the surface of the marsh, and the fauna of the pools.

The Fauna of the Surface of the Marsh.

The fauna of the marsh surface can be divided into two groups: animals visiting the marsh to feed, and animals living permanently on the marsh.

In the first group come sheep, rabbits, rats and mice, and a large number of birds. Since most of the birds come to feed on the animal life of the marsh their importance in the economy of the area is great, especially in times of drought when the water in the pools is shallow or has even disappeared. At such times the mud shows the tracks of innumerable waders which have crossed the mud in all directions in their search for the small crustacea, insect larvæ and worms which form their food. The numbers of these destroyed during the summer must be enormous in a secluded place, but at Aberlady a main road runs along the side of the marsh, and the activities of many of the shier birds are limited to the early hours of the morning.

In the second group are animals living on the surface of the marsh. This region is of interest from the point of view of respiration rather than from that of adaptation to changing salinity. Most of the species inhabiting it belong to the class Insecta, and, owing to their chitinous covering they are probably unaffected by saline conditions acting during short periods of time. On the other hand, they are all air breathers, and are cut off from their source of supply every time the marsh is covered by the tide. It is possible, however, that sufficient air is retained in their tracheæ to keep them alive in an inactive state until the water again recedes, or that they breathe anærobically during the short period. Slater (1930) has shown that it is possible for the Cockroach to remain in an oxygen-free atmosphere for as long as two hours without being permanently affected. It is seldom that any of the marsh is covered for as long a period.

At high-water mark a thick layer of weed, dead leaves, bits of wood and rubbish of all sorts, accumulates, forming a moist, warm region with a plentiful food supply. These conditions are taken advantage of by a number of animals, mostly Crustacea and Coleoptera. On the right bank the following species occur.

Annelida.
Enchytraeus albidus.
Crustacea.
Orchestia gammarella.
Porcellio scaber.
Philoscia muscorum.
Myriopoda.
Cylindroiulus britannicus.
Brachyiulus pusillus.
Polydesmis sp.
Insecta.
Campodea palustris.
Anthomyid larvæ.
Tachinus rufipes.
Quedius maurorufus.
Lestiva longelytrata.
Pterotrichus diligens.
Dichirotrichus pubescens.
Arachnida.
Lycosa palustris.

On the left bank the drift is not so dense, and is deposited on long stiff grass so that the region is never so moist as on the right bank. The following species are found.

Crustacea.
Orchestia gammarella.
Porcellio scaber.

Myriopoda.
Brachyiulus pusillus.

Insecta.
Campodea palustris.

On the right bank, where most of the soil is sandy, the surface of the marsh is dry, and the following species occur.

Crustacea.
Orchestia gammarella.

Insecta.
Podura marina.
Campodea palustris.
Tachyporus hypnorum.
Atheta triangulum.
Atheta vestita.
Cantharus rusticus.
Dichirotrichus pubescens.

Arachnida.
Lycosa palustris.

On the left bank this type of surface is not represented.

Wherever mud accumulates the ground becomes wet and waterlogged. On this type of surface on the right bank the following species are found.

Crustacea.
Sphæroma rugicauda.
Orchestia gammarella.
Carcinus maenas.

Mollusca.
Hydrobia ulvæ.
Littorina saxatilis.

Insecta.
Podura marina.
Campodea palustris.
Tachyporus hypnorum.
Atheta triangulum.
Atheta vestita.
Dichirotrichus pubescens.

Arachnida.
Lycosa palustris.

Along the edge of the marsh, in crevices in the muddy bank and round the edges of the lowest pools, three other species occur: a small reddish turbellarian *Uteroporus vulgaris*, and an isopod, *Paragnathia maxillaris*, are numerous, but the third species, the mollusc, *Phytia myosotis*, is rare. Since it occurs commonly at the Tynninghame marsh near Dunbar, a search was made at Aberlady, and one large specimen and two small ones were obtained from among the grass roots.

On the left bank the ground is so wet that only the following species can live there.

Annelida.
Enchytræus albidus.

Crustacea.
Orchestia gammarella.
Sphæroma rugicauda.
Carcinus maenas.

Mollusca.
Hydrobia ulvæ.

Insecta.
Podura marina.
Campodea palustris.
Dichirotrichus pubescens.

Arachnida.
Lycosa palustris.

The surface fauna of the marsh is derived from three sources. Species such as *Dichirotrichus pubescens*, *Atheta vestita*, *Orchestia gammarella*, *Phytia myosotis* and *Podura marina* occur only in regions within reach of the tide, and are found commonly on salt-marshes. Other species such as *Porcellio scaber* and *Philoscia muscorum*, *Atheta triangulum*, *Campodea palustris* and *Lycosa palustris* are commonly found away from the coast, but are not inconvenienced by a certain amount of salt water. Others such as *Hydrobia ulvæ*, *Sphæroma rugicauda*, *Carcinus maenas* and *Littorina saxatilis* are brackish-water or marine species which have been washed on to the marsh from the estuary, and which are able to survive in the moister parts in crevices and under banks.

The Fauna of the Pools.

The pools on the marsh can be roughly divided into two groups: those which are situated near the top of the marsh, and are seldom reached by the tides, and those which are entered by many tides.

The less saline pools.

During the greater part of the year the first type of pool is almost fresh having a salinity of about 1·0°/₀₀. Immediately after a spring tide, however, the salinity may be as high as 15·0 °/₀₀. It falls rapidly under normal circumstances, and in a week or two it has reached its ordinary low value (Fig. 14, p. 245). These pools contain little vegetation ; a few are filled with *Scirpus lacustris* var. *tabernæmontani*, a few with *Zannichellia palustris* and *Equisetum limosum*, but the greater number are devoid of plant life except for a few diatoms and green flagellates. The bottoms of the pools are of soft mud mixed with dead leaves, overlying sand on the right bank and stiff clay on the left. The permanent fauna of these pools is limited to a few species, some of which may be found in neighbouring ponds, others are definitely brackish-water animals which are able to live in low-average salinities.

Fresh water species.

Insecta.
- *Cricotopus vitripennis.*
- *Culicella* sp.
- *Agabus bipustulatus.*
- *Hydroporus planus.*
- *Hydroporus palustris.*
- *Hydroporus nigrita.*
- *Hygrotus inæqualis.*
- *Helophorus viridicollis.*

Brackish water species.

Crustacea.
- *Gammarus duebeni.*
- *Tachedius brevirostris.*
- *Cyclopina gracilis.*
- *Eurytemora velox.*

Insecta.
- *Aëdes detritus.*
- *Ochthebius marinus.*

In addition to these animals which live and breed in the pools, others derived from the same sources are accidental visitors, which only find a temporary footing in the marsh when the conditions are suitable, and disappear again when these conditions change.

Fresh water species.

Mollusca.

Limnœa truncatula.

Insecta.

Sigara sahlbergi.

Anopheles bifurcatus.

Culex pipiens.

Chloeon sp.

Amphibia.

Molge palmata.

Bufo vulgaris (tadpoles).

Brackish water species.

Annelida.

Nereis diversicolor.

Crustacea.

Sphæroma rugicauda.

Corophium volutator.

The more saline pools.

The remainder of the pools on the marsh must be considered under one head from the point of view of salinity. Owing to their small size they are so greatly influenced by factors such as the rainfall, the rate of evaporation and the amount of drainage water entering them that they cannot be further subdivided on a salinity basis. The fauna of the pools, however, is by no means uniform, but differences in it can best be correlated with differences in the amount of vegetation and in the consistency and nature of the substratum rather than with arbitrary differences in the salinity.

Many of the pools contain an abundant supply of weed which in some consists of a luxuriant growth of *Ulva lactuca*, *Enteromorpha intestinalis*, *E. compressa* and *Polysiphonia elongata*, growing on the grass roots which form an overhanging mat round the margin. The bottoms of such pools may consist of bare mud covered at certain times of the year by a brown scum of diatoms. Other pools have a dense bottom vegetation as well as the fringing weed. In some this consists of *Zostera marina* (in one pool of *Z. nana* which was, however, killed off by the hot summer of 1932, and has not yet recolonised the marsh, although it is common on the muddy banks of the river), in other pools dense mats of species of Chætomorpha cover the bottom, and in others *Vaucheria littorea* fills the pools. In some, where solid objects such as stones, old tin cans or waterlogged wood occur on the substratum, *Enteromorpha intestinalis* and *Ulva lactuca* grow thickly. By far the most luxuriant of the algæ, however, is the Vaucheria which entirely covers the bottoms of many of the pools in the early spring and largely dies down by the end of May. In all pools where the substratum is exposed to light, in the spring and early summer a dense brown felt of diatoms is formed, and at the same season the fronds of the Zostera and the grass roots are covered with gelatinous masses of diatoms.

The nature of the substratum in the pools varies considerably. In a few, the bottom is covered with coarse gravel and stones ; in some it is sandy, particularly on the right bank of the burn, but in the majority it is covered to a depth of eight or nine inches with soft black mud, the surface inch of which is in a semiliquid state, becoming progressively firmer as greater depths are reached. The consistency of the mud is of great importance to some of the animals living in the pools and depends on the relative proportions of sand and silt, all grades between hard sand and almost liquid mud being represented. Since these differences are probably much more important than the exact salinity in determining the distribution of the fauna in a marsh such as this, the habitat has been divided according to the vegetation and to the nature of the bottom, and the associated faunas are listed separately.

The free swimming fauna.

A few free swimming forms occur which are independent of either the nature of the bottom or the kind of vegetation.

Brackish water species.

Rotifera.
Brachionus mulleri.
Crustacea.
Neomysis vulgaris.
Insecta.
Aëdes detritus.
Pisces.
Gasterosteus aculeatus.

Fresh water species.

Rotifera.
Notholca acuminata.
Crustacea.
Eurytemora velox.
Tachedius brevirostris.
Cyclopina gracilis.

In addition to these, adult specimens of *Aurelia aurita*, *Pleurobrachia pileus* and *Beröe cucumis* are occasionally carried into the pools by the tide and survive for a short time.

The fauna of the weed.

The following species occur on the vegetation fringing the edges of the pools.

Brackish water species.

Cœlenterata.
Syncoryne sarsi.
Crustacea.
Sphœroma rugicauda.
Mollusca.
Limopontia capitata (small).
Embletonia pallida.
Hydrobia ulvæ.

Marine species.

Annelida.
Dinophilus tæniatus.
Nemertina.
Lineus gesserensis.
Crustacea.
Carcinus maenas (small).

In addition to these species the following occur among the bottom vegetation.

Brackish water species.

Protozoa.
- *Pulvinula repanda.*

Crustacea.
- *Jæra marina.*
- *Melita palmata.*
- *Gammarus duebeni.*

Mollusca.
- *Alderia modesta.*
- *Limopontia capitata.*

Marine species.

Protozoa.
- *Polystomella striatopunctata.*

Annelida.
- *Eulalia viridis.*

Mollusca.
- *Mytilus edulis.*

Fresh water species.

Insecta.
- *Chironomus aprilinus.*
- *Procladius choreus.*
- Trichopteran larvæ.

Most of these are not confined to any one species of weed, but *Melita palmata*, *Alderia modesta* and *Limopontia capitata* when full grown are seldom found except on Vaucheria.

The fauna living on the substratum.

The following species occur in pools with stony bottoms.

Brackish water species.

Crustacea.
- *Gammarus duebeni.*
- *Jaera marina.*

Marine species.

Cœlenterata.
- *Aurelia aurita* polyps.

Crustacea.
- *Balanus balanoides.*

Mollusca.
- *Chiton marginatus.*
- *Mytilus edulis.*
- *Littorina saxatilis.*
- *Littorina littorea.*

None of the marine species are at all common, but they appear to be maintaining a precarious footing in a few of the pools.

The following species occur in pools with sandy bottoms.

Brackish water species.

Mollusca.
- *Hydrobia ulvæ.*

Pisces.
- *Gobius microps.*

Marine species.

Crustacea.
- *Carcinus maenas.*
- *Crangon vulgaris.*

Mollusca.
- *Littorina littorea.*
- *Littorina saxatilis.*

The following species occur in pools with muddy bottoms.

Brackish water species.	Marine species.
Cœlenterata.	Crustacea.
Protohydra leuckarti.	*Crangon vulgaris.*
Pisces.	
Gobius microps.	

In the two last types of pool the following Protozoa are found on the surface of the substratum. *Chlamydodon triquetra*, *Euplotes charon*, *Loxophyllum rostatum*, *Lacrimaria olor*, *Uronychia transfuga*, *Pulvinula repanda* and *Polystomella striatopunctata* besides many other smaller species which have not been identified.

Pandalus annulicornis and *Pleuronectes flesus* also occur as occasional visitors.

The fauna living in the substratum.

The following species are found buried in the floor of pools with sandy bottoms.

Brackish water species.	Marine species.	Fresh water species.
Annelida.	Annelida.	Insecta.
Nereis diversicolor.	*Arenicola marina.*	*Chironomus aprilinus.*
Manyunkia estuarina.	*Pygospio elegans.*	
Crustacea.	Mollusca.	
Corophium volutator.	*Macoma balthica.*	
	Mya arenaria.	

The following species are found burrowing in mud.

Brackish water species.	Marine species.	Fresh water species.
Annelida.	Annelida.	Insecta.
Nereis diversicolor.	*Arenicola marina.*	*Chironomus aprilinus.*
Manyunkia estuarina.	Crustacea.	
	Carcinus maenas.	
	Nemertina.	
	Lineus gesserensis.	
	Pisces.	
	Anguilla vulgaris.	

It is impossible to distinguish exactly between these two types of bottom, and only the fauna of the two extremes is given. Even so a considerable number of species occur in both.

The Fauna of the Estuary.

The estuary in the immediate vicinity of the marsh (Fig. 2) can be divided into four regions each showing slight differences in the fauna.

The mud. This region is best developed on the banks of the Peffer burn east of the foot bridge. The mud is soft and sticky and has a thick covering of *Zostera nana*. The following species are found.

Annelida.
Nereis diversicolor.
Crustacea.
Corophium volutator.

Mollusca.
Macoma balthica.
Scrobicularia piperata.
Hydrobia ulvæ.

A similar fauna is found in the mud along the left bank of the burn near the hulks.

The sand. This region lies on the right bank of the burn west of the foot bridge. The following species occur.

Annelida.
Arenicola marina.
Nereis diversicolor.
Nemertina.
Tetrastemma melanocephala.

Mollusca.
Hydrobia ulvæ.
Cardium edule.

Tetrastemma is not common and is found only under a few stones, although large numbers are present nearer the sea.

The stony mud. This region lies on the left bank between the marsh and the pure mud edging the bed of the burn at low water. It consists of gravelly mud on which rest stones of various sizes. The following species occur.

Annelida.
Nereis diversicolor.
Nemertina.
Lineus gesserensis.
Crustacea.
Balanus balanoides.
Corophium volutator.

Mollusca.
Chiton marginatus.
Mytilus edule.
Littorina littorea.
Littorina saxatilis.
Hydrobia ulvæ.

The bed of the burn at low water. This region always has running water varying in salinity from $0{\cdot}8°/_{oo}$ when the tide is out, to $33{\cdot}0$ to $35{\cdot}0°/_{oo}$ when the tide is full. A number of large stones lie in the stream which afford protection to the Mysids from the current. The following species are found.

