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THE ECOLOGY OF THE TAMAR ESTUARY

VII. OBSERVATIONS ON THE INTERSTITIAL SALINITY OF INTERTIDAL MUDS IN THE ESTUARINE HABITAT OF *NEREIS DIVERSICOLOR*

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(Text-figs. 1–5)

INTRODUCTION

The polychaete *Nereis diversicolor* F. O. Müller is one of the most characteristic elements of the brackish-water fauna of north-western Europe, and inhabits an extremely wide range of salinities. As a background for comparative physiological studies of chloride regulation in worms from different parts of the geographical range, the writer has attempted to describe the salinities and the variations in salinity endured by populations of *N. diversicolor* in ecologically distinct and geographically well separated areas. Three principal environments have been studied:

(1) *Relatively stable high salinity*. Since it was initially hoped to study *N. diversicolor* in a 'marine' habitat, a study was carried out at Kames Bay, Millport, on a presumably marine beach, but it was found that *N. diversicolor* was restricted to a brackish zone produced by underground seepage of fresh water (Smith, 1955*a*). Since I have been unable at any time to find this species except in areas subject to some lowering of salinity, my general conclusion has been that in a 'marine-dominated' habitat *N. diversicolor* behaves as a brackish-water animal and is to be found in the least saline portion of the available ground. A similar conclusion was reached after studies in the Isefjord, Denmark, where the general level of salinity is about 20‰ and quite stable (Smith, 1955*b*).

(2) *Relatively stable low salinity*. The most obvious contrast to the marine-dominated intertidal habitat is found in the inner Baltic Sea, wherein *N. diversicolor* reaches the less saline limit of its ecological range. In these tideless waters the salinity is low and, over most of the year, fairly constant. Studies carried out near the Zoological Station, Tvärminne, South Finland, have also been reported (Smith, 1955*b*). In this region the distribution of *N. diversicolor* is surprisingly unlike that seen in Britain. Whereas in British estuaries the species has been observed to penetrate into nearly fresh water, and much farther than any of its usual brackish-water associates, in the Baltic the reverse is found. The range of *N. diversicolor* is limited at summer salinities in excess

of 4‰, and a number of its brackish-water associates (*Cardium*, *Mytilus*, *Macoma*, *Balanus improvisus*) penetrate into less saline waters. The answer to this paradox may lie in the fact that although the inner Baltic is of fairly stable salinity during most of the year, there is an annual lowering of salinity as a result of melting snows, occurring when temperatures are still very low, and possibly at the breeding period of *N. diversicolor*. Whether the limiting factor is the effect of low salinity upon the adult population (whose osmoregulatory capabilities may be temporarily reduced by low temperature) or upon some phase of reproduction is not yet clear. We must consider, however, that whatever the mode of action, the special hydrographic characteristics of the inner Baltic are important in limiting the spread of *N. diversicolor* into waters of low salinity.

(3) *The estuarine habitat.* In comparison with the two sorts of environment mentioned above, the estuarine habitat is characterized by marked salinity *variation* resulting from tidal action. The present paper discusses this third type of salinity regimen, and completes the series of three studies on the distribution of *N. diversicolor* in relation to salinity which the writer was able to carry out in 1953–54. Most of the observations have been made in the estuary of the River Tamar, with additional observations near the head of the Kingsbridge Estuary.

Any estuary exhibits a complex pattern of salinity changes, and individual estuaries may differ very greatly from each other. Day's review (1951) provides a most useful general account, while Rochford's classification of Australian estuaries (1951) illustrates the great diversity which may exist among estuaries in respect to their pattern of salinity variation. In attempting to consider the physiological adaptations of an estuarine animal, we must consider not only mean salinity, which over the range of *N. diversicolor* varies from over 25‰ down to nearly fresh water, but the extent of salinity variation as well. The difficulty of characterizing in any simple way the salinity to which a given population is exposed is very great. At each point within an estuary there may be noted maximum and minimum salinities, but the magnitude of these extremes does not tell the whole story, for their duration and the rates of change of salinity must also be considered (Bassindale, 1943). These factors differ not only horizontally as one proceeds up an estuary from the sea and vertically with intertidal height, but also they vary with time, in all but an idealized estuary where tidal ingressions of sea water were regular from day to day, and freshwater inflow constant and uniform. In actuality, tidal ingressions vary daily throughout the lunar tidal cycle, and are markedly affected by local wind conditions, while freshwater inflow is subjected to seasonal or erratic variation in rainfall. The character of estuaries varies topographically according to volume and configuration of the estuary bed, and with the relative volumes of estuary bed and daily freshwater inflow.

For purposes of the present study, the estuary of the River Tamar has offered the advantages of being relatively accessible from the laboratory at Plymouth, of possessing a long salinity gradient inhabited by *N. diversicolor*, and of being an estuary about which much useful published information is available to the newcomer. Much, however, remains to be learned, and it is hoped that the data presented in this paper will extend the existing knowledge somewhat. Time has not permitted a comprehensive or complete survey, but the effort has been made to base these studies upon reliable previous work, and to relate what has been learned to the total picture.

The most useful introduction to the River Tamar is given by Hartley & Spooner (1938), whose paper should be consulted by any reader not familiar with the locality. By reference to the map (Fig. 1) it may be noted that the lower 10 km of the estuary lies below the confluence of the Tamar and the River Tavy, and that this common estuary is joined by the Lynher River some 5 km from the mouth, which opens into Plymouth Sound. Above the entrance of the Tavy, the Tamar gradually narrows and becomes winding. *N. diversicolor* extends to the vicinity of Calstock (22·5 km from Plymouth Sound), above which point the vegetation and bottom fauna are essentially fresh water, although tidal action extends another 7 km to Weir Head.

The fauna of the Tamar Estuary has been described qualitatively by Percival (1929), whose account is generally useful, although little indication of abundance of individual species is given. It may be noted that Percival worked in a dry summer, and recorded upstream limits for planktonic organisms and certain crustaceans (e.g. *Carcinus* present at Calstock) which may be somewhat atypical. Spooner & Moore (1940) have given a thorough quantitative account of the macrofauna of the intertidal muds of the Tamar as far upstream as North Hooe (18 km). I have been able to add very little general information to their excellent account, except for additional observations on *N. diversicolor* at stations upstream from the limit of their survey. Spooner & Moore reported *N. diversicolor* present scatteringly in St John's Lake, 'apparently here confined to the lower tidal levels', increasing in abundance up-river, and reaching its greatest density at their uppermost station, North Hooe. This increase was believed to be independent of substrate, since equivalent muds are available over more than the entire range of the species in the river. In the lower reaches of the estuary, *N. diversicolor* was found at a lower-intertidal position, but over most of its range was reported to have its maximum density above mid-tide.

The pattern of salinity variation in the Tamar is unquestionably complex, and in comparison with the amount of information available on the fauna, the published data on salinity are still far from complete enough to give an overall picture of the salinity of the *N. diversicolor* habitat. Percival (1929) gave salinity values at or near high and low water for a number of stations from the lower estuary up to the head of tidal action, and the distribution of salinities

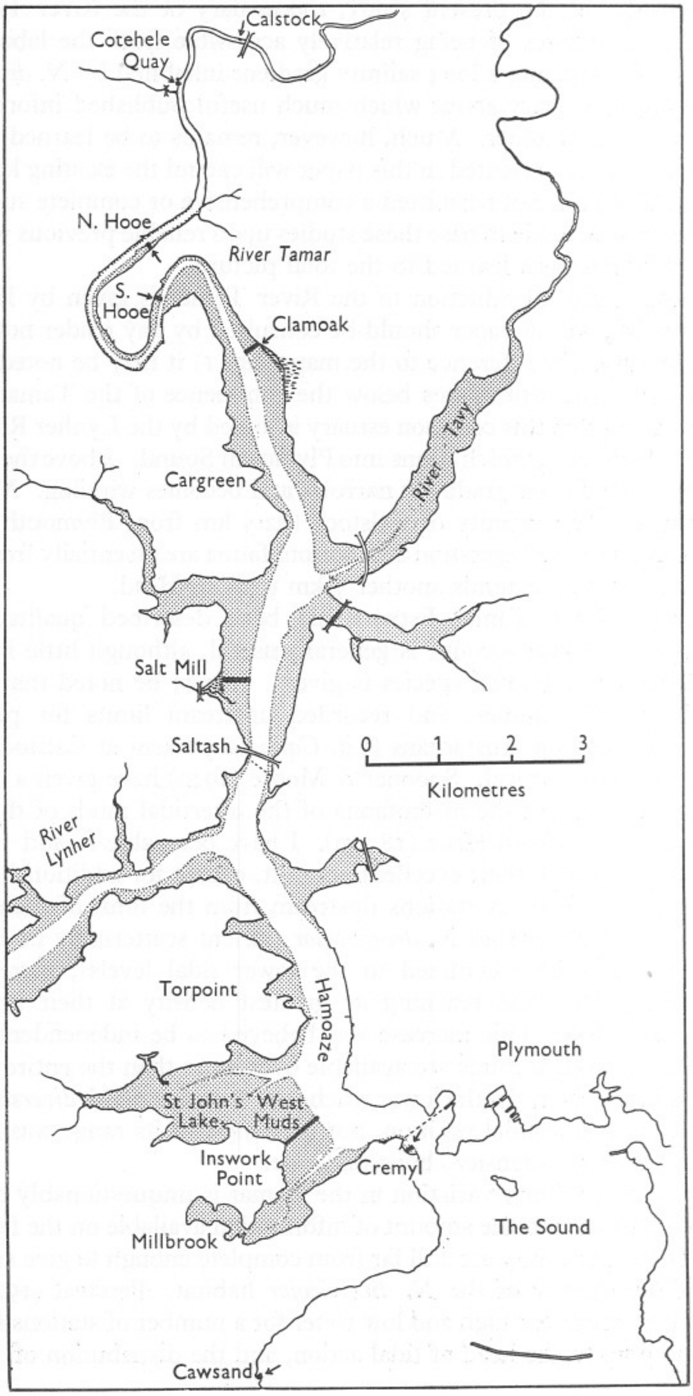

Fig. 1. Sketch-map of the Tamar Estuary showing location of stations and points mentioned in the text. Stippled areas represent intertidal muds between H.W.M. and L.W.M. of ordinary tides. Compiled from various sources. A more detailed map is found in Hartley & Spooner (1938).

correlates well with the reduction of the marine fauna as one passes up-stream. Most of Percival's data were obtained during a summer of 'negligible' rainfall (86 mm at Plymouth in 86 days), hence they probably do not represent the lower and perhaps limiting salinities reached in winter and spring. Percival judged from his salinity data that the main body of inflowing sea water did not pass Cargreen (11 km from the mouth) and that the greatest drop in surface salinity took place between Cargreen and the region about Calstock. In this same stretch of river occurred the greatest differences in salinity between high and low tide. Milne (1938) recorded salinity stratification in May–June on one rising and one falling tide in a cross-section of the estuary 7·7 km from the mouth, between Saltash and Neal Point and thus within the wide portion of the river strongly influenced by salt-water ingression (salinity range *c.* 15–32‰). Milne calculated salinity fluctuation at various intertidal heights, and showed that organisms living near low-water mark must suffer the greatest change of salinity at a tidal cycle; those near high-water mark must experience the least change in salinity; those at mid-tidal positions and those living subtidally are subjected to fluctuations intermediate in magnitude between those at the first two levels. Additional data for the lower estuary are given, and for a few up-stream points values which are in general agreement with Percival's data, emphasizing the marked drop in mean salinity and the considerable salinity variation of the River Tamar up-stream of its union with the River Tavy. However, the available data are insufficient to define the up-stream limits of *N. diversicolor* in terms of salinity. It has, therefore, been necessary to seek additional data in the region above the middle reaches of the estuary.

Methods

Field work was carried out from April to mid-June and from late September into December 1954. Since physiological studies on *N. diversicolor* inhabiting the less saline reaches were the main objective, most observations have been confined to the region from Clamoak to Calstock, with comparative observations in the lower reaches (Salt Mill and St John's Lake) as well as in the 'marine-dominated' Kingsbridge Estuary. In the early weeks of work the extent and complexity of the Tamar Estuary were not fully appreciated; in the last few weeks bad weather contributed to incompleteness of the record.

With the limited available time and the difficulty of securing boats when and where needed, it was felt that the usual method of obtaining samples of water close above the mud at representative intertidal levels and at enough different stages of tide would be impractical. The expedient was therefore adopted of measuring the salinity of water contained in the mud itself by means of a series of samples forming a transect of the exposed shore at each station. It is obvious that the salinity of interstitial water reflects in some degree the salinity of the water that has lain above the mud. Precisely what the relationship is between interstitial salinity and the varying salinities of the overlying water is not known. At present it certainly cannot be claimed that the salinity of the interstitial water represents the mean salinity of the overflowing water—it can merely be said that the interstitial salinity must be the resultant of the varying overlying salinities and the duration of the exposure. Until the actual time-course of salinity changes of the water just above a given intertidal point is worked out, it does not appear possible to give a significant 'mean', either arithmetic or harmonic, for salinity at this point. If the change of salinity with time followed a symmetrical pattern (e.g. sinusoidal), the median value would approximate a mean value, but if, for example, the time course followed a pattern wherein one extreme (at high water) acted for a much longer time than the opposite extreme (at low water), then the 'mean' of isolated values taken at high and low water would represent only a median value, and not anything like a true mean. We may assume that the values of interstitial salinity in mud would be subject to the time factor of the salinity variation. We may also assume that under conditions of seasonal variation in the 'mean' salinity at a given point in an estuary—as when the freshwater inflow is elevated during prolonged rains—the salinity of the interstitial water would be shifted in corresponding fashion. But it must be emphasized that no precise measurement of the lability of the interstitial salinity has yet been attempted. The present study was timed, although not intentionally, in such a way that the variability of interstitial salinity with seasonal rainfall has been indicated.