Crustacea.
Corophium volutator.
Sphæroma rugicauda.
Gammarus duebeni.
Hyale nilsoni.
Neomysis vulgaris.
Crangon vulgaris.

Mollusca.
Hydrobia ulvæ.
Littorina littorea.
Littorina saxatilis.
Pisces.
Gasterosteus aculeatus.
Pleuronectes flesus.
Gobius microps.

Although most of the species occurring in the estuary are the same as those found in the marsh, the following were found in the estuary only, *Scrobicularia piperata, Cardium edule, Hyale nilsoni* and *Tetrastemma melanocephala*.

Numbers of Animals in the Marsh.

The number of animals in the marsh is difficult to estimate, but is in some instances very large. For example, in one pool in June in an area of one square foot of mud there were 8890 young Nereis. Counts of the three principal inhabitants of the mud, *Corophium volutator*, *Chironomus aprilinus* and *Nereis diversicolor*, gave the following figures. These are for an area of one square foot and are the averages of five samples made at different times throughout the year.

TABLE I.

Species.	Pool II.	Pool III.	Pool VII.	Pool IX.	Pool XI.
Corophium volutator .	64	84	36	108	15
Chironomus aprilinus .	519	1239	1	66	81
Nereis diversicolor . .	36	3	9	48	60

Estimates of the numbers of the larger animals in some of the pools were also made, partly by sampling, partly by actual counts of random areas. The results are given in the following table.

TABLE II.

Species.	Pool VIII.	Pool IX.	Pool XI.	Pool XII.
Limopontia capitata	22	0	0	0
Hydrobia ulvæ	46	0	108	0
Mya arenaria	0	(41)*	(2)	0
Nereis diversicolor . . .	3	10	6	0
Arenicola marina . . .	4	(10)	(4)	0
Corophium volutator . . .	0	3	34	322
Chironomus aprilinus . . .	3672	572	8	78
Gobius microps	0	(3)	(1)	0

Notes on the Fauna.

Protohydra leuckarti. Protohydra is common at certain times in some of the pools. During May and June, 1931, it was present in large numbers in Pool VII. It was still abundant in October, but died out during the winter, and was not rediscovered until the summer of 1933, when it reappeared in Pool IV. The uneven distribution and the difficulty of

* The figures in brackets are for the whole pool, not per square foot.

seeing the animal probably accounts for the few records of its occurrence in Britain. Up to the present it has been recorded by Hickson only from Southampton and Plymouth, but a search in a small marsh at Torridon in Western Ross-shire revealed large numbers, again in one pool only, so that it is probably widely distributed.

Arenicola marina. The castings of this worm are to be found in pools of an average salinity as low as $15^{\circ}/_{\circ\circ}$. In these pools the salinity does not often fall below $8^{\circ}/_{\circ\circ}$. The nature of the bottom does not appear to affect the distribution, except that the worms do not occur in pools with gravelly bottoms. They are numerous in only a few pools, the maximum number recorded being 61 individuals of all sizes per square yard, the average number being 4 or 5.

The Copepods. The three species of Copepod which have been identified are most abundant in the fresher pools, although they also occur in some of the salter ones. In addition several species of Harpacticids are common in the fresher water, while a minute bottom living species is abundant in the surface layer of the mud of most of the salter pools.

Corophium volutator. The distribution of Corophium is determined firstly by the salinity, secondly by the type of bottom. In the upper pools of a salinity of about $5^{\circ}/_{\circ\circ}$ it only occurs as an occasional visitor. Hart (1930) states that Corophium when full grown is able to withstand immersion in fresh water for 16 days, but that the young die at the first moult. Only adults have been seen in the fresher pools. In the salter pools the distribution of Corophium is dependent on the type of bottom as Hart points out, being most abundant in muddy pools without vegetation. In one such pool the total number of animals per square foot was 322, exclusive of most of the smaller individuals which passed through the wire sieve. In sandier pools the numbers are low, for example, 34 per square foot, and in pools with black mud they may be absent.

Paragnathia maxillaris. This species occurs in burrows probably made by Orchestia, on the seaward edge of the marsh, above the bridge on the right bank only. The females are distended with fluid of a yellow colour. The young are found attached to Gasterosteus in the estuary, as many as seven being found on one fish.

Gammarus duebeni. This species is most abundant in the fresher pools round Pool XIII, on the right bank, and in the fresh water drains which traverse the marsh. It is sparingly distributed over the rest of the marsh but is common in the estuary. It breeds all the year round.

Neomysis vulgaris. This Mysid is common in the estuary as far up as the bridge but is local in its distribution in the marsh. In June, 1931, it was present in Pools III and VI only, but by September had spread to the surrounding pools. In 1932 specimens could be taken from many parts of the marsh but it appeared to be breeding only in a few pools.

After the hot summer it disappeared from all except Pool III, and from there died out during the winter. Since then it has not reappeared in the marsh although it is present in large numbers in the estuary. This may be due to the relatively low rainfall since the summer of 1932, causing much higher salinities in the pools. In the estuary, on the other hand, the Mysids are still subjected to almost fresh water conditions for the greater part of the twenty-four hours.

Carcinus maenas. Small specimens up to half an inch carapace width are common among the weed in the pools and also under dry overhanging banks on the marsh. They appear to be resistant to drought over long periods of time. Larger specimens are, however, present in considerable numbers in burrows from three to nine inches long under the overhanging banks of the pools and in the soft bottom mud. When the pools dry up they may be dug out, but are otherwise seldom seen as they emerge from their burrows only during the night.

Aëdes detritus. This mosquito is stated by Marshall (1925) to occur in stagnant full strength sea water as well as in brackish water. In the marsh, however, the larvæ are found only in pools of low average salinity. Since the eggs are scattered indiscriminately over the surface of the marsh and only hatch in suitable situations, one might expect to find a certain number of larvæ in all the pools. Gasterosteus and Gobius eat them however with avidity and probably clear any pool of the early stages, so that the larvæ should only be found in the upper pools where fish are absent. This cannot be the only controlling factor since fish are absent from many of the lower pools, yet Aëdes is never found in them.

Chironomus aprilinus. The larvæ of this species do not appear to be affected by the salinity since they occur in all pools, provided that the substratum is sufficiently soft. In some pools enormous numbers are present; 3660 per square foot were counted in Pool VIII. In others, such as Pool XI, which is sandy, only 10–20 per square foot may be present.

Culex pipiens. Although this species occurs with *Culicella morsitans* and *Anopheles bifurcatus* in the neighbouring ponds, it has been found only once in the marsh pools. In June, 1931, it occurred in enormous numbers in Pool X. The salinity at the time was between 1·3 and 0·9°/₀₀, but, although as low salinities are common in certain pools, the larvæ have never again been found in the marsh.

Alderia modesta. This nudibranch occurs in large numbers among the Vaucheria in the pools. It arrives in the marsh at the same time as Limopontia and behaves in the same way.

Limopontia capitata. This small nudibranch is of considerable interest. Although reported occasionally from rock pools near high-water mark, its most characteristic habitat is the pools of salt-marshes, but its appearance there is seasonal. The molluscs were first observed at Aberlady in June, 1931, but had entirely disappeared by October. In 1932 and 1933 they appeared after a high tide in the middle of February. Breeding began almost at once and spawn was found as late as June. Small Limopontias were found from March onwards in the weed fringing the pools, while the adults were entirely confined to *Vaucheria littorea*, or to the pools where it had been. During the winter of 1933–34 the characteristic egg masses of Alderia were observed in a pool at the end of November and a search revealed immature Limopontias also. They quickly increased in size and began to spawn in January. This early arrival in the marsh may have been due to the hot summer and the exceptionally open winter. The complete life-history of these molluscs is not known. The eggs hatch as veligers, but the later stages have never been seen in the pools, neither are their winter quarters known nor their method of arrival in the pools.

Hydrobia ulvæ. This species occurs in the pools with a firm substratum and along the banks of the stream. In pools where the mud is in a semi-liquid condition a few specimens may be found, but unless weed is present on which the animals can crawl, they are not abundant. Robson (1920) showed that in an Essex marsh the numbers of *Hydrobia ulvæ* were controlled by the distribution of *Ulva lactuca* on which, he says, they were feeding. This association is by no means universal. At Aberlady the Ulva is remarkably free from Hydrobia which occurs much more frequently among Enteromorpha. The greatest numbers, however, are to be found in the sandy pools on the right bank which dry up completely between tides. Counts were made in a number of these pools and 360 to 590 individuals per square foot were often found. In selected parts the population was as high as 2570 per square foot. Above the bridge on the bare mud of the right bank 3020 animals per square foot were present and on the clean sand below the bridge 830. In all these places *Ulva lactuca* was completely absent. Specimens of an average length of 9 mm. have been taken from the muddy flats of a salt marsh at Tynninghame in East Lothian, and from the sand at the head of some of the long inlets on the west coast of the Outer Hebrides, where there is no Ulva. An examination of the stomach contents shows that Hydrobia is a detritus feeder. It is likely that its occurrence on Ulva in the Essex marsh was connected with the soft nature of the substratum and not with the food supply.

Mya arenaria. Mya occurs in the marsh particularly in Pools III, IX, and XI. The first of these has a sandy bottom while the others have soft mud. The salinity in all three is usually high. During the summer of 1933 a Mya in a pool with a muddy bottom which had dried up was kept under observation. After five weeks of drought the animal was still alive. By the end of the summer, however, it had died. During 1934, when Pool XI was dry for many periods during the summer, nearly all the Mya were killed, but those in Pools III and IX did not suffer although the salinity rose considerably above that of the outside sea water. These pools never dried up.

Gasterosteus aculeatus. These fish are evenly distributed throughout all the salter pools in the marsh between the end of February and the end of August. The nests are made of weed and placed in the open on the mud. In contrast to the early arrival of the nudibranchs, the first sticklebacks were not seen in 1934 until the beginning of April, and the main body arrived still later. The adults and young are often almost entirely killed off by the drying up of the pools during the summer. This occurred in 1933 and as a consequence the fish were present in smaller numbers in 1934.

Gobius microps. The adults and young of these small fish inhabit the pools all the year round. They spawn during the month of June, attaching the eggs to the under sides of shells, bits of paper or dead leaves, the fish congregating in numbers round suitable objects.

Bufo vulgaris. Although toads breed freely in the fresh water ponds at Aberlady and are known to be tolerant of a certain amount of salt, eggs and larvæ have been seen in only one pool, the salinity at the time being $0{\cdot}2°/_{oo}$. In other marshes they have been found in a salinity of at least $4{\cdot}8°/_{oo}$.

Molge palmata. A single specimen of this newt was taken in Pool XIII in the spring of 1934. The salinity at the time was $0{\cdot}8°/_{oo}$. Earlier in the spring, when salinities were higher, dead specimens of *Rana temporaria* were common in the pools in this region.

THE ENVIRONMENT.

The Salinity.

i. *The conditions in the pools.*

The salinity of the pools is influenced by four main factors.

(1) Tides.
(2) Rainfall.
(3) Evaporation.
(4) Interchange of water between the mud and the overlying water of the pool.

The effect of the first and the last of these factors depends on the previous history of the pool under consideration; for instance, a tide entering a pool after a period of wet weather raises the salinity, a tide entering the same pool after prolonged drought lowers it.

The Tides.

Only a certain number of tides in the year affect the conditions in the marsh, since the water must rise at least sixteen feet above datum before it enters any of the pools. Thus the maximum numbers of tides entering the lowest pool on the marsh would be, according to the Admiralty Tide Table, twenty-five per year, that is, at every new and full moon. Pools situated at the top of the marsh are, of course, reached by fewer tides. The wind may cause an appreciable variation in these conditions. A strong offshore wind coinciding with a poor tide may prevent sea-water reaching some of the pools. Conversely, under the influence of an onshore

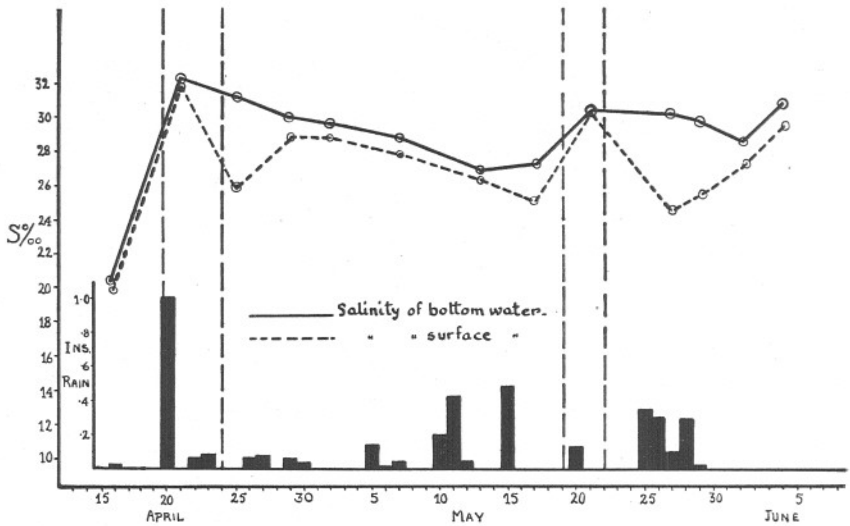


Fig. 3.—The salinity changes in Pool VII during the spring of 1932 showing the effect of tides entering the pool when the rainfall and the amount of evaporation have been approximately equal. The vertical lines show the limits of the periods during which tides entered the pool.

wind, the sea water may enter pools on the marsh which it would not normally have reached. The effect of an onshore wind is intensified by the funnel-like shape of Aberlady Bay. The number of tides entering a pool depends also on the height above datum of the lowest part of the rim of the pool and not on its position in the marsh, since the surface is by no means level and certain pools are raised many inches above their neighbours.

The effect of a tide entering a pool is determined by the previous weather conditions in the district. If, since the last high tides, the amount of rain and the amount of evaporation have been approximately equivalent, the passage of a tide over the marsh has little effect on the salinity of the water of the pools. Approximately these conditions are illustrated in Figure 3 for Pool VII during the period April 16th to June 4th, 1932. Tides entered the pool between April 20th and 24th and between May 19th and 22nd. In the intermediate period the rainfall was slightly greater than the evaporation and the salinity of the bottom water fell from 32·5 to

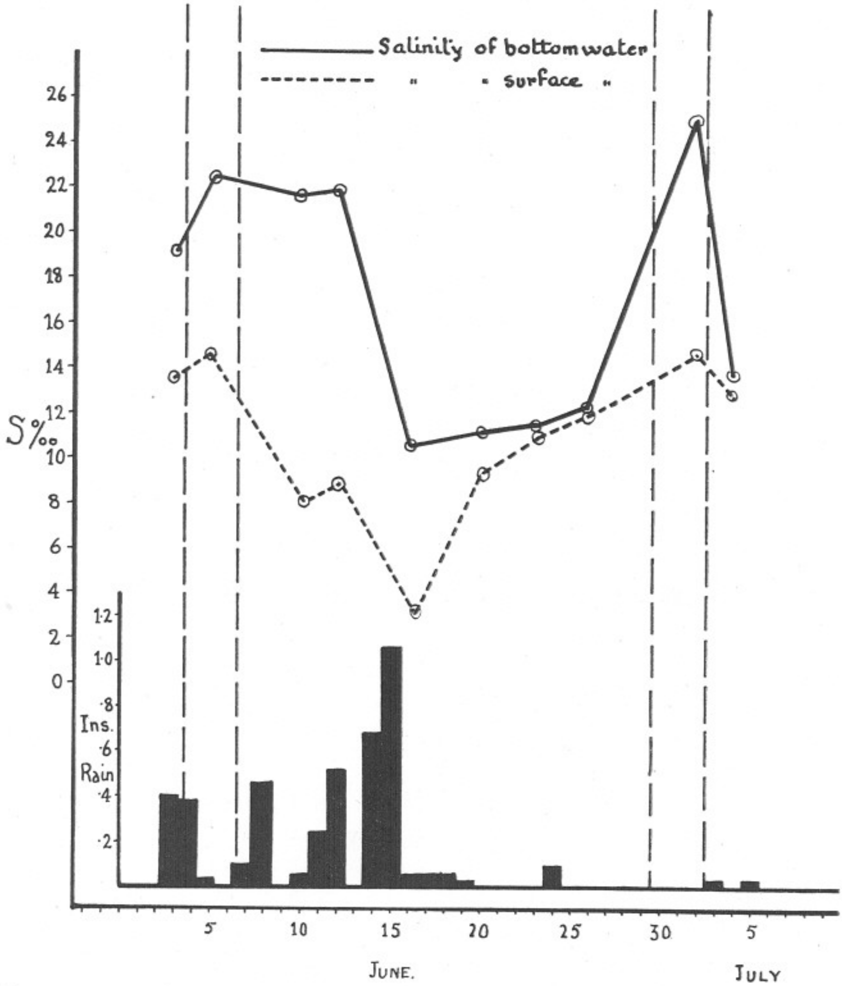


Fig. 4.—The salinity changes in Pool III during June, 1931, showing the effect of tides entering the pool when the rainfall has been greatly in excess of the evaporation. The vertical lines show the limits of the periods during which tides entered the pool.

27·0‰. The surface water showed greater changes, falling from 32·0 to 25·0‰ following heavy rain. If these conditions are compared with those in Pool III during a period of very wet weather (Fig. 4) the comparative slightness of the salinity changes will be appreciated. If, since the last tides, the rainfall has greatly exceeded the evaporation, a tide covering the marsh raises the salinity of the water. This condition is shown in Figure 4 which illustrates the changes in Pool III during the period June 3rd to July 5th, 1931. Tides entered the pool on June 4th to 6th and from June 30th to July 2nd. The salinity of the surface and bottom water fell from 14·5 to 3·0°/$_{\circ\circ}$ and from 22·5 to 10·5°/$_{\circ\circ}$, changes three times as great as those illustrated in Figure 3. If, however, the rate of evaporation has exceeded the rainfall since the last tide, then water entering the pool lowers the salinity. This condition is illustrated in Figure 5 for Pool III during part of May and June, 1933, when the salinity of both surface and bottom water rose from 32·0°/$_{\circ\circ}$ on May 18th to 38·0

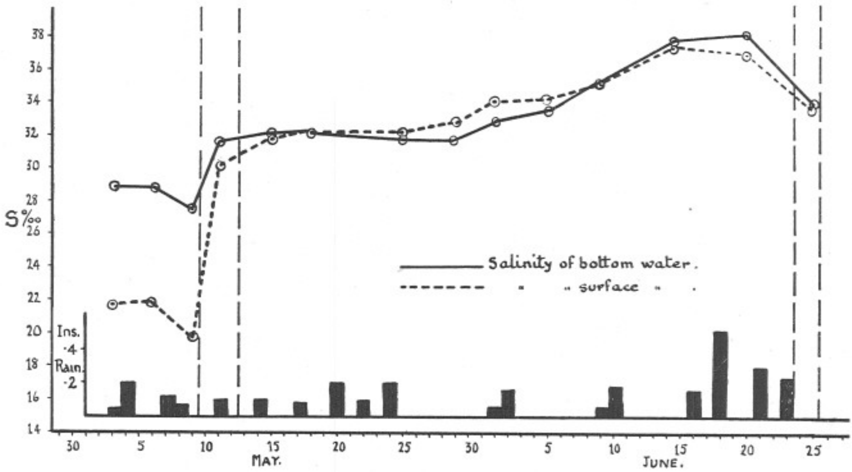


FIG. 5.—The salinity changes in Pool III during May and June, 1933, showing the effect of tides entering the pool when the evaporation has been in excess of the rainfall. Inverse layering of the water has taken place. The vertical lines show the limits of the periods during which tides entered the pool.

and 37·0°/$_{\circ\circ}$ respectively on June 20th. On June 24th and 25th tides just reached the pool, lowering the salinity to 33·5°/$_{\circ\circ}$.

Rainfall.

The rainfall can influence the salinity of the pools in three ways: directly; by drainage into the pools from a higher level; or by flooding at the time of high tides.

The direct effect of rainfall is often well marked, as in Pool III (Fig. 4) during the month of June, 1931. The first half of the month was abnormally wet, with a total of 3·95 inches of rain in fifteen days. This rain, particularly that which fell on the 14th and 15th, is clearly reflected in the salinities of both the surface and bottom water, which fell from 14·5 to 3·0°/$_{\circ\circ}$ and from 22·5 to 10·5°/$_{\circ\circ}$ respectively. Vertical mixing of the water must have taken place here to a considerable extent for the bottom

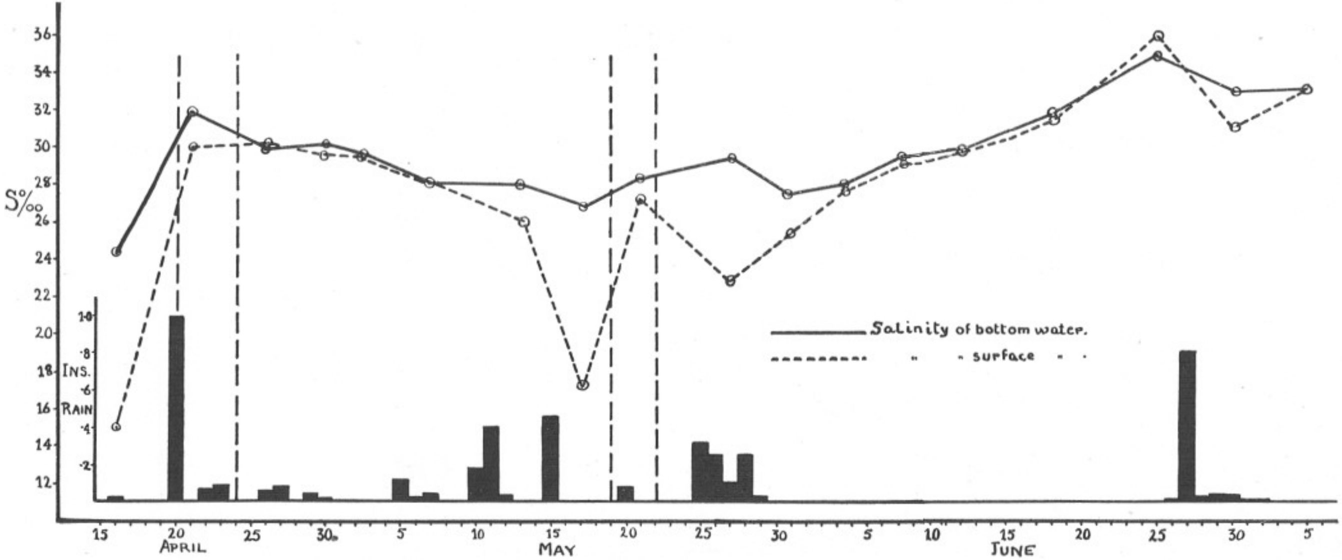


FIG. 6.—The salinity changes in Pool III during the spring of 1932 showing the lowering of the surface salinity by heavy rain and the effect of evaporation. The vertical lines show the limits of the periods during which tides entered the pool.

water to be so greatly affected. When there is no wind to bring this about the surface salinity is alone affected as in Figure 6, which shows the effect of rain unaccompanied by wind on the salinity of Pool III. Heavy rain between the 10th and 15th and the 25th and 28th of May lowered the

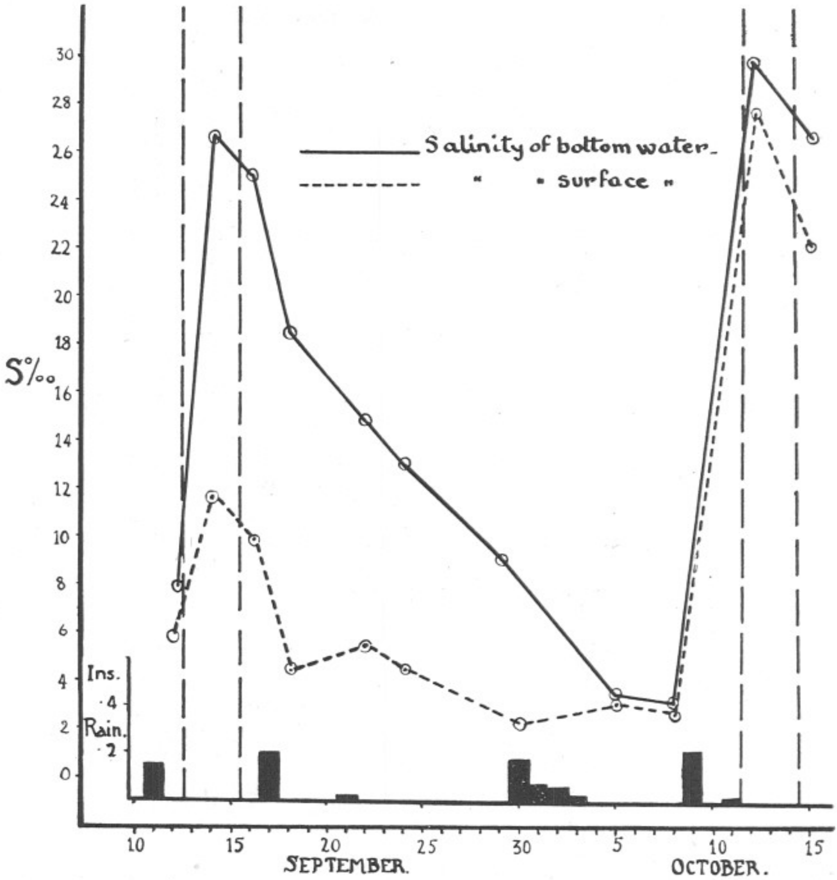


Fig. 7.—The salinity changes in Pool X during the autumn of 1931 showing the effect of drainage water. The vertical lines show the limits of the periods during which tides entered the pool.

surface salinity from 28·0 to 17·0 and from 27·0 to 23·0‰ without appreciably affecting the salinity of the bottom water.

The indirect effect of rainfall through drainage is well marked in certain pools near the top of the marsh, especially on the right bank, although it is often difficult to distinguish from that of direct rainfall accompanied by wind. When, however, a dry period follows rain, drainage into the pools from the land behind continues for some time, and the effect is easily seen as in Figure 7 for Pool X. The first fortnight of September, 1931, was fairly wet, 1·2 inches of rain falling in fifteen days, and tides entered the pool on September 13th to 15th, raising the salinity of the bottom water to 26·5 $^\circ/_{\circ\circ}$, but the surface water only to 11·5$^\circ/_{\circ\circ}$. After rain on the 17th the surface salinity fell to 4·5$^\circ/_{\circ\circ}$, and later to between 2 and 3$^\circ/_{\circ\circ}$. During the same period the salinity of the bottom water fell steadily until it became almost the same as that of the surface water. While mixing may have played some part, it is probable that drainage into the pool from the land behind was chiefly responsible for the large and steady decrease in salinity of the bottom water and the production of uniform conditions throughout. Confirmation of this is obtained from the changes in the alkali reserve. During the same period the alkali reserve of the bottom water rose steadily from 0·0022 N. to 0·0076 N., which would not have occurred had the fall in salinity been due to direct rainfall.

The rainfall also acts indirectly by affecting the salinity of the water entering the pools at each tide. Since Aberlady Bay drains dry at low tide, the water of the Peffer Burn does not accumulate in the bay but is carried out to sea and does not affect the salinity of the Forth appreciably. The data given in the Hydrographical Tables of the Conseil International pour L'Exploration de la Mer (1925–31) show that the salinity of the water at the mouth of the bay varies only slightly, the maximum values for the period 1925–31 at the surface and at 10 metres being 34·28 and 34·26$^\circ/_{\circ\circ}$ and the minimum 33·6 and 33·78$^\circ/_{\circ\circ}$ respectively. The effect of the incoming tide will be, however, to dam back the water of the burn in the region of the marsh, and this water, mixing to various extents with the sea-water, spreads over the marsh as the tide rises. The amount of water coming down the Peffer fluctuates considerably. The following rough estimates were made of the volume of water flowing per minute under varying weather conditions.

TABLE III

	Gallons.
October 24th, 1933, after a very dry summer . .	2,800
November 27th, 1933, after slight rain . . .	3,100
April 14th, 1934, after 10 days' heavy rain (2·83 in.) .	48,000
April 24th, 1934, after 10 days' dry weather (0·61 in.) .	5,200
May 31st, 1934, after another 5 weeks' dry weather (1·51 in.)	2,700
June 14th, 1934, after another 2 weeks' drought (0·23 in.)	1,700

During wet weather then, large quantities of fresh water flow down the stream and are met by the incoming tide, a certain amount of mixing finally taking place. The effect of this is clearly shown in Figure 8, which gives the conditions in Pool XI in June, 1931, when the first half of the month was abnormally wet. Tides entered the pool during three periods, June 3rd to 6th, 17th to 20th, and June 29th to July 3rd. The first group of these tides only raised the salinity from 11·5 to 12·0°/$_{oo}$, owing to the large amount of flood water. On the 16th the rain practically ceased,

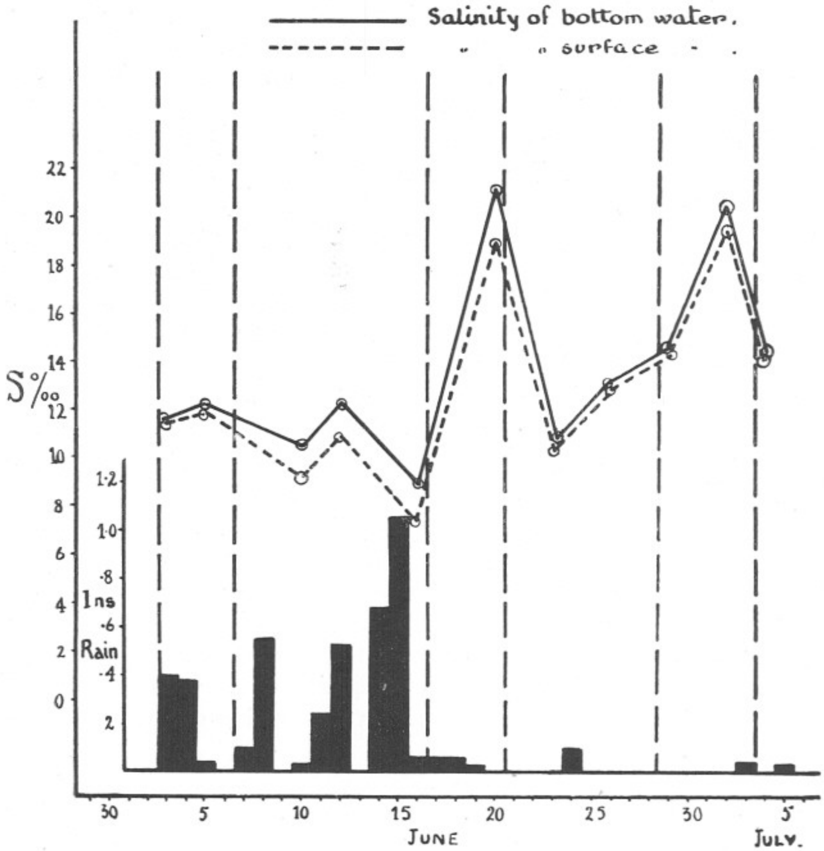


FIG. 8.—The salinity changes in Pool XI during June, 1931, showing the effect of the damming back of the flood water of the Peffer Burn by the incoming tide. The vertical lines show the limits of the periods during which the tides entered the pool.

although flood water was still coming down, for the second batch of tides raised the salinity of the top and bottom water of the pool only to 19·0 and 21·0°/$_{oo}$, and the third to 19·5 and 20·5°/$_{oo}$. Under ordinary weather conditions a spring tide would raise the salinity of this pool at least to 30°/$_{oo}$. In calm weather the water of the Peffer Burn does not mix completely with the water coming in from the sea, but flows out over the surface as a layer of almost fresh water. The following table gives the salinity at the footbridge in the centre of the estuary, and at various depths under various weather conditions.