Method of Determining Interstitial Salinity in Mud

The mud of the *N. diversicolor* habitat in the Tamar is soft and usually of a sticky consistency, apparently with considerable admixture of clay. Draining, sucking, or centrifuging water from it is hardly practical. In this survey the simplest methods were adopted, it having been felt not worth while to invest time in more elaborate procedures or equipment until a preliminary survey had indicated the usefulness of such an approach. Samples were taken at low tide at a series of points from the highest level of the mud-flat down to the water-line. The top inch or so of mud was scraped aside, several samples were scooped up with the fingertips from the area thus exposed, and these were packed together in a 175 ml. honey jar, which was filled to capacity to prevent any evaporation. In the laboratory two 30–40 g samples were spooned out from each collecting jar into wide shell vials and weighed immediately to the nearest 0·01 g. Samples were then dried to constant weight in an electric oven at $105 \pm 2^\circ$ C, a process requiring 3 or 4 days. The loss of weight represented the water content of each sample. Into each vial was then pipetted 25 ml. of distilled water, each dried sample was crushed with a small, flat-ended glass rod, the samples were covered to check evaporation, and were allowed to stand for 24 h. The glass pestle was left in each vial, and twice more during the soaking period was used to stir up the contents and to crush any solid lumps. In samples with much clay present this task proved troublesome. Finally, after settling, two 1 ml. aliquots were pipetted from the more or less clear supernatant and titrated with silver nitrate as earlier described (Smith, 1955*a*). From the chloride value obtained on the 25 ml. of added water, and the original water content as obtained by drying, the chloride of the originally contained water was calculated. Salinities were approximated by multiplying the chloride values by 1·81.

The method, as described above, is based upon several assumptions. It is assumed that all samples were taken at about the same depth, roughly the second inch beneath the surface in spots typical of the general area at that level, that no loss of water by evaporation took place before weighing or during the soaking process after drying, that the osmotically active chloride of the originally contained water was quantitatively recovered in the extraction step, and that no such chloride was bound permanently or lost during the drying process. It is further assumed that drying at 105° C did not release constituent water of clay. The method should in theory be unaffected by the actual interstitial water content or by the degree of drainage of the sample, provided no evaporation is permitted. The water-retaining qualities of soils, especially when clay is present, are complex (Baver, 1948), but as far as I have been able to determine, the method described is in principle free of serious theoretical sources of error. In its present form it is admittedly tedious, and, in any future survey, would need to be reduced to a routine to ensure more reproducible results. In particular, a standard method of taking groups of core samples should be employed, and a stricter control of the depth of sample is essential, for we must assume that the salinity of interstitial water in the uppermost layer is more labile than that of deeper-lying water. Further, a standard method of mechanical shaking during the extraction process and a simplified routine for chloride analysis would be necessary before a large-scale survey were undertaken. Present results may indicate whether or not the taking of interstitial salinities is likely to be of value in ecological surveys of estuaries.

Methods of Obtaining Levels

At each sampling station a profile of the exposed shore was determined by means of a dumpy level and a metric surveying staff. Distances of less than 50 yd. were measured with a length of cod line marked off in 5 yd. intervals (always used wet); greater distances were measured by use of the vertical angular adjustment of the dumpy level. The instrument was probably not very accurate for levelling or distance-ranging at distances over 150 m, and its use was not attempted on the wide flats of St John's Lake. In order to assign absolute heights relative to Ordnance Datum, three established Bench

Marks were used. Their heights relative to the newer (Newlyn) datum were furnished by the Ordnance Survey Office:

Location of Bench Mark	National Grid (10 m) Reference		Height above Ordnance Datum (Newlyn)		Height above Chart Datum (Devonport)	
			Feet	Metres	Feet	Metres
South face of west pier of Saltash Bridge to north of ferry landing	SX 4337	5877	6·76	2·06	15·68	4·78
West angle of barn at Clamoak	SX 4378	6421	18·61	5·67	27·53	8·40
South-east face of barn at Cotehele Quay	SX 4236	6803	11·64	3·55	20·56	6·27

At Clamoak and Cotehele Quay, the height of the mud flats could be determined directly. To determine the height of the flat at Salt Mill Creek, markers of the type used by Spooner & Moore, consisting of glass tubes lined with gelatine containing silver chromate and having a capillary at the bottom to damp out wave action, were placed near the Bench Mark at the west end of the Royal Albert Bridge at Saltash. A similar marker was set out on a stake in the mud-flat at Salt Mill Creek. The high-water mark at Salt Mill was thus recorded, and was levelled in relation to the top of the mud flat, top of salting, and to the Admiralty Boundary Stone no. 10, which is conveniently located nearby. The height of this stone is not recorded in Ordnance Survey files, but I have calculated its height, by the method described, as 2·31 m above Ordnance Datum (Newlyn). Returning to Saltash, I related the height of high water as recorded on the indicator to the known height of the Bench Mark, and so was able to assign an absolute level to H.W.M. here and at Salt Mill, and to the profile of the shore at the latter station. Similarly, levels at North and South Hooe were determined with reference to the Bench Mark at Clamoak, and at Calstock with reference to Cotehele Quay. At Calstock and North Hooe the point of high water had to be observed directly, since in December of 1954 salinities above South Hooe were too low to discolour the silver chromate indicator (this difficulty might be eliminated in future by placing a little NaCl solution in each tube before allowing the tide to elevate the water within it). My methods have not differed in principle from those of Spooner & Moore, except that I have used several Bench Marks well up in the estuary rather than a single mark on the shore of Plymouth Sound. The up-river readings were taken at high slack water on windless days, and despite the large freshwater inflow are probably close enough together to rule out error caused by any slope of water in the estuary bed. Like the previous authors, I claim no great accuracy.

Method of Estimating Nereid Population Density

The taking of quantitative worm samples while working alone in the extensive Tamar muds proved difficult, and was attempted only occasionally. At the extremes of the range (St John's Lake and Calstock) only impressions can be given. At Salt Mill, North Hooe, and Cotehele Quay, a metal frame of 0·1 m^2 area was pressed into the mud, the enclosed mud dug out to a depth of about 10 cm, and washed through a pair of sieves of 3–4 and 1·5 mm mesh. Before sieving, the soil was broken apart by hand and as many worms as possible removed intact. The results are inadequate in a quantitative sense but some idea of relative abundance was gained in the effort to be quantitative.

Field Observations

Weather

The present study was done partly during May and June and partly in the autumn, mostly under wetter-than-normal conditions. While it is difficult to evaluate the effect of rainfall in a region where local as well as year-to-year variation in rainfall is the rule, it may be noted that May and June of 1954 were months of above-normal rainfall, but followed an unusually dry April, so that the River Tamar was not abnormally swollen, and studies at this time probably reflected conditions not far from normal. However, the

Table I

	Rainfall (mm)		
	Average normal	6-year average 1948–53	1954
January	159	153	81
February	147	124	184
March	136	116	167
April	102	107	28
May	88	109	167
June	84	80	157
July	112	112	169
August	137	180	157
September	105	161	201
October	174	158	198
November	188	208	313
December	229	156	164
Totals	1648	1650	1984

summer and autumn of 1954 were, subjectively, among the wettest in local memory, and flooding on the Tamar occurred after a series of autumn storms. Conditions in November 1954 were regarded as severe, and the salinity in the estuary probably approached a minimal level. These subjective estimates are to some extent supported by the rainfall records published in the Monthly Weather Reports of the Meteorological Office. Unfortunately there are no rainfall-gauging stations on the watershed of the River Tamar proper, and it was felt that rainfall at Plymouth or along the lower estuary was less critical than that on the high moors to the north. Accordingly, Table I was compiled from the records for Tavistock and Princetown on the watershed of the River Tavy. The values given are the averages of data from these two stations. Although the records show great variation in a given month from year to year, and from station to station in any given month, the general character of the rainfall in the study area in 1954 is indicated, as well as the 'normal' pattern.

Distribution of Nereis diversicolor *and salinities at selected stations (see Fig.* 1)

'Marine' situations

Careful search was made on each of two occasions in spring at Cawsand and on the shore south of the quay at Cremyl. The substrates consisted of sand among boulders, and at both stations there was clear evidence of some fresh-water seepage. No *N. diversicolor* were found at any intertidal level despite the fact that the substrata appeared in no way unsuitable. At the Plymouth Laboratory *N. diversicolor* is regarded as a mud-dweller rather than a sand-dweller, but at Millport and in the Baltic it is commonly in sand, so that its absence does not appear attributable to a lack of suitable substrate. At no time in the course of over a year's work have I found this species in a situation which could be described as fully 'marine'. Undoubtedly, individuals may be found from time to time in marine water adjacent to populous brackish habitats. Salinities at Cawsand may be assumed to be high; Cremyl may occasionally receive brackish water from the Hamoaze, but no lowered salinities were recorded at this place in ordinary rainy weather. As Spooner & Moore (1940) state: 'In the Plymouth District the status of *Nereis diversicolor* as a marine species is doubtful. Though recorded occasionally from the Sound, it probably never establishes itself in permanent full salinity sea water.'

West Muds (St John's Lake)

Two visits were made in May, and the area from Inswork Point north-west to the channel edge studied at low tide. The exposed muds are here over 400 m wide, and a profile was not attempted. The greater part of the distance from the shore is occupied by an imperceptibly sloping, shell-covered, soft mud-flat, which probably lies close to Ordnance Datum as shown by Spooner & Moore's figure 7 which is a profile of a nearby area. At an estimated 300 m from shore the shelly flat changes to a noticeable slope of finer and even softer mud, which drops to a level very close to chart datum (tide-table level 0·0 ft, or 2·7 m below O.D., Newlyn). Here, at about the mean low-water mark of spring tides (M.L.W.S.T.), the mud slope terminates in a firm bench or flat strip of hard ground overlain by 2 or 3 in. of soft deposit. The fauna of the upper flat is as described by Spooner & Moore; that of the mud slope is far scantier, including mainly *Arenicola marina* and *Nephthys* sp.; that of the hard flat at M.L.W.S.T. is more abundant, including *Sabella pavonina*, *Nephthys* sp., *Melinna palmata* in large numbers, and *Nereis* (*Eunereis*) *longissima*, fairly abundant. In contrast with the findings of Spooner & Moore, I note the following. Large specimens (> 0·7 g) of *N. diversicolor* occur scatteringly on the outer portions of the shell-strewn flat, apparently below mid-tide level, as the above authors found on the St John's Lake flats (st. B-3, B-5), but I found none on the softer mud slopes, nor on the hard flat at the channel edge. Spooner & Moore report the largest counts of *N. diversicolor* on this 'bare mud...rather firm' area (their stations D-4 at -2.2 m and C at -1.8 m). Since they do not mention *N. longissima*, which is conspicuously present at this level, there is a possibility of a misidentification, regarding which I can draw no conclusions. They also report *N. diversicolor* present at levels as low as -2.0 m in the secondary channel of St John's Lake. This is fully consistent with observations I have made in the Salcombe Estuary near Kingsbridge—there is no question but that *N. diversicolor* may be quite abundant at low-intertidal levels in steep banks of erosional channels in marine-dominated mud-flats (Fig. 5), but I have not found it present in the depositional slopes of very soft silty mud such as occur along the main channel at West Muds. The question of its occurrence on the firmer flat bench at the foot of such slopes is a problem which should be re-investigated. It should be noted that *N. diversicolor* is also found abundantly at high levels along the shore at Inswork Point, in sand black with organic matter, associated with *Cardium*, *Macoma*, and capitellids. Its occurrence here is possibly correlated with freshwater seepage from the land. Samples of water from this sand had salinities of 23·1–30·2‰, whereas the salinity in the main channel on the same day varied from 32·4‰ at extreme low water to 34·4‰ at mid-tide, and was probably even higher at high tide. The population at this upper level, estimated at about 1·0 m above O.D., contained medium and small individuals; it is probably a breeding population, and may be the source of the scattered large individuals on the outer flats. Spooner & Moore consider that salinities below 30‰ are not encountered at St John's Lake even in winter, except possibly at L.W.M.S.T., and Milne's data are in agreement. Apart from the high-level population, which is in a somewhat special situation, *N. diversicolor* seems to occupy a marginal position on the West Muds and seems to be near its seaward limit.

Salt Mill

The transect, at 7·8 km from the Sound, corresponds closely with that worked by Spooner & Moore, and may be levelled with reference to Admiralty Boundary Stone no. 10, whose mark I have estimated as 2·31 m above O.D. (Newlyn). The essential results of observations made on 17 June and 12 October are set forth in Fig. 2. *N. diversicolor* is found in small numbers (but of large individuals) from -1.3 to $+0.8$ m relative to O.D. (Newlyn). The population does not extend inshore to the edge of the salting, despite the presence of suitable substrate, and its maximum density lies above mid-tide level. Its zonal position is a little lower than that indicated by Spooner & Moore and, furthermore, seems to have a natural upper limit, not set by the actual edge of the mud-flat. The salinity profile indicates a stable situation with no significant seasonal shift; interstitial salinities over the area inhabited by *N. diversicolor* vary only from 25 to 29‰. On 12 October, salinities of the rising surface water were taken as the tide covered the flat. These values (Fig. 2) range from 18 to 25‰, and are lower than those of the interstitial water of the underlying mud. They are also lower than the surface salinities obtained by Milne, in 1937, very near this spot. The low values of the present study undoubtedly reflect the greater rainfall in 1954. The fact that interstitial salinities are higher than those of the advancing water suggests that the former are relatively unaffected by the brief contact with surface water of low salinity during tidal rise and fall, and that at high tide the nereid zone receives water of a salinity greater than 25‰.