The first set of figures was obtained in June, 1933, when the river was low and the weather calm. The second set was obtained in April, 1934, on a calm day after ten days' heavy rain.

TABLE IV

Time.	Depth of sample.	Depth of water.	Salinity °/₀₀.
12.15 p.m. . . .	Surface	6 in.	1·0
	Bottom		1·0
12.45 p.m. . . .	Surface		24·8
	1 ft. below	2 ft.	26·8
	Bottom		27·6
1.15 p.m. . . .	Surface		29·4
	1 ft. below	3 ft. 4 in.	30·6
	Bottom		30·6
1.45 p.m. . . .	Surface		31·0
	1 ft. below	5 ft. 9 in.	31·5
	4 ft. below		31·7
	Bottom		32·2
2.15 p.m. . . .	Surface		29·8
	1 ft. below		29·8
	4 ft. below	5 ft.	29·9
	Bottom		29·9
	High water 2.03 p.m.		
11.45 a.m. . . .	Surface	1 ft.	0·8
	Bottom		0·8
12.30 p.m. . . .	Surface	1 ft.	0·8
	Bottom		0·8
1.45 p.m. . . .	Surface		2·8
	1 ft. below	2 ft. 8 in.	12·6
	Bottom		13·4
2.30 p.m. . . .	Surface		13·2
	1 ft. below	4 ft. 6 in.	28·5
	Bottom		29·3
3.15 p.m. . . .	Surface		21·4
	1 ft. below	6 ft. 3 in.	31·1
	4 ft. below		32·0
	Bottom		32·6
	High water 3.15 p.m.		

The effect of this layering of the estuarine water can be seen in the salinity curves for various pools. In Figure 7 the condition is particularly well shown for Pool X during part of September and October, 1931. The first half of September was wet, 1·2 inches of rain falling, and a considerable amount of water was flowing in the Peffer. On September 13th a tide entered the pool and must have raised the salinity to at least 26·5°/₀₀. On the following day, which was windless, the tide just reached the pool by creeping between the grass stems. Water samples taken immediately after the tide receded showed that although the salinity of the bottom water was as high as 26·5°/₀₀ the surface water was only 11·5°/₀₀. Water samples taken in the estuary at high tide showed that there was a marked difference between the salinities of the surface and bottom water, the value for the former being 5·5 and for the latter 31·3 °/₀₀ ; so that the water reaching Pool X must have been surface water of low salinity, thus giving the low value for the surface water of the pool. A similar discrepancy between top and bottom water is well marked in Figure 4 for Pool III at both periods of high tides.

Layering of the water. During periods of dry weather following a high tide the salinity of the water may be the same throughout. Such a condition is well shown in Figure 6, giving the salinities in Pool III, where, on June 4th, the salinity of the surface and bottom water was almost the same, and remained so during the next three weeks. If the pool is shallow, even during wet weather there may be little difference in the salinity at different depths. This is shown in Figure 8 for Pool XI where the maximum depth was five inches, and sufficient mixing took place to keep the salinity constant. Conditions of equal salinity are the exception, however, and there is often a marked difference between the surface and bottom layers. This difference may be due to two causes :

(*a*) Rain.
(*b*) Evaporation.

When heavy rain falls a layer of fresh water is formed on the surface of the pool, which during calm weather mixes slowly by diffusion. Figure 9*a* shows the conditions in Pool III. On October 20th, immediately after a high tide and before rain, the salinity was practically uniform throughout (Curve A). On the 22nd heavy rain fell, and on the 23rd the surface and bottom salinities were 17·6 and 31·2°/₀₀ respectively (Curve B). Between the 23rd and 26th it was windy and vertical mixing of the water took place, a condition of almost equal salinity being again achieved at about 26·5°/₀₀ (Curve C). If, on the other hand, the wind and the rain come together, then a definite layer of fresh water is not formed on top and mixing takes place rapidly until a uniform condition is again reached. This condition is shown in Figure 9*b*, for Pool V, where Curve A shows the condition of uniform salinity immediately after a high tide; Curve B, the condition two days later after wind and rain—mixing has already taken place to within two inches of the bottom; and Curve C, three days later, when the salinity has again become uniform throughout. The rainfall can also bring about layering of the water by means of drainage. This drainage water flows through the soil from the land behind the marsh, particularly in certain places, and reduces the salinity of the mud and overlying water. Figure 9 *c* shows the effect of drainage water on Pool XI. On October 26th (Curve A) conditions were fairly uniform. Rain

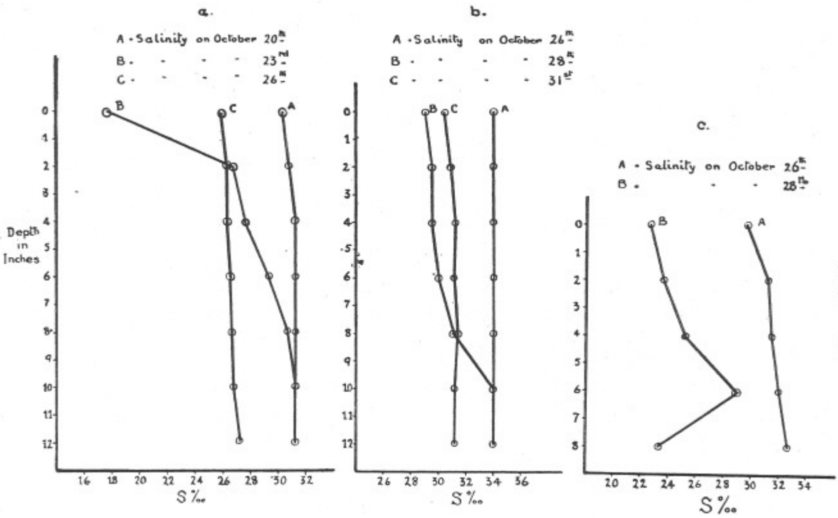


FIG. 9.—The salinity of certain pools at different depths to show (*a*) the effect of heavy rain in calm weather and the effect of wind in restoring conditions of equal salinity; (*b*) the effect of rain accompanied by wind; (*c*) the effect of drainage water.

accompanied by wind lowered the salinity of all the water to a certain extent (Curve B). The water at the surface of the mud, however, shows a markedly lower salinity than the water two inches above, which is probably due to drainage water. Inverse layering may also be produced if the weather is hot and dry.

Evaporation. Evaporation is always taking place from the surface of the pools, but its effect is usually so overlaid by other factors such as rainfall and the incidence of the tides that it is completely masked. During dry sunny weather, however, its results are well shown as, for instance, in Figure 6 for Pool III. The surface salinity first rose from 22·8 to 27·8°/₀₀ on June 4th, then both surface and bottom salinity rose together to 36·0 and 35·0°/₀₀ respectively on the 25th, after which rain fell. During the summer of 1933 the effect was even more pronounced, when, in spite of constant small amounts of rain, the salinity of Pool III rose from an average of 31·0°/$_{oo}$ on May 11th to 37·5°/$_{oo}$ on June 20th, after which a tide entered the pool and lowered the salinity (Fig. 5).

In warm, dry weather evaporation can proceed so rapidly that inverse layering takes place, the surface water being at a higher salinity than the water below. An example of this is shown also in Figure 5 for Pool III, where, from May 18th to June 9th, the salinity of the surface water was slightly higher than that of the bottom water. A certain amount of mixing, however, takes place all the time in the pools, and the difference can never be very great.

It is only during exceptionally hot, dry weather that the salinity in the pools rises above that of the Firth of Forth. This happened in the early summer of both 1932 and 1933. In the latter year the salinity rose as high as 38·2°/$_{oo}$ on the 20th of June, after which the records had unfortunately to be discontinued.

Interchange between the mud and the overlying water. The effects of the interchange between the mud and the water cannot in most cases be estimated, since they are obscured by the effects of mixing, drainage and rain water. Under exceptional conditions, however, the rate of exchange can be observed. In October, 1933, Pool I was dry, but on the 23rd heavy rain fell, filling the pool to a depth of two inches. On the 24th the salinity of the bottom water was already 6·4°/$_{oo}$ and of the surface water 5·8°/$_{oo}$. On the 27th the bottom salinity had risen to 21·0°/$_{oo}$, and the surface to 6·8°/$_{oo}$. On the 30th rain fell and drainage water began to run in, lowering the salinity of both top and bottom water.

ii. *Conditions in the mud.*

Up to the present only the conditions in the water have been considered. However, since many salt-marsh animals inhabit the mud in the bottom of the pools, the conditions there are of equal importance. There seem to be two main factors involved :

(*a*) the salinity of the overlying water.
(*b*) the amount of drainage water.

Under conditions of drought, however, a third factor, evaporation, comes into play ; after the overlying water of the pool has disappeared the heat of the sun and the wind act directly on the surface of the mud and profoundly alter the salinity.

The salinity of the overlying water. Table V gives the conditions in Pool XI, which can be taken as typical of the conditions in pools frequently entered by the tides.

TABLE V

SALINITY $^\circ/_{\circ\circ}$.

	April.				May.			
	19th.	22nd.	25th.	29th.	3rd.	6th.	9th.	11th.
Bottom water	24·8	20·8	18·4	17·4	14·2	12·8	30·6	32·0
Mud 0–1 in.	30·4	24·2	22·0	19·9	13·7	12·1	23·4	31·4
1–2 in.	24·3	25·0	22·9	18·3	16·7	15·9	17·2	23·5
2–3 in.	28·5	25·5	23·2	21·4	20·0	18·1	18·3	20·6
3–4 in.	27·6	26·1	25·5	21·9	21·7	19·4	21·3	19·3

	May.				June.			
	15th.	18th.	26th.	30th.	2nd.	6th.	9th.	13th.
Bottom water	27·6	26·4	19·6	18·6	17·6	16·0	31·2	30·6
Mud 0–1 in.	29·6	30·4	21·0	19·5	18·5	18·2	30·0	29·9
1–2 in.	28·7	26·3	22·4	18·8	17·7	16·8	24·8	29·0
2–3 in.	26·5	24·7	22·9	22·3	18·6	15·2	18·7	27·0
3–4 in.	23·6	20·8	21·6	23·2	20·1	18·8	25·0	26·6

Tides entered the pool on April 16th (the record commenced on the 19th), May 8th to 12th, and again on June 8th to 11th. The fluctuation in the salinity of the bottom water is considerable, and shows a maximum range of 19·2$^\circ/_{\circ\circ}$. The salinity of the surface inch of mud follows that of the water fairly closely, but shows a considerable lag in reaching its maximum and minimum values, and seldom reaches the same extremes of salinity. An exception to this occurred on May 6th, when the salinity of the mud actually fell below that of the water, possibly due to subterranean drainage water after fairly heavy rain on May 4th (for the rainfall record see Fig. 13). The maximum range is 19·3$^\circ/_{\circ\circ}$. The layer of mud 1–2 in. below the surface shows a similar lag, and the maxima and minima are less extreme, the total range being 13·1$^\circ/_{\circ\circ}$. In the deeper layers this is more and more marked, the range of salinity for the layer 2–3 in. below the surface being 11·9$^\circ/_{\circ\circ}$, and for that 3–4 in. down 8·8$^\circ/_{\circ\circ}$. At slightly greater depths it is reasonable to suppose that a condition of uniform and moderate salinity would be reached, at any rate, in pools with this type of bottom.

Drainage water. Drainage water can be of two kinds, fresh water coming from the land and salt water coming from the sea. It is impossible to say how far the second influences the condition in the marsh, but in certain regions there is a layer of coarse sand some inches below the surface, along which water appears to be pushed by the rising tide, altering the salinity of the mud in certain pools. In other regions the pools are unaffected by any tides except those reaching them in the normal manner. The effect of both kinds of drainage water is shown for Pool XIII during the spring of 1933 in Table VI.

TABLE VI.

Salinity $^{\circ}/_{\circ\circ}$.

	April. 19th.	22nd.	25th.	29th.	May. 3rd.	6th.	9th.	11th.
Bottom water	14·6	12·6	10·1	9·2	6·9	6·5	5·6	4·6
Mud 0–1 in.	11·9	12·3	8·2	6·5	6·0	5·6	3·9	5·9
1–2 in.	4·6	8·8	6·1	5·0	5·6	3·5	4·4	3·0
2–3 in.	2·2	2·6	2·8	3·4	3·5	2·4	5·1	6·0
3–4 in.	1·5	1·5	1·5	1·5	2·0	1·0	4·4	2·8

	May. 15th.	18th.	26th.	30th.	June. 2nd.	6th.	9th.	13th.
Bottom water	3·7	2·6	2·0	1·7	1·4	1·6	1·6	1·6
Mud 0–1 in.	4·9	4·5	2·3	1·7	1·7	2·0	1·0	1·0
1–2 in.	3·3	3·6	2·7	2·4	1·8	1·1	2·0	1·2
2–3 in.	2·3	2·2	2·5	1·8	2·8	2·2	2·2	1·5
3–4 in.	2·9	3·0	2·1	2·0	1·9	2·1	2·8	2·0

From April 19th till May 9th the salinity of the mud was lower than that of the bottom water, and, as the salinity of the latter fell under the influence of drainage water, that of the mud fell also. As the mud continued to have a lower salinity than the water it also was being affected by drainage water. On May 9th the salinity of the mud began to be considerably disturbed, rising and falling in an irregular manner for some days. This period of disturbance coincided with the high tides, which, forced in by a strong wind, covered the marsh to within about 20 feet of Pool XIII from the 9th to the 12th. It is probable that the salter water was forced up by the tide along the sandy layer under the pools which is present in this region, and caused the salinity changes in the mud. Similar though less well marked disturbances coincided with the next batch of high tides between June 9th and 12th, and confirmation of the results was obtained from other pools at the same time.

Evaporation. During the summer the tides may fail to reach the marsh pools for as long as six weeks, and if these periods coincide with periods of dry weather, then many of the pools dry up entirely, leaving the mud below directly exposed to the heat of the sun. The resulting changes vary with the type of bottom. In a pool floored with stiff mud the surface dries and cracks, and finally, if the drought is prolonged, the top inch of the mud cakes hard and can be lifted off. All animals living in this layer dry up unless they can burrow deeper into the mud. Small Corophium, Chironomus larvæ and young Nereis, as well as surface-crawling forms, are killed, but the layers below do not show an abnormal amount of drying or a very high chlorine content, so that deep-burrowing animals such as Mya, adult Nereis and Arenicola stand a good chance of surviving drought. Figure 10 shows the conditions in one such pool in the summer of 1932. Owing to the effects of drainage water the salinity of the water of the pool was low during the early part of May. On June 4th, just before drying up, the salinity of both top and bottom water was 10·5°/$_{oo}$, or 5·8 gm. of chlorine per litre. At the same time, the values for the water contained in the mud were slightly higher, varying between

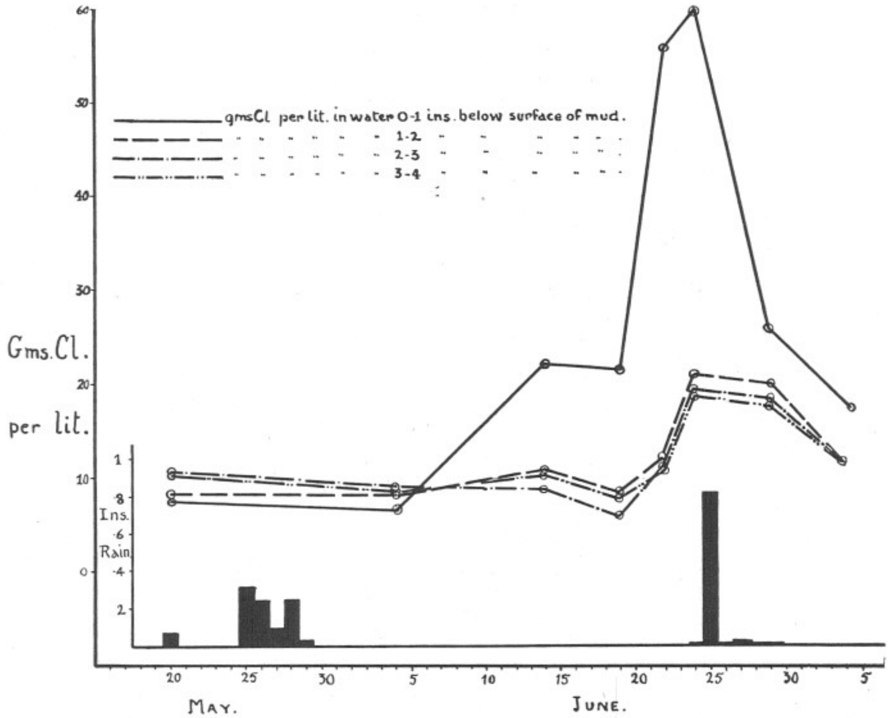


Fig. 10.—The changes in chlorine content of the water in the upper layers of the mud in Pool I during a period of prolonged drought.

6·5 and 9·5 in the top four inches of mud. As soon as the pool dried up completely the surface layer of mud also began to dry and the chlorine content of the water to rise. By the 14th it had reached 22·0 gm. per litre, and by the 24th 60·0 gm. per litre. The layers below the surface inch of mud differed very little in their chlorine content. By the 14th they had risen to between 8·5 and 10·5, and by the 24th they had only risen to between 18·5 and 21·0 gm. of chlorine per litre, about one third of the value for the surface inch. A downpour of rain on the 25th caused a drop to 26·0 gm. per litre without appreciably altering the chlorine content of the layers below. By the 4th of July drainage had lowered the surface layer to 17·4, and the layers below to 12·0 gm. of chlorine per litre.

As a contrast to the conditions in a muddy pool, the conditions in Pool XI can be taken. Here the bottom is sandy and when the pool is dry the top layer does not cake into a protective covering but remains free and porous. The result is that the layers below dry to a much greater extent than in a muddy pool. This particular pool contained a number of Mya and Macoma, which were all killed in 1933, when the pool was subjected to many recurring periods of dryness. The following table gives the values of the chlorine content of the water during one such period. It can be seen that although the surface inch gives some protection, there is not the marked difference between the layers that there is in Pool I with a muddy bottom. The drop in chlorine content on the 6th was due to a tide, which just reached the pool but did not leave any standing water.

TABLE VII

Depth.	Chlorine in gm. per litre.						
	May.			June.			
	18th.	26th.	30th.	2nd.	6th.	9th.	13th.
Bottom water	8·4	8·6	—	—	—	17·1	17·0
0–1 in.	10·0	9·6	20·8	27·5	13·5	12·5	15·0
1–2 in.	11·6	10·5	15·6	19·6	13·0	11·5	14·9
2–3 in.	13·7	8·0	14·1	17·0	13·4	10·9	13·4
3–4 in.	8·5	7·2	13·1	15·9	11·1	11·7	13·2

The Oxygen Content.

The oxygen content of the pools is influenced by several factors of which the numbers and relative proportions of plants and animals are the most important. During the night both plants and animals are using up oxygen, while during the day the former are giving it off to the surrounding water. Other factors are also important, such as the length of day, intensity of illumination and temperature, but their effects are mainly produced through their influence on the organisms inhabiting the pools.

The presence or absence of green plants is thus of paramount importance in determining the amount of oxygen present in a pool. The vegetation of the marsh pools includes flowering plants such as *Potomageton pectinatus*, and *Zostera marina*, various algæ such as *Ulva lactuca* and *Enteromorpha intestinalis*, also diatoms, peridinians and other green flagellates. None of the pools appears to be entirely devoid of plant life, a few small diatoms and filamentous algæ being present in all of them.

The Diurnal Variation in Oxygen Content.

An examination of the changes in the oxygen content was made throughout the hours of daylight in three types of pool, one containing large quantities of Enteromorpha, one containing diatoms only, and

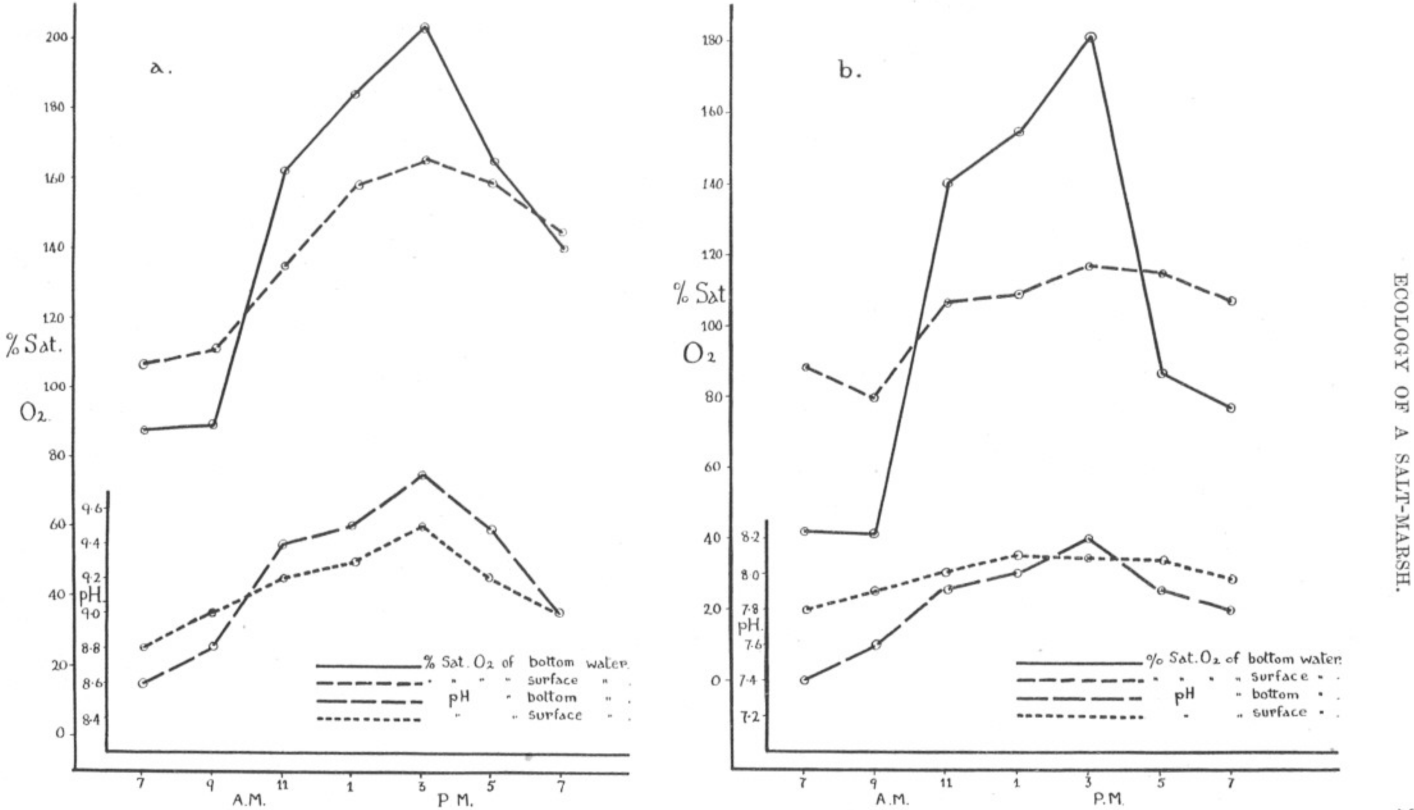


FIG. 11 *a* and *b*.—The percentage saturation with oxygen and the hydrogen ion concentration of the water of (*a*) Pool V containing Enteromorpha and Ulva ; (*b*) Pool IX containing diatoms.

one in which plant life of any kind was scarce. A bright day was chosen at the end of October when daylight began a little before 7 a.m. and finished just after 5 p.m. Observations were made every two hours from 7 a.m. to 7 p.m. The results are recorded in Figure 11, which gives the percentage saturation with oxygen in the three types of pool at the salinity and temperature recorded. Figure 11*a* gives the condition in Pool V, containing a mass of Enteromorpha. Both the top and bottom water

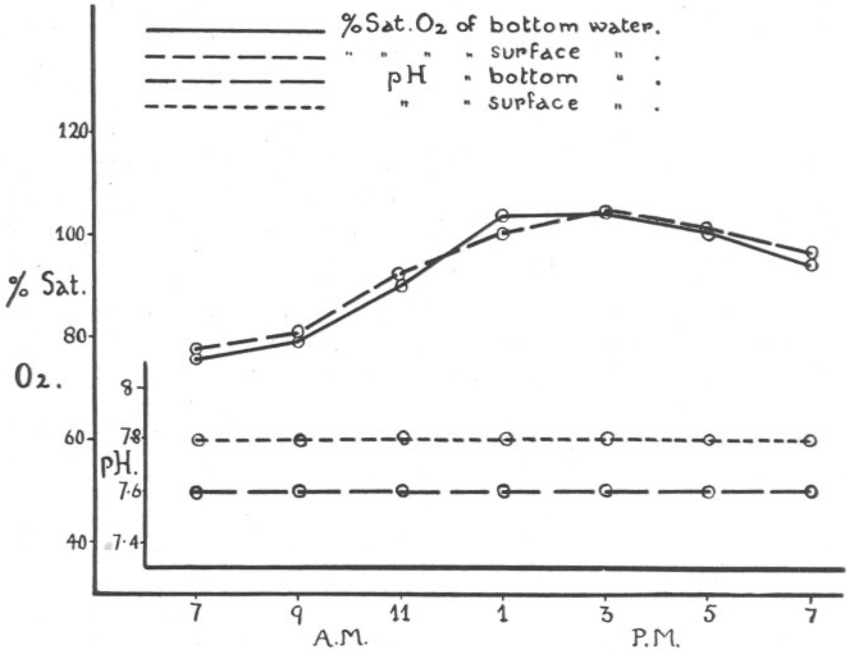


FIG. 11 *c*.—The percentage saturation with oxygen and the hydrogen ion concentration of the water of Pool XIII containing no plant life, during the hours of daylight on October 27th, 1933.

show the same changes, a slow rise from 7 to 9 o'clock, when the sky was overcast, a rapid rise till 3 o'clock when the light intensity was at its maximum, followed by a fall in oxygen content. Unfortunately it was not possible to extend the observations during the night, but without doubt this fall would have continued throughout the hours of darkness, until a minimum value was reached before dawn the next morning. The bottom water shows a rise of 110% while the surface water shows a rise of only 59%. This discrepancy may have been due to the fact that a strong breeze was blowing, causing loss of oxygen from the surface, but is more likely to have been caused by the concentration of the algæ at the bottom of the pool. This is further suggested by the fact that the oxygen content of the bottom water had fallen below that of the surface water during the night owing to the amount used up by the plants and animals at the bottom in respiration. Figure 11*b* gives the conditions in Pool IX, containing diatoms only. The curves follow the same general form as the last, but the great power of diatoms to saturate the water is well marked. In October diatoms are by no means at their maximum numbers, yet in this pool the increase in saturation of the bottom water was 142%, actually greater by 32% than that in Pool V crowded with Enteromorpha. This can be explained by the small size of the individual diatoms and the absence of storage space in their tissues, causing minute bubbles of oxygen to be liberated which pass at once into solution, as Butcher, Pentelow and Woodley (1931) have pointed out. In Pool XIII (Fig. 11*c*) where the plant life is scarce, consisting largely of minute green flagellates, the increase in oxygen is much less and the water hardly supersaturated even at 3 p.m. The curves for both top and bottom water are almost the same, rising from 77% to 104%, an increase of only 27%.

These observations are of interest when compared with those of Gessner (1931) for salt-marsh pools on Hiddensee. There many of the fresher pools are densely packed with *Ranunculus baudottii*, yet in May Gessner, making observations at midday and at midnight, found a change of only 50%, while even at midday the water was only slightly supersaturated. Pool V, containing Enteromorpha, shows a change of from 59 to 110%, with a shorter day and a lower light intensity, which suggests that algæ, as well as diatoms, possess the power of saturating the water with oxygen to a much greater degree than the higher plants.

Changes in Oxygen Content during longer periods.