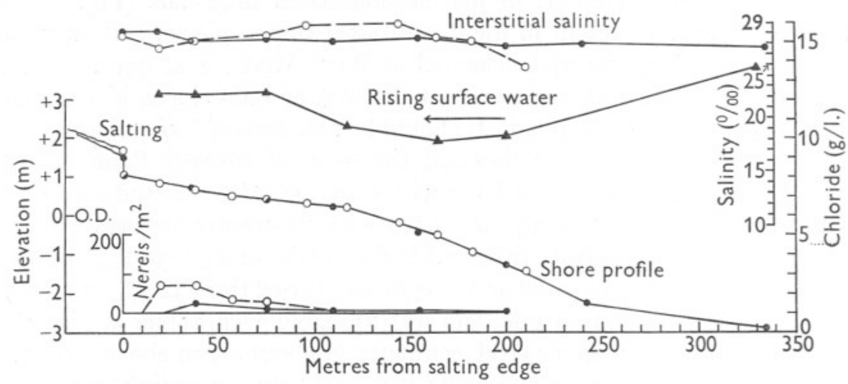

Fig. 2. Salt Mill: upper curves, salinity of interstitial water of mud, below which is a curve (triangles) showing salinity of rising surface water as it covered the flat on 12 October 1954. Middle curve, shore profile. Lower inset, distribution of *N. diversicolor*. Open circles represent values obtained in June; solid black circles, points obtained in October.

Clamoak

This station lies near the upper end of the straight and open part of the estuary, in a region where salinities have started to decline, but where the flats are still quite wide. Saltings are well developed here, 12·5 km from the Sound. *N. diversicolor* is abundant, especially at the upper or inshore levels of the flat and in muddy channels in the salting. It is found from a height of about 0·5 m above O.D. to the foot of the salting at about 0·9 m, and in the channels of the latter to about 1·25 m. No quantitative samples were taken. The salinity profile (Fig. 3A) taken in June showed the salinity across the flat to be as high as that at Salt Mill, except for a pronounced drop near low-water mark. This drop in interstitial salinity coincides with a sharper slope of the outer edge of the mud-flat, suggesting current-scouring of this zone by water of low salinity at low tide. The interstitial salinity of 10 December shows a profound drop to salinities of 5·8‰ inshore and rising to 10·9‰ near L.W.M. This reversal of slope of the salinity profile strongly suggests a salinity stratification such that the higher levels of the intertidal muds are exposed to much lower salinities than the muds near L.W.M. The possibility of freshwater drainage from the adjacent land may well add to a general lowering of salinity near the banks; on 10 December, following prolonged rains, the flat at Clamoak seemed much wetter than usual at low tide, and one had the impression that it was receiving much freshwater drainage from the near-by saltings. A check of the sheet of surface water showed salinities of less than 3‰, while the river water at low tide was as low as 0·4‰. But from the interstitial salinities it is apparent that ingression of salt water even at this period had provided the *Nereis* zone with salinities at least as high as 10‰ at the lower levels and not less than 6–7‰ at the higher levels. In contrast to the lower estuary, this section of the Tamar is clearly one of great seasonal as well as tidal salinity changes, and the salinity profiles of the interstitial water of the exposed shore seem to provide a reasonable picture of the extent of the changes that occurred between June and December 1954.

South Hooe

A station was selected just around the first major bend of the river, 14·8 km from the mouth. The mud-flat is here distinctly narrower than the preceding; the interstitial salinity profile taken in June is lower and drops more sharply toward L.W.M. (Fig. 3B). The December salinity profile shows both a lowering and a reversal of slope quite comparable to and more exaggerated than that observed at Clamoak. *N. diversicolor* is abundant and occupies a wide band vertically from $-1·65$ m to $+1·18$ m, O.D. (Newlyn). No population counts were made.

North Hooe

This spot lies 3 km upstream of South Hooe, around the second major bend of the river. At North Hooe the salinity profiles of 6 June and 10 December are still lower, and the seasonal difference is very great, amounting to about 18‰ difference between summer and winter values for the main nereid zone (Fig. 3C). Salinities near the low-water mark are considerably more stable, although not very high: 9–11‰ in summer and 3·5–4·5‰ in winter flood. A count of *N. diversicolor* had been made in May, 400 m downstream, where the mud-flat is somewhat wider. The nereid population was most dense in the upper levels, exceeding 800 per m^2 even before reaching the highest level where the burrows were more numerous than in the spots sampled. A few small *Nephthys* sp. were taken at this point, and dead shells of *Scrobicularia* were seen at North Hooe. Spooner & Moore reported the highest density of *N. diversicolor* at the latter point, where their survey ended.

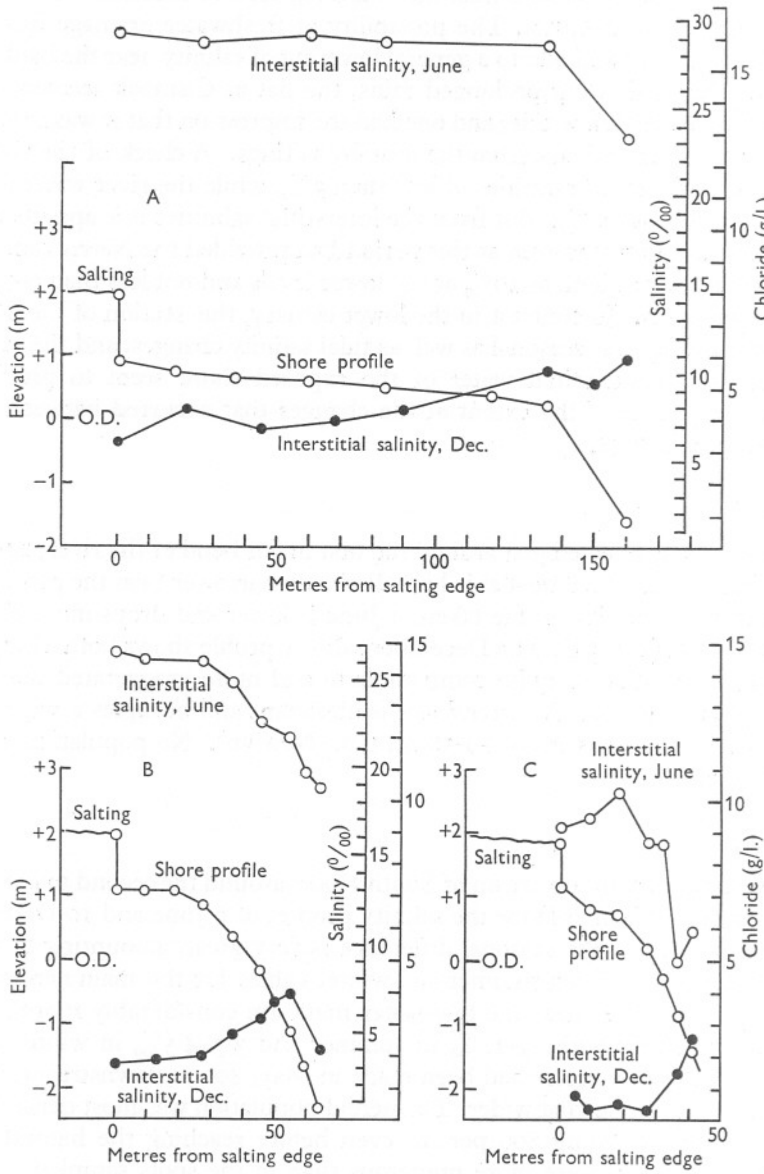

Fig. 3. Shore profiles (June) and interstitial salinity profiles for June (open circles) and December (solid circles). A, Clamoak; B, South Hooe; C, North Hooe.