The oxygen content of the pools at the same hour varies greatly from day to day, and this variation depends largely on the intensity of illumination and the temperature at the moment of sampling. The hours of sunshine have been taken as a measure of the intensity of illumination. These records are for the nearest meteorological station, North Berwick, eight miles away, and three sources of error arise : (i) the local conditions at Aberlady ; (ii) the distribution of sunshine during the day (two days having the same number of hours of sunshine might have it either in the morning or afternoon, and this difference would be shown in the oxygen samples made at midday, but not in the sunshine record) ; (iii) the hours of sunshine are not an accurate measure of the intensity of illumination. On the whole, however, it will be seen that the amount of oxygen present in the pools depends fairly closely on the number of hours of sunshine.

Figure 12 shows the oxygen content in percentage saturation of two pools during June, 1931. Curve A gives the conditions in Pool V rich in

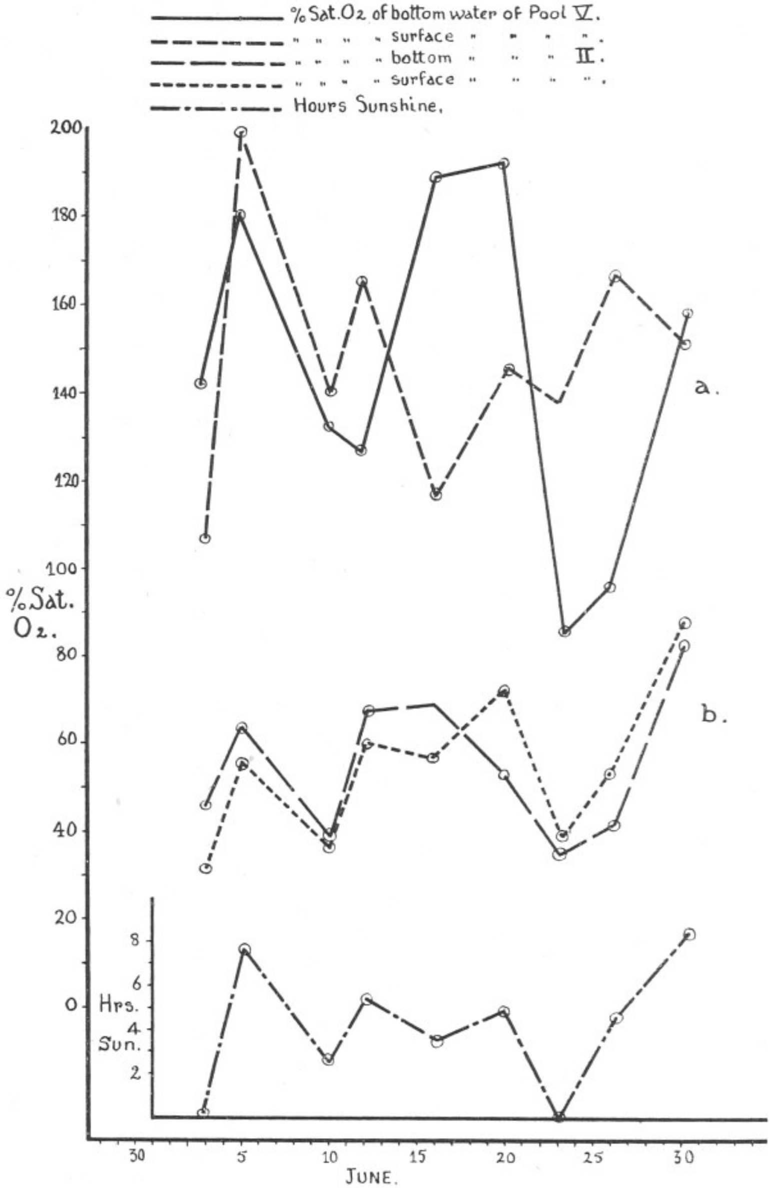


FIG. 12.—The percentage saturation with oxygen of the water of (*a*) Pool V containing much green weed, and (*b*) Pool II containing a few diatoms only.

algæ, and Curve B the conditions in Pool II with no large algæ and few diatoms, but with a fauna of Gobius, Gasterosteus, Corophium, Carcinus, Crangon, Neomysis and Nereis. In Pool V at midday the water is between 100 and 200% saturated with two exceptions, on June 23rd and 26th. On the first date the day was overcast and raining, and on the second, although four hours' sunshine is recorded, it is probable that they occurred in the afternoon after the water samples had been taken. In Pool II, on the other hand, the water is never fully saturated, and often has an oxygen content of 2·5 cc. per litre, less than 40% saturated, even at midday. The hours of sunshine are also recorded, and it can be seen that with the single exception already mentioned the oxygen curves follow fairly accurately that for the hours of sunshine.

The Alkali Reserve.

The alkali reserve of any natural water is important, as on it largely depends the amount of carbon dioxide available for photosynthesis, thus influencing indirectly the supply of oxygen in the pools. It is also closely related to the hydrogen ion concentration.

The alkali reserve of water from the open sea lies between ·0023 N. and ·0026 N., but that of fresh water varies between wide limits ; at Aberlady the alkali reserve of the Peffer Burn is ·0040 N. The water of the salt-marsh pools is derived from direct rainfall, from the sea, and from the land by drainage. It is clear therefore that alterations in the relative volumes of water contributed by these three sources will produce corresponding changes in the alkali reserve of the water of the pools. In addition the amount of evaporation will affect the alkali reserve to a lesser extent.

Direct Rainfall.

The effect of direct rainfall is, naturally, to reduce the alkali reserve of the surface water by dilution, at the same time as the salinity is reduced. If the rain is accompanied by wind the bottom water will also be affected. The effect of rain alone is clearly seen both in Figure 14 and in Figure 15, after the rain of April 24th, when both the alkali reserve and the salinity of the surface water fell considerably. The effect of prolonged wet weather is to lower the alkali reserve of all the water in the pools very considerably. In 1931 after a very wet spring 3·95 inches of rain fell in the first fortnight of June, and the alkali reserve of the pools became very low. The following table gives the values for some of the pools. As soon as the rain ceased the alkali reserve began to rise owing to the effects of drainage water which had previously been masked by the rainfall.

TABLE VIII.

Pool		June 5th.	16th.	20th.	26th.
II	Surface water . .	·0012 N.	·0025 N.	·0028 N.	·0031 N.
	Bottom water . .	·0012 N.	·0034 N.	·0034 N.	·0034 N.
X	Surface water . .	·0025 N.	·0049 N.	·0057 N.	·0059 N.
	Bottom water . .	·0023 N.	·0052 N.	·0064 N.	·0072 N.
IX	Surface water . .	·0009 N.	·0017 N.	·0019 N.	·0027 N.
	Bottom water . .	·0009 N.	·0017 N.	·0018 N.	·0031 N.

Sea Water.

The effect of a tide entering a pool is usually to lower the alkali reserve. This is clearly shown in Figure 13 for Pool XI during April and May, 1933. In the periods between the high tides the alkali reserve rose steadily under the influence of drainage water, but there is a sharp drop each fortnight coinciding with the first of each group of tides. The amount of lowering depends on the alkali reserve of the water entering the pool, and that in turn depends on the ratio between the amount of sea and

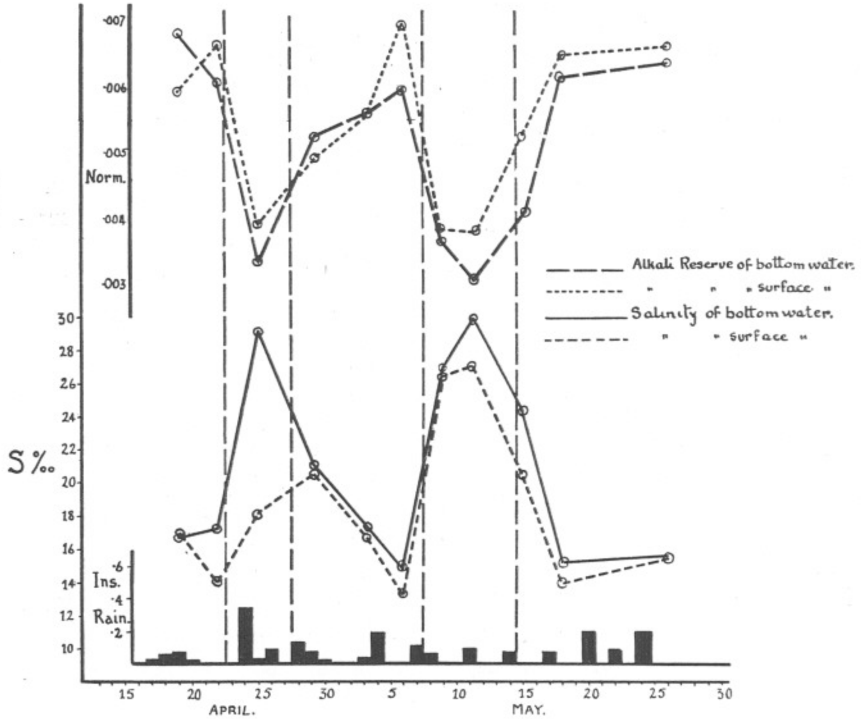


FIG. 13.—The effect of evaporation on the alkali reserve of the water of Pool XI during the spring of 1933. The vertical lines mark the limits of the periods during which tides entered the pool.

river water. As already stated, the alkali reserve of sea water lies between ·0023 N. and ·0026 N., while that of the water of the Peffer Burn is about ·0040 N. For instance, on April 25th the alkali reserve of the bottom water of Pool XI fell to ·0033 N., while on May 11th it fell to ·0030 N. In the first instance, following heavy rain in the night, there was a greater proportion of river water than in the second, so that the alkali reserve did not fall so much. Again the estuarine water during a period of high tides may not have a uniform alkali reserve throughout. Both on April 25th and May 11th the alkali reserve of Pool XI was higher at the surface than at the bottom, showing that the river water had flowed out on the surface of the sea water. This is confirmed by the lower salinity of the surface water.

Drainage water.

The effect of drainage water on the alkali reserve of the marsh pools can sometimes be clearly followed. The water reaching the marsh from the land percolates through sandy soil rich in the remains of marine shells on the right bank, and on the left through soil overlying and partly derived from limestone strata, consequently it has a high alkali reserve. During the spring of 1933 the effect of drainage water was clearly marked. The early part of April was wet, but later little rain fell though drainage water

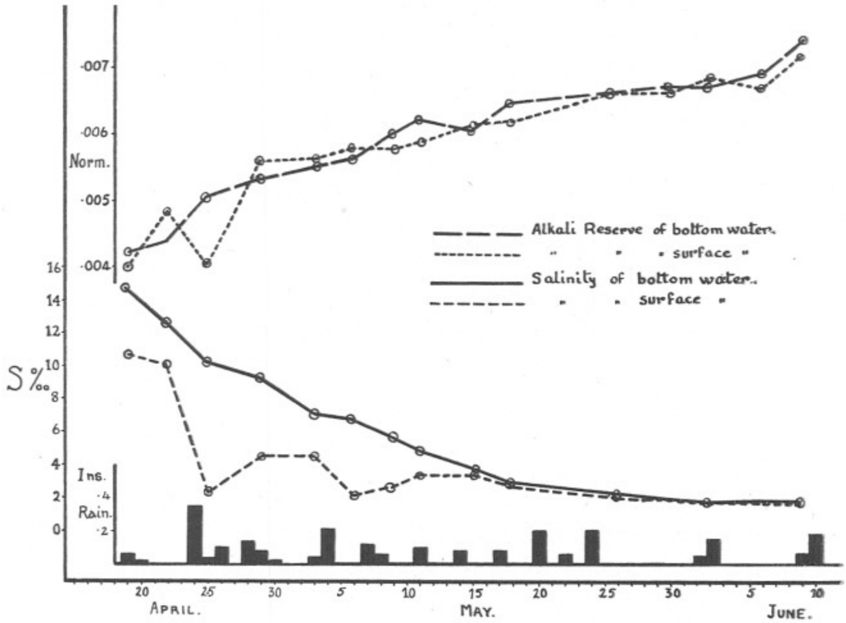


Fig. 14.—The effect of drainage water on the alkali reserve of the water of Pool XIII during the spring of 1933.

continued to be abundant, and, percolating through the soil, lowered the salinity of the pools at the same time as it raised the alkali reserve. A good example of this is shown in Figure 14 for Pool XIII. A tide entered the pool on April 14th, and five days later the salinity of the surface water

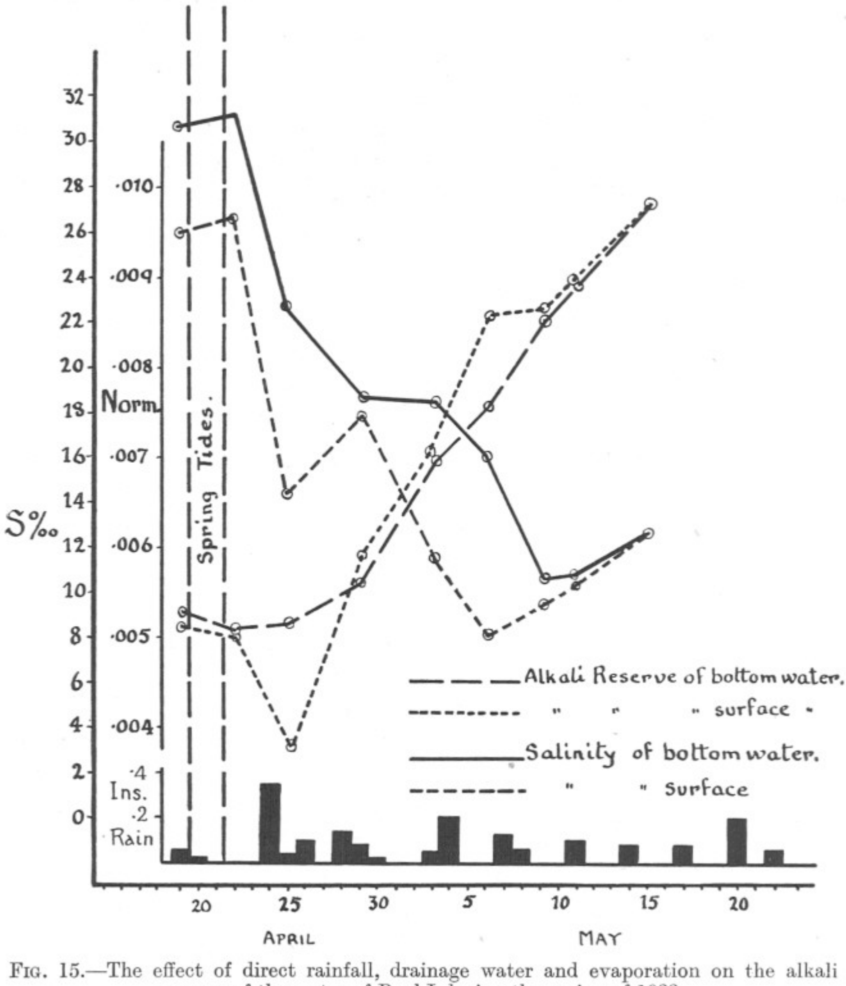


Fig. 15.—The effect of direct rainfall, drainage water and evaporation on the alkali reserve of the water of Pool I during the spring of 1933.

was 10·6°/₀₀, and the bottom water 14·8°/₀₀. After that, until June 17th, when the records stopped, the salinity fell steadily and the alkali reserve rose from an average of ·0041 N. to ·0073 N. Similar results were obtained for Pool I on the left bank, and are illustrated in Figure 15. Here, as the salinity fell (although the pool was gradually drying up), the alkali reserve rose from ·0052 N. to ·0098 N.