Cotehele Quay

At this point, 20·5 km from the mouth of the estuary, the river and the bordering mud-banks have become distinctly narrow, and reeds (*Phragmites*) have supplanted typical saltings vegetation. On the stone quay grows a broad band of *Fucus vesiculosus* (det. Dr Elsie Burrows), extending vertically from 1·02 m above O.D. down to 0·52 m below O.D. (Newlyn). In terms of Chart Datum (Devonport) this is from +12·26 ft. to +7·22 ft. tidal height. Percival listed North Hooe as the upstream limit of *Fucus*; this may indicate that the species has spread 2·5 km upstream since 1929, for the growth is extensive enough to have attracted attention had it been growing at Cotehele Quay at that time. Below the *Fucus* is a rich growth of the hydroid *Cordylophora*, typical of oligohaline waters. *N. diversicolor* occurs in considerable density although the available habitat is of small area. Observations were made on a small flat protected from erosion by stone quays (Fig. 4A). The lower part of the steeply sloped mud-bank is poorly consolidated and much gullied. The maximum density of nereids (*c.* 600 per m^2) occurred at the edge of the land vegetation at 1·3 m above O.D., and the population was reduced to scattered individuals at about O.D. level. The population seemed healthy and, judging by the number of small worms present in June, had been breeding. Salinities in the mud were low, varying from 2·6‰ in June to about 0·3‰ in November after a period of flood.

At this time an observation was made which suggested that salinity stratification in these upper reaches of the estuary may be an intermittent phenomenon. Salinity samples were taken at the surface as the tide fell past the zone of *Fucus* (Fig. 4B). A salinity of 0·2‰ was found at high water, when the river lay smoothly, with a gentle downstream drift apparent on the surface. As the tide fell the current gathered strength, a counter-current developed along the quay face where grew the *Fucus*, and the salinity rose to 1·0‰ by 2 h past high tide, by which time the river presented a strong downstream sweep of current. Surface salinity then dropped again until at 3 h past high tide it had reached 0·11‰. The only explanation I can offer is that at high water there is salinity stratification, and that as the ebb develops frictional turbulence is set up, bringing water of higher salinity to the surface. This provides a maximum surface salinity at about the middle of the *Fucus* zone. Later in the ebb the saline water has moved downstream, and the salinity drops sharply. A study of the stability of salinity stratification near Cotehele Quay might prove of interest in connexion with the algal zonation.

At this point, although salinities are generally very low, the tidal and seasonal salinity variation is also nearly minimal. It should be noted that the nereid population at Cotehele Quay, although far denser than any observed in Finnish waters, is living at a salinity of less than half that which characterizes the limit of the species in the Baltic Sea. In the Tamar, as on the south

Finnish coast, both *N. diversicolor* and attached *Fucus vesiculosus* stop together at about the same summer salinity, although this value is much lower in the Tamar than in the Baltic.

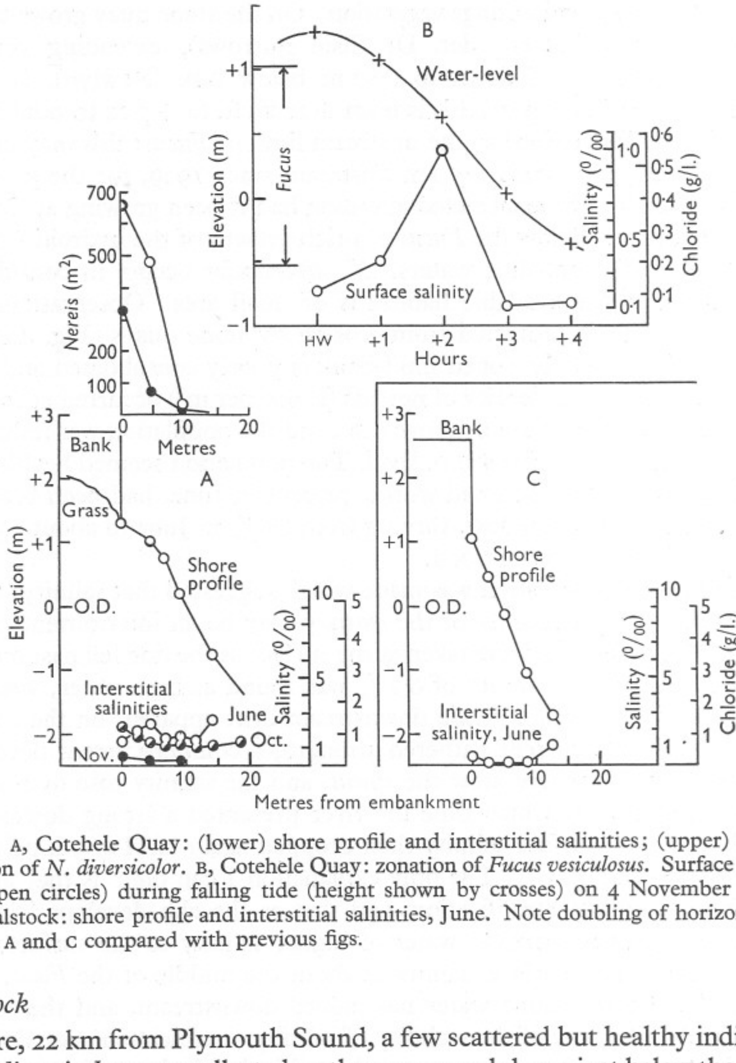

Fig. 4. A, Cotehele Quay: (lower) shore profile and interstitial salinities; (upper) distribution of *N. diversicolor*. B, Cotehele Quay: zonation of *Fucus vesiculosus*. Surface salinities (open circles) during falling tide (height shown by crosses) on 4 November 1954. C, Calstock: shore profile and interstitial salinities, June. Note doubling of horizontal scale in A and C compared with previous figs.

Calstock

Here, 22 km from Plymouth Sound, a few scattered but healthy individuals of *N. diversicolor* were collected on the upper mud slopes just below the railway bridge, always in spots where the mud was of somewhat firmer consistency. The worms were restricted to a narrow vertical band, from O.D. to about 0·5 m higher (Fig. 4C). Associated with them were very abundant tubificid worms, dolichopodid dipteran larvae, and leeches (unidentified) found buried in the mud. Salinities in the mud of the nereid zone were almost nil (less than

0·5‰) but increased to 1·1‰ near low-water mark where the mud was so disturbed as to be apparently devoid of fauna. Percival reported the up-stream limit of *N. diversicolor* as half a mile above Calstock. Careful search at Okeltor, 1 mile upstream, failed to reveal it in a suitable substrate. No other animals or plants of marine affinity were seen at Calstock.

Discussion

The interstitial salinity profiles in Figs. 2–4C show a clear pattern of salinity variation in the River Tamar. If one compares the spring salinities, which were obtained under fairly 'normal' conditions, with those obtained in autumn, three major sections of the estuary can be recognized. (1) A lower estuary, which may be called 'marine dominated', is characterized by wide flats, relatively high salinities, and interstitial salinities little decreased with elevation intertidally and little affected by periods of freshwater flooding. (2) A middle region is characterized by intermediate salinities, with marked variation in salinity with intertidal level, and with a marked lowering of interstitial salinity and a reversal of slope of the interstitial salinity profile at times of freshwater flooding. It may be that excess freshwater discharge is strongly stratified, so that the upper intertidal is more particularly affected; possibly the 'salt-water piston' of the summer is transformed to a deep-lying wedge of lesser volume by the sheer mass of fresh water flowing down above it; perhaps lateral freshwater intrusion from the banks at low tide plays a part. The down-stream limit of this suggested middle estuarine region is perhaps below Clamoak, a point which in summer would seem to be much like the lower estuary but which in winter flood is clearly comparable to points up-stream. The up-stream limit must lie above North Hooe. (3) The upper reaches, characterized by virtual absence of 'flats', show low salinities at all seasons, and little change of salinity either with intertidal level or with season. The down-stream limit in the Tamar is near or below Cotehele Quay. However, these limits cannot be sharp, and it might be best to regard them as entirely labile. If one could imagine a year of low enough rainfall, salinities characteristic of the lower estuary would extend to Calstock, in what we now regard as the upper reaches. Indeed, if we turn not far away, to the Kingsbridge Estuary, we can see this possibility realized.

The freshwater inflow into the Kingsbridge Estuary is so slight, relative to the volume of the estuary bed, that the fauna near Kingsbridge, almost at the very head, is strikingly comparable to that of St John's Lake. A series of observations were made on the flats 1 mile below Kingsbridge (Fig. 5) at a point where the main mud flat is separated from the stony beach by a secondary channel. Because of failure to locate a Bench Mark, the levels shown in Fig. 5 were estimated from the predicted heights of high and low water on 10 October 1954 as corrected for Kingsbridge. This method is particularly subject to error at a point so removed from the sea, and the results may be inaccurate to the extent of perhaps ±0·3 m. The general level of the mud-flat is estimated as close to O.D. (Newlyn) and is thus approximately the same as the flat of St John's Lake as described by Spooner & Moore (1940). *N. diversicolor* was found to be extremely abundant low in the relatively firm erosional slopes of the secondary channel, a position comparable to its occurrence in St John's Lake as reported by the latter authors. In agreement with my findings at West Muds, *N. diversicolor* is also present on the higher shores, where smaller

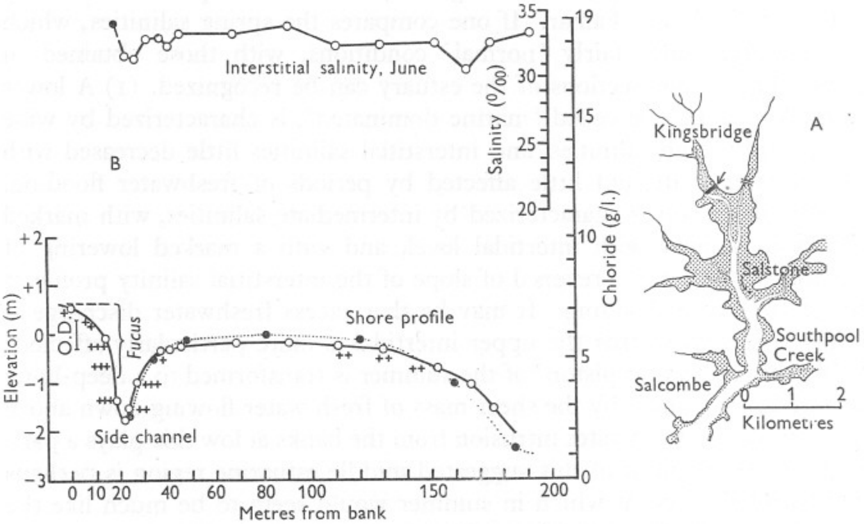

Fig. 5. A, Sketch map of the Kingsbridge (Salcombe) Estuary to show collecting station and points mentioned in text. Stippled areas represent intertidal exposed between H.W.M. and L.W.M. of ordinary tides. B, at top, interstitial salinity profile (June) across flats below Kingsbridge. One point (solid circle) taken in October. At bottom, shore profiles: open circles, June; closed circles, October. Vertical height of *Fucus* zone shown by bracket; estimated relative abundance of *N. diversicolor* shown by groups of crosses. Vertical bar by O.D. represents a possible estimated error in level of ±0·3 m.

individuals are numerous in muddy sand under rocks up to the upper limit of *Fucus* (+0·6 m), and also in pockets of soft mud held in the remains of hulks on the shore. Along the main channel *N. diversicolor* seemed common on the edge of the flat, but was absent from the soft outer slope and from the firmer bench at L.W.M., quite as at West Muds. The salinity profile (June) is higher than that for Salt Mill, but was not studied after the November rains. There is some indication of a drop in interstitial salinity at the edges of the main flat and in the banks of the secondary channel, which is consistent with the distribution of the estuarine *N. diversicolor*. In general, the salinities at this station were high; the lowest observed was no less than 28‰, obtained in the water of the main channel at low tide in June, and a similar value in the secondary channel in October, both at times of fair weather. However, the nearness of the site to the head of the estuary makes it likely that occasional periods of heavy freshwater run-off might effect a greater lowering of salinity than my brief studies encountered.

Lower in the estuary, near the Salstone, *N. diversicolor* is also present, but scarce. A few large individuals were taken in the muddy banks of channels behind the Salstone reef; their position was roughly mid-tidal, comparable to the position observed at West Muds. The species, where found, was associated with the polychaetes *Arenicola*, *Melinna*, *Nephthys*, and capitellids. It was absent from the lower levels inhabited by *Sabella*, *Lanice* and *Eunereis longissima*, and from the very soft mud occupied by *Myxicola*. It is evident that the Kingsbridge Estuary as a whole is, in Rochford's terminology, 'marine-dominated', and only near its head is *N. diversicolor* abundant. Existing reports suggest that this species is scarce in the Kingsbridge (Salcombe) Estuary; Marine Biological Association (1931), following Allen & Todd (1900) reports it numerous only in Southpool Lake, 'in a small gully traversed by a stream of fresh water'. In view of these earlier reports, the abundance of *N. diversicolor* near Kingsbridge deserves mention. As is well known, the marine-dominated Kingsbridge Estuary stands in marked contrast to the Tamar Estuary, which for the greater part of its length is 'gradient-dominated', and characterized by large salinity variations, both spatial and seasonal.

As for the use of interstitial salinities of intertidal mud as indicators of the salinity characteristics of an estuary, it is felt that the results give a picture of what is happening even though the quantitative relationship between salinity in the substratum and the variable salinity of the overlying water is still not understood. The method may be of value to the individual field worker who must sample several localities on the same day, especially if he must travel by land. Certainly less labile than salinities of tidal water, the interstitial salinities are still labile enough to give some picture of changes within past weeks, although how responsive these interstitial salinities actually are, or how stable, remains to be determined. Possibly one could use the surface layer of mud as an indicator of recent changes in salinity, and deeper layers as indicative of general conditions over a longer period. Mud-dwelling animals, by the irrigation of their numerous burrows, may profoundly influence the speed of adjustment of interstitial salinities to variations in the environmental salinity.

Muds represent extremely complex physico-chemical systems (Baver, 1948), of which the detailed composition doubtless varies a great deal within the bounds of a single estuary, so that generalizations as to their water-holding properties should be made with caution. As pointed out by Bourcart & Francis-Boeuf (1942) in their useful discussion of the properties of mud, the chloride values of re-wetted dried samples of marine muds may differ from those based upon the natural water content. These authors make the statement

(p. 27) that the chloride of interstitial water of marine sediments is always higher than that of the overlying water, and suggest that this may be attributable to desiccation during periods of low tide. While this may be a factor in certain estuaries in regions of low rainfall, the intertidal flats of the Tamar would seem as likely to experience lowering of salinity by dilution with rain-water as concentration by evaporation. In situations where, as at Salt Mill, interstitial salinities higher than that of the overlying water are observed, I am inclined to regard this as the result of failure to measure salinity in the lower strata of water at flood tide. In any estuary where salinity stratification is marked, surface salinities will be expected to be lower than interstitial salinities over all but the highest intertidal shores. The presence of a given interstitial salinity at any spot on an intertidal mud slope probably indicates that the spot is bathed by water of at least that salinity at high tide. In certain situations, as described for Kames Bay (Smith, 1955*a*), subterranean intrusion of fresh water may produce local lowering of interstitial salinity, but no instance of this has been seen in the Plymouth area. Instances of intertidal muds retaining a high salinity beneath freshwater streams at low tide are too well known to be cited specifically; they are in no way inconsistent with the general view that the retained interstitial salinities in intertidal muds reflect in general the higher salinities of the tidal water which reaches them.

The chief objective of the present study, to characterize the salinity and the pattern of salinity variation of the habitat of *N. diversicolor* in a typical estuary, requires recognition of the region of greatest abundance of the species. This aspect of the problem has proved beyond the author's capabilities in the field studies described, but fortunately the careful quantitative work of Spooner & Moore (1940) is available and has undoubtedly been applicable in 1954. In Table II their data on the distribution of *N. diversicolor* are summarized, the values being based only upon those stations where the species was actually taken.

TABLE II. DATA OF SPOONER & MOORE (1940)

Location	Range of densities in worms per m²	Mean of densities recorded per m²
St John's Lake	2–56	20
Thanckes Lake	1–350	130
Salt Mill and Ernesettle	4–770	186
Cargreen-Weirquay	8–590	251
Clifton-South Hooe	>22–>1020	>786
North Hooe	400–3030	1715

The data of the present study, treated in the same way, are given in Table III. The total data agree in indicating a maximum abundance somewhere in the region of North Hooe, that is to say, in that part of the river where salinity variation is the greatest. One point of caution should be noted: no data on weight of worms per unit of area are available, and it is notable that where

N. diversicolor is at a high density in the Tamar, the population is of small individuals, rarely exceeding 0·15–0·20 g. On the other hand, the scattered worms at Salt Mill and St John's Lake are mostly of very large size. Dales (1951) has pointed out that a population of *N. diversicolor* may have a low percentage of males, not over 10%, and that these must be sought out by the females if reproduction is to be accomplished. Females ordinarily spawn and die at an age of 1 year or less. However, those females which fail to find a male may survive for 18 months or perhaps 2 years, and grow to very large size.

TABLE III. DATA OF THE PRESENT STUDY

Location	Range of densities in worms per m^2	Mean of densities recorded per m^2
Salt Mill	3–70	28
Clamoak	(Abundant)	—
South Hooe	(Very abundant)	—
North Hooe	45–>800	436
Cotehele Quay	5–660	204
Calstock	(Occasional)	—

The occurrence of scattered large worms may thus be indicative of a non-reproductive population, perhaps rendered so by such wide spacing that encounters between the sexes are unlikely. On this assumption, the large worms at St John's Lake and Salt Mill would not, despite the high weight per unit area they represent, be considered as anything but a marginal population. It must be added, however, that large worms may occur in quite dense populations in mud, as at Millbrook Lake and near Kingsbridge, and the problem requires clarification. In respect to the River Tamar population of *N. diversicolor*, the optimal region seems to lie up-stream from the region reached by the main mass of tidal sea water, and to centre in the region of maximum salinity variation.

In summing up the series of studies, of which this article is the third, on the distribution of *N. diversicolor* in relation to salinity, it is well to point out that no simple relationship has been detected. We have seen (Smith, 1955*a*) that the apparent zonation of the species on the sandy beach at Kames Bay, Millport, is correlated with a zone of lowered interstitial salinity. This may in part be the result of abundance of *N. diversicolor* in areas where less inter-specific competition is encountered. A clearer example of this sort of limitation is seen in the Isefjord (Smith, 1955*b*), where the apparent restriction of *N. diversicolor* to zones of very low salinity is the result of its exclusion from a large part of its former range as a result of competition and/or predation by another species of nereid. In the Tamar, *N. diversicolor* is most abundant in areas which other polychaetes are unable to utilize, but it is also abundant in the more saline head of the Kingsbridge Estuary where competition by other, more marine, species must be severe. Interspecific competition is perhaps not a factor of over-riding importance in limiting the distribution of *N. diversicolor* in the Plymouth region, although it may be so in certain situations elsewhere.

Tidal factors *per se* are also difficult to evaluate, but are probably of secondary or indirect importance. *N. diversicolor* is characteristically an upper mid-tidal form in the Tamar, but can occupy lower positions, as it does in the banks of secondary channels in St John's Lake and near Kingsbridge. Here we find a slightly firmer substrate, as well as somewhat lower salinities, than in adjacent higher areas. Over most of its range in the Tamar, *N. diversicolor* is characteristic of the 'flats', which, as noted by previous workers, show a relatively greater area of intertidal mud above mid-tide level as one goes upstream (Hartley & Spooner, 1938). The level of the saltings which border the upper Tamar at many points is said to be quite constant. The pertinent data on heights of mud-flats and saltings obtained in the present survey are given in Table IV.

TABLE IV. HEIGHTS IN METRES ABOVE O.D., NEWLYN

Location	Top of salting	Highest level of mud	General level of 'flat'
Calstock	(Embanked)	1·04	0·1 to 0·5
Cotehele Quay	(Embanked)	1·30	0·7 to 1·3
North Hooe	1·83 to 1·88	1·15	0·7 to 1·0
South Hooe	1·85 to 1·90	1·18	1·13 to 1·15
Clamoak	1·93 to 1·96	0·90	0·40 to 0·75
Salt Mill	1·50 to 1·70	1·05	0·25 to 0·8
St John's Lake (from Spooner & Moore)			−0·2 to +1·0

These slight figures suggest a constant level of about 1·8–2 m above O.D. for the tops of saltings (the lower salting at Salt Mill may be eroding away). Also fairly constant is the highest point of the mud (i.e. the foot of the salting cliff) at about 1 m above O.D. The general level of the main flat is not precisely determined, but shows an increase in level from the lower estuary up to the first great bend in the river at South Hooe. Above this point, with the narrowing and steepening of the intertidal mud, the 'flats' themselves seem to become more inclined, and the outer edge lower, possibly as the result of current scouring.

At Cotehele Quay and up-stream, flats are almost indefinable, and since at both Cotehele and Calstock the measurements are at spots disturbed by man-made embankments, no conclusions should be drawn. It