Evaporation.

The effect of evaporation is to raise the alkali reserve as well as the salinity, and this effect is shown in Figure 16 for Pool III during May and June, 1933. A high tide entered the pool on May 11th, raising the salinity to 30·6 and 32·2°/₀₀, and lowering the alkali reserve to ·0032 N. and ·0028 N. for the surface and bottom water respectively. After that the salinity and the alkali reserve rose steadily until June 17th, when

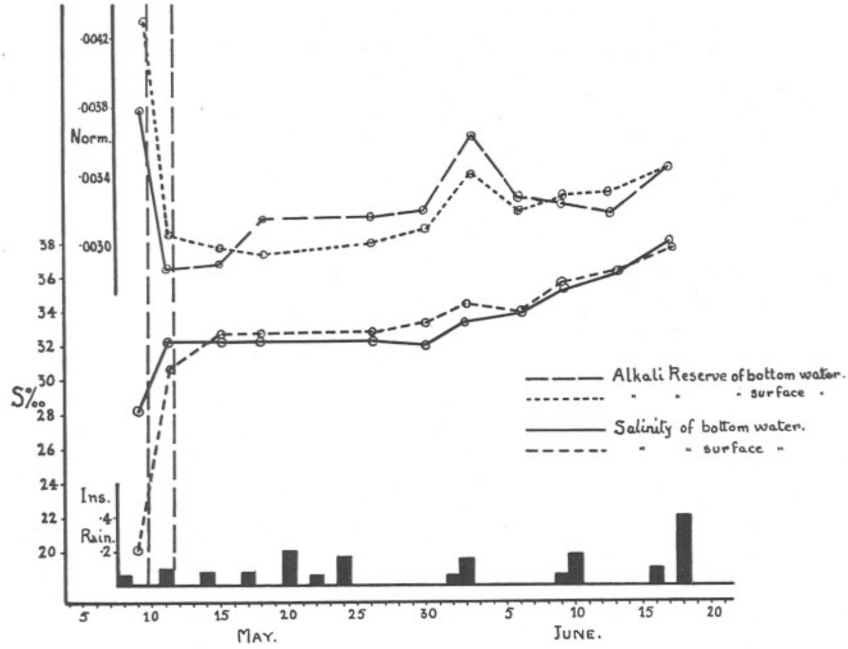


FIG. 16.—The effect on the alkali reserve of the water of Pool III of a tide entering it during the spring of 1933. The vertical lines mark the limits of the periods during which tides entered the pool.

the records stopped. The final salinities were 38·0 and 37·6°/₀₀, and the final alkali reserve for both top and bottom water was ·0034 N.

THE HYDROGEN ION CONCENTRATION.

The hydrogen ion concentration in a particular pool depends on the alkali reserve of that pool, and on the carbon dioxide tension in the water. The carbon dioxide tension, on the other hand, depends on the intensity of photosynthesis and on the amount of animal life in the pool. Since the alkali reserve is usually high and the pools are not, as a rule, crowded with animal life, the chief factor responsible for the control of the hydrogen ion concentration is the amount of vegetation present.

Diurnal variation.

The hydrogen ion concentration, being closely connected with the amount of photosynthesis, may be expected to show a diurnal variation with a minimum value (i.e. maximum pH) at the same time as the maximum oxygen content of the pools, and a maximum (minimum pH) during the night, when the respiration of both plants and animals tends to saturate the water with carbon dioxide. Such diurnal variations are shown in Figure 11 along with the percentage saturation with oxygen. In Figure 11*a* the condition is shown in a pool containing much Enteromorpha, and in Figure 11*b* the condition in a pool containing diatoms only. In both the pH curve follows the oxygen curve, rising to a maximum at 3 p.m. and falling again towards evening. The maximum rise in both pools is about pH 1·0, and is greatest in the bottom water, which also shows the greatest rise in oxygen content. In Figure 11*c* the conditions in a pool containing very little plant life are shown. The increase in oxygen is very much less than in the other pools, and the hydrogen ion concentration is unchanged. In this pool the alkali reserve was much higher, ·0072 N. as against ·0031 N. in the others, and was probably instrumental in reducing the effect of such photosynthesis as took place in this particular pool.

The Hydrogen Ion Concentration during Longer Periods.

A similar relationship between the hydrogen ion concentration of a pool and the oxygen content can be shown for longer periods of time.

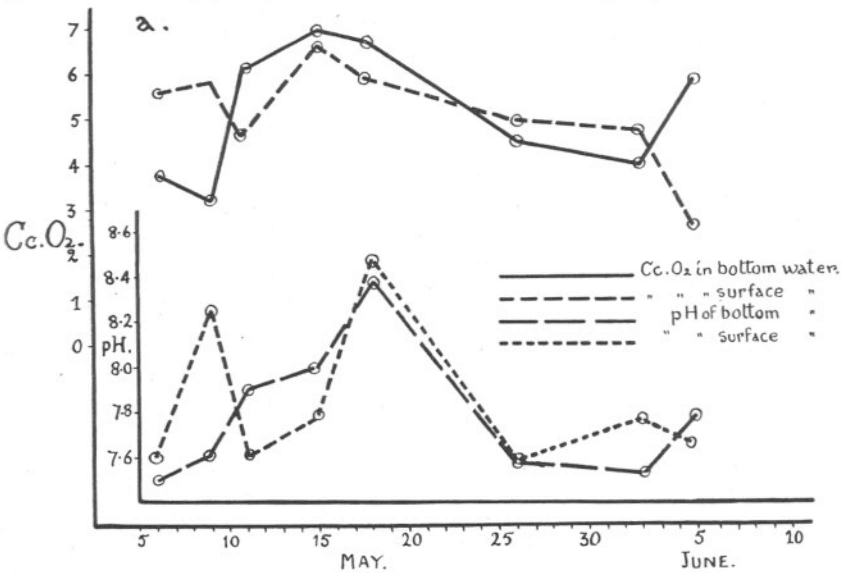
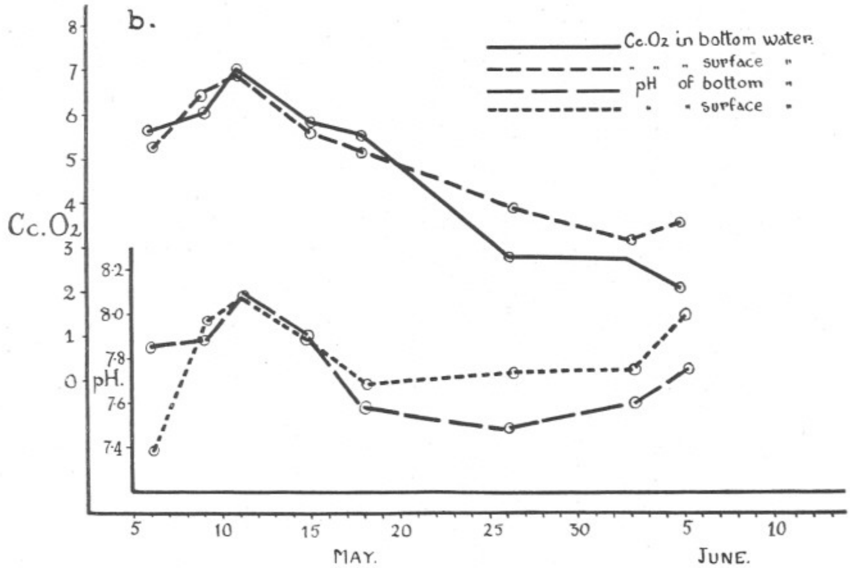
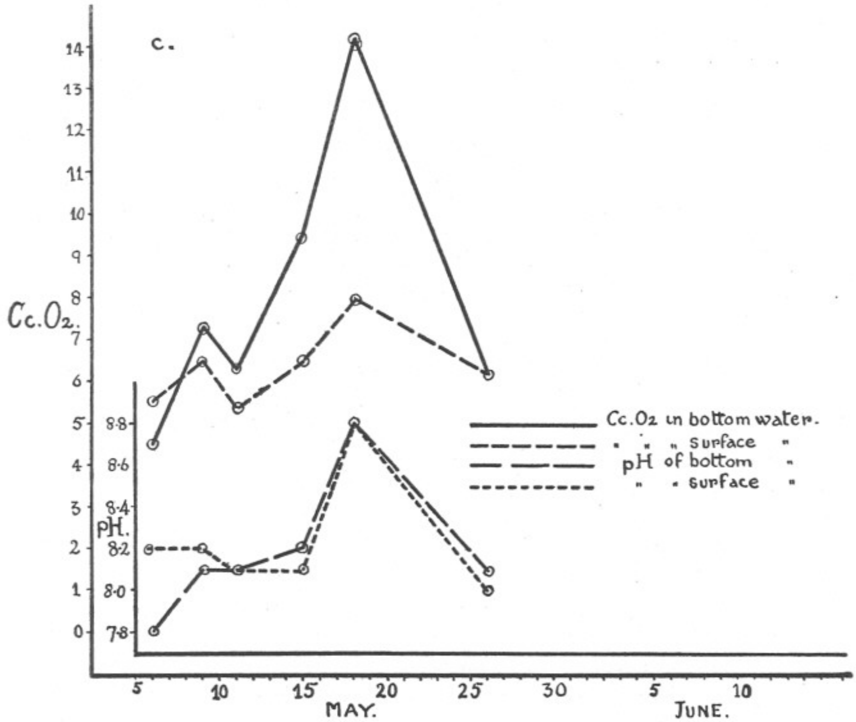


FIG. 17.—The changes in hydrogen ion concentration and in the oxygen content of the water of three pools during the spring of 1933. (*a*) Pool XIII.



(*b*) Pool V.



(*c*) Pool IX.

Fig. 17. (*contd.*)

In Figure 17 the conditions in three different pools all containing a considerable amount of plant life are given for the month of May and part of June, 1933. In all of them the oxygen and pH curves agree closely, the maximum and minimum values falling approximately on the same days.

The Range of Hydrogen Ion Concentration.

The total pH range in the marsh pools varies from a minimum of pH 6·8 to a maximum of 9·6, but these extreme values were not recorded from the same pool. The highest pH values are obtained in the pools with the greatest amount of weed. The following tables give values for the three pools previously discussed.

TABLE IX.

	Pool V. Enteromorpha.		Pool IX. Diatoms.		Pool XIII.	
Date.	Top pH.	Bot. pH.	Top pH.	Bot. pH.	Top pH.	Bot. pH.
5.6.31	9·6	9·0	7·7	7·5	7·4	7·0
10.6.31	8·0	8·8	7·6	7·4	7·2	7·2
23.6.31	9·2	9·2	8·2	7·7	7·4	7·4
19.4.33	8·0	8·0	7·9	8·0	7·5	7·4
9.6.33	8·2	8·2	8·2	8·0	7·6	7·6

THE TEMPERATURE.

The Daily Variation.

The daily variation of temperature in the pools was not studied exhaustively since no night observations were made. The following figures are typical for the hours of daylight.

TABLE X.

Date.	Pool.	Depth.	Temperature in °C. Max.	Min.
June 14th, 1932	V	Top	21·5	14·0
		Bottom	19·0	13·5
October 27th, 1933	V	Top	5·5	4·5
		Bottom	6·0	5·0

The Seasonal Variation.

During cold weather all the pools of the marsh may be covered with a sheet of ice, the thickness of which depends on the salinity of the surface layer of water. This is particularly marked when the frost follows a period of calm wet weather and a layer of almost fresh water lies on top of the salter water in the pools. During hard frost the pools may be covered with one to four inches of ice for several weeks at a time, as in January, 1933.

During the summer the average temperature is considerably above that of the open sea, and the following temperatures are typical for the months of June and July.

TABLE XI.

Depth.	Temperature °C.				
Surface water	24	27	24	25	27
Bottom water	23·5	26	25	24	24
Surface mud	23	24·5	25	24	24

Higher temperatures have often been recorded in shallow pools densely crowded with weed. The highest figure was 32·5° C., on June 17th, 1933. This temperature did not appear to be harmful to the animals living among the weed, *Sphæroma rugicauda*, *Melita palmata*, *Hydrobia ulvæ* and *Limopontia capitata*, all of which appeared normally active.

Temperature in the Mud.

The temperature in the mud varies very little from that of the overlying water, but may show a lag of a degree or two with rapidly rising or falling temperatures.

When, however, the pools are dry, then the temperature of the mud is often very high at the surface and progressively lower at greater depths. The following table gives some temperatures at different depths in the mud of dry pools on June 17th, 1933, when the sun temperature was 30·5° C. and the shade temperature 25° C.

TABLE XII.

Depth Below Surface.

½ inch.	2 inches.	4 inches.
31·5	22·0	—
28·0	22·0	—
29·0	24·0	18·0
28·0	22·5	18·0
31·0	26·0	22·0
29·0	26·0	24·0
33·0	27·0	24·0

DISCUSSION.

The particular interest of a salt-marsh lies in the fact that it is one of the meeting-places of the fresh-water and marine faunas. As a result of prolonged acclimatisation a specialised brackish-water fauna has been derived from both sources, much of which seems to have become incapable of living for any length of time in its old environment. A similar specialised fauna is found in estuaries, land-locked seas, lagoons and salt-marshes all over the world, and, to a lesser extent, in inland saline lakes. In temperate regions the number of species forming the community is relatively small, but in tropical waters it is very large, the fauna of any big estuary or brackish lagoon showing numerous endemic species as well as many others of wider distribution (Annandale, 1922).

Remane (1934) gives graphs to show that the number of marine species in brackish water of varying salinity decreases steadily as the salinity falls. Similarly the number of fresh-water species falls as the salinity rises. Where the distribution curves overlap the minimum number of species occurs. Contrary to what one might expect, this poor fauna is not found where the water is of intermediate salinity at about 17·5°/₀₀, but lies at a point between 5 and 8°/₀₀. Although in a large estuary or body of water such as the Baltic this observation can be easily checked, in a salt-marsh the salinity changes are so large and erratic that it is difficult to classify the pools on a salinity basis. It is, however, clear that the pools with a salinity of between 15 to 20°/₀₀ support the richest fauna from the point of view of number of species. In pools entered by fewer tides fewer species occur, *Nereis diversicolor*, *Corophium volutator* and *Gammarus duebeni* forming the greater part of the fauna, while in the freshest pools again, although the marine animals have disappeared, the number of species is again larger owing to the predominance of fresh-water animals.

In discussing a problem such as this the need is at once felt for some convenient basis of classification of the environment. An attempt has been made to supply this by Redeke (1922 and 1931), who takes the chlorine content of the water as the limiting factor in the distribution of members of the brackish-water fauna. The following is his scheme of classification :

		Cl. gm. per lit.	S°/₀₀.
Fresh Water	. . . .	0·0— 0·1	0·0— 0·2
Brackish Water	Oligohaline	0·1— 1·0	0·2— 1·9
	Mesohaline	1·0—10·0	1·9—18·6
	Polyhaline	10·0—17·0	18·6—31·8
Sea Water	. . . .	17·0+	31·8+

These divisions, he states, correspond closely to the differences in the fauna, no matter what type of brackish water is investigated.

The oligohaline region has few characteristic animals, the bulk of the fauna being formed by fresh-water species which are able to withstand a certain amount of salt. Redeke (1922) cites *Eurytemora affinis* and *E. velox*, *Cordylophora lacustris* and *Dreissenia polymorpha* as typical of this region. To these should be added *Gammarus duebeni*.

The mesohaline zone is inhabited by the most characteristic brackish-water species, such as *Brachionus mulleri*, *Manyunkia estuarina*, *Nereis diversicolor*, *Sphæroma rugicauda*, *Corophium volutator*, *Neomysis vulgaris* and *Gobius microps*, which, although found also in other regions, reach their maximum numbers in the mesohaline zone.

Just as the bulk of the oligohaline fauna is composed of fresh-water species, so the greater part of the polyhaline fauna is derived from the sea. *Corophium crassicorne*, *Gammarus locusta* and *Eurytemora hirundo* are given by Redeke as typical polyhaline animals.

Although this classification has been found to be satisfactory when applied to lagoons and large estuaries, when an attempt is made to apply it to small bodies of water such as salt-marsh pools it breaks down completely owing to the fact that every tide and every shower of rain alters the composition of the water in the pools, which may pass from a polyhaline to an almost oligohaline condition in a few days, so that only animals which are able to withstand the whole range of salinities for an appreciable length of time will be able to survive permanently in the small pools of a salt-marsh. Under these circumstances isolated observations on the salinity of such pools are useless as indicators of the conditions under which an animal is living. Redeke himself admits the breakdown of his scheme when dealing with the conditions in small estuaries where the salinity during the intertidal period ranges from almost pure sea water to fresh water. As a consequence of this the salinity of the pools at Aberlady can only be regarded as controlling between wide limits the distribution of the fauna. The average conditions of salinity throughout the year show that the greater part of the Aberlady marsh belongs to the mesohaline zone, and as such supports a typical brackish-water fauna. All the characteristic species given by Redeke are present, and, in addition, a number of species which cannot be regarded as typical since they do not occur in estuaries. This difference is correlated with one important characteristic of salt-marsh pools, namely, the stillness of the water. This absence of movement makes it possible for fresh-water animals in particular, living in neighbouring ponds and lakes, to invade the less saline pools of the marsh. At Aberlady the pools of low average salinity are limited in size and number, and are liable to be invaded by sea water, so that the fresh-water fauna found in them is sparse. The majority of the species can be traced to the neighbouring ponds from which successive waves of colonisation take place during each period of low salinity. Certain brackish-water species also only occur in still water. Some of these such as *Aëdes detritus* are directly dependent on lack of current, others such as *Chironomus aprilinus*, *Protohydra leuckarti* and *Cricotopus vitripennis* appear to depend on a substratum of soft mud, which is most commonly laid down in still water, while yet others are found only on certain kinds of algæ. Some of these algæ are non-rooting, and can occur only in still water. *Melita palmata*, *Procladius choreus*, *Alderia modesta* and *Limopontia capitata* are species which, absent from estuaries, are dependent on marsh vegetation.

One point of widespread interest is suggested by an examination of any fauna list of brackish-water species, and a consideration of the relative proportions between the fauna derived from the sea and from fresh water. Once the power to colonise a new type of habitat has been developed, and the old habitat entirely abandoned, it is more difficult to return to the original environment than it was in the beginning to become acclimatised to the new. Colonisation of fresh water began in the Devonian (Sollas, 1905), has proceeded ever since under suitable circumstances, and is proceeding at the present day. From this steady influx of marine species first into brackish, then into fresh water, has been derived the present-day fauna of rivers and lakes. Yet during all that time few species have returned to brackish water, fewer still to the sea. By far the larger number of animals in brackish water are derived direct from the marine fauna, and only a few from the fresh water. Of these few the majority belong to the insects which, being encased in a chitinous covering, are relatively independent of the environment.

When the changing conditions in the marsh are compared with those of the open sea it is possible to understand some of the difficulties which confront animals attempting to colonise such an environment. The ocean shows small seasonal and daily variations in salinity, in oxygen content, in hydrogen ion concentration, and in temperature ; the salt-marsh water is constantly changing, showing in twenty-four hours far larger fluctuations than can be found in the open sea in six months. The gap between the two extremes is partially bridged by the conditions found in inshore waters and the mouths of estuaries, but there the lines of retreat from too unfavourable conditions are always open. In small estuaries, for instance, the change from salt to almost fresh water is rapid, occurring twice in the twenty-four hours, but animals attempting to gain a footing there have three ways of escape from the extremes : they may retreat down the estuary with the falling tide and return again with the flood as do crustacea such as *Praunus flexuosus*, or they may burrow deep in the mud as do worms and molluscs such as *Arenicola marina* and *Scrobicularia* *piperata*, and so escape both the high salinity of full tide and the low salinity of the river water; or again they may allow themselves, like *Carcinus maenas*, to be left behind by the falling tide to take refuge in crevices or under moist weed, and so avoid the lowest salinities. The animals in the salt-marsh pools are offered no alternatives. They cannot go out to sea, they cannot permanently remain deep in the mud, they cannot leave the pools for an indefinite period; if they are to survive at all it must be by their power of adaptation to circumstances and not by avoiding them.

The greatest difficulty for the salt-marsh animals is that of the changing salinity owing to the osmotic effect on their body fluids. A few animals such as *Gasterosteus aculeatus* and *Anguilla vulgaris* are known to be able to withstand sudden changes from salt to fresh water. It is animals such as these that are the most successful colonisers. In many instances, however, it has been shown that marine animals can be acclimatised to low salinities and even to completely fresh water by lowering the salinity gradually (Beudant, 1816). The success of the experiment depends, however, on the slow rate of change, a sudden lowering of the salinity by even a few parts per thousand causing death. It is just this problem of the rate and degree of change which is so vital in the salt-marsh, since the fluctuations there are so great from day to day.

Early work on the body fluids of marine animals suggested that their osmotic pressure was always identical with that of sea water, but recent work has established that in nearly every case the osmotic pressure is very slightly higher than that of the surrounding medium. When, however, the salt content of the environment is reduced by dilution this high osmotic pressure is not maintained, it drops rapidly owing both to the passage inwards of water and to loss of salts, and, if the dilution is great enough and the time of exposure long, death follows. In those animals able to withstand large changes of salinity, however, this is not the case. The osmotic pressure is maintained at a level well above that of the surrounding water, very little swelling takes place and the animals remain active indefinitely in the diluted medium. A comparison between closely related forms from the open coast and from estuaries, such as *Nereis cultrifera* and *Nereis diversicolor* (Beadle, 1931), shows that the fall in osmotic pressure and the swelling due to uptake of water occurs in the animals from both localities, but that in the brackish-water species the process is quickly arrested and no loss of activity ensues. Further investigation shows that this arrest is accompanied by a rise in the oxygen consumption, which reaches a maximum and then gradually falls to a level somewhat above the normal and continues there indefinitely. This increase in oxygen requirements suggests that the difference between the external and internal osmotic pressure can only be maintained by the expenditure of energy on the part of the animal. An interesting point arises here, namely, that an initial rise in oxygen consumption was also present in *Nereis cultrifera*, but was not maintained as the osmotic pressure began to fall, suggesting that marine animals are potentially able to control the osmotic pressure of the internal medium. Schwabe (1932) has recently shown that the ability to maintain osmotic control in brackish water is not equally strong at all periods of the life history, but depends on the physiological condition of the animal at the time. His experiments show that during periods of prolonged hunger the osmotic pressure of the body fluids of various crabs kept in diluted sea-water falls slowly until the animals become distended with water and die. He also shows that after moulting the osmotic pressure drops considerably below the normal in diluted sea-water and that the same thing occurs during the period when the female is carrying eggs. This last observation probably explains why, although several kinds of crustacea penetrate right into fresh water, they are never known to breed there (Gurney, 1923 ; Annandale, 1922 ; Peters and Panning, 1933).

The rise in the oxygen requirements shown by Schleiper (1931), and also by Beadle (1931), constitutes a second difficulty for salt-marsh animals. Beadle shows that *Nereis diversicolor*, on being moved from 100% to 16·5% sea water, more than doubles its oxygen requirements, while Schleiper gives similar figures for *Carcinus maenas*, and it is probable that a comparable rise occurs in all brackish-water animals. Schwabe (1932) has also shown that keeping *Carcinus maenas* under conditions of low salinity combined with low oxygen tensions has a deleterious effect on the activity of the crab, and that the osmotic pressure of the blood of such animals falls considerably lower than that of animals subjected to low salinities with a plentiful supply of oxygen. In the salt-marsh temperatures are often high, increasing the activity of the animals and reducing the oxygen capacity of the water. Oxygen, although often abundant during the day, is scarce during the night, and it is conceivable that after rain this oxygen lack might have a disastrous effect on the animals, already faced with the difficulties of diluted salinities.

An observation by Bateman (1933) may have some bearing on the problem of survival in brackish water. He states that in captivity *Carcinus maenas* placed in half-strength sea water can only survive between pH 6·0 and 9·0. Above pH 9·0 death occurs within thirty-six hours. In the marsh small crabs appear to be evenly distributed, and are found among the weed in pools with a pH as high as 9·6. It is, however, only during the day that this high value is found, during the night it may be as low as pH 8·0. Either Carcinus can survive a high pH over short recurring periods, or, under natural conditions, changing hydrogen ion concentrations have no effect. It may be significant that in the Aberlady salt-marsh the pools with the highest pH are also the pools with the highest salinity. It is generally considered that normal variations in the hydrogen ion concentration of the open sea do not affect the fauna adversely (Harvey, 1928), but in an atypical marine habitat such as a salt-marsh, showing large fluctuations, the hydrogen ion concentration may be of considerable importance.

Von Martens (1857) has suggested that a possible reason for the greater number of animals of marine origin in brackish and fresh water in the tropics lies in the more even temperature conditions throughout the year. The work of Giard (1883) showing that Gasterosteus is only able to withstand sudden changes from fresh to salt water and vice versa provided that the temperature is kept even, supports this view. Whether the temperature is the principal factor involved in successful colonisation of brackish water is another matter. The temperature variations in the temperate zone are certainly much greater than in the tropics, not only in fresh water but also on the seashore. Southern (1915) gives 16·5° C. as the maximum seasonal variation, and 4·1° C. as the maximum variation in twenty-four hours, for the water of Ballynakill harbour. The changes in rock pools must be much greater. Many of the colonisers of salt-marshes live normally in this littoral zone, and are already acclimatised to very variable temperatures. An increase in temperature leads to an increase in the rate of respiration and to a lower saturation point of the water with oxygen. On the other hand, the rate of photosynthesis is increased and the water of the pools is readily supersaturated, so that only in those devoid of all vegetation would an oxygen shortage be likely to occur during the summer. The density of population is sometimes great, but the size of the animals is small, so that it is doubtful whether high temperatures alone present any difficulties to salt-marsh animals derived from the littoral zone.

Little is known of the effect of other factors on the vitality of animals in brackish water. Pantin (1931) finds that the presence of calcium in the water has a marked effect on the power of *Gunda ulvæ* to withstand low salinities and suggests that the distribution of Gunda is limited to small streams of hard water ; 15% of the calcium found in sea water appears to be sufficient for the needs of the animal. Although the amount of calcium in the water at Aberlady was not directly investigated, in view of the situation of the marsh on an old raised beach in close proximity to calciferous strata, it is permissible to assume that the alkali reserve of the water consists almost entirely of calcium salts. If this is so the calcium content of the water has not been observed to fall seriously below 50% of that found in pure sea water, and in many instances, when drainage water is abundant, is three or four times as great. Under the circumstances it is unlikely that calcium shortage plays any part in the economy of a marsh such as that at Aberlady. In other marshes, however, situated in peat districts, as on the west coast of Scotland and in Ireland, it may be of considerable importance, especially as it has been shown by Ellis (1933) that in *Nereis diversicolor*, a typical salt-marsh species, the absence of calcium in the water causes an increase in weight, followed by loss of movement greater than that occurring ordinarily in diluted sea water, and that addition of calcium instantly starts a return to normal conditions.

SUMMARY.

The salt-marsh under investigation is situated at Aberlady Bay on the south shore of the Firth of Forth, fifteen miles east of Edinburgh.

The marsh is small and occurs at the mouth of a stream. The character of the soil on the two banks differs, being on the one side muddy with permanent pools, and on the other sandy, so that the pools tend to drain dry. The vegetation of the pools is variable, some containing species of Zostera, Ulva, Enteromorpha and Vaucheria, others having only diatoms.

The surface of the marsh has a characteristic fauna of species such as *Orchestia gammarella*, *Paragnathia maxillaris*, *Podura marina*, and *Dichirotrichus pubescens*. The pools can be divided into two groups, those having a low average salinity of less than 5 $^{\circ}/_{\circ\circ}$, and those having an average salinity of 15 to 20$^{\circ}/_{\circ\circ}$. In the former brackish-water species such as *Aëdes detritus*, *Gammarus duebeni* and *Helophorus viridicollis* occur in numbers as well as fresh-water species such as *Agabus bipustulatus*. In addition, during periods of very low salinity, species such as *Culex pipiens* and *Limnæa truncatula* colonise the pools from the neighbouring marshes. In the pools of higher salinity *Gobius microps*, *Neomysis vulgaris*, *Corophium volutator* and *Nereis diversicolor* are common. *Alderia modesta*, *Limopontia capitata* and *Protohydra leuckarti* also occur in certain pools in large numbers. Marine forms such as *Macoma balthica*, *Mya arenaria* and *Arenicola marina* are also found.

Detailed observations were made on the conditions under which the animals in the pools are living.

The salinity of any pool is determined by the salinity of the water entering it at the last high tides and by the subsequent weather conditions. In hot weather during the summer the salinity of some pools may be as high as 40$^{\circ}/_{\circ\circ}$, in wet weather as low as 8$^{\circ}/_{\circ\circ}$. Other pools reached by fewer tides fluctuate between 15 and 0·5$^{\circ}/_{\circ\circ}$.

The oxygen content of the water depends largely on the amount of vegetation in the pool. Large daily fluctuations take place, the water on a sunny afternoon being as much as 200% saturated, and in the same pool at dawn as little as 40%.

The alkali reserve of the pools is high, being largely derived from drainage water percolating through an old raised beach behind the marsh. It may reach as high a value as ·0098 N., but a tide reaching the pool may lower it to ·003 N. During very wet weather it may be as low as ·0009 N.

The hydrogen ion concentration varies between pH 6·8 and 9·6, depending on the amount of vegetation and on the hours of sunshine.

During the summer the temperature may reach 32° C., while in winter even pools of high salinity may be frozen over for several weeks at a time.

The composition of the fauna and the relationship of the conditions to the life of the animals is discussed in connection with recent work on the physiology of some of the inhabitants of brackish water.

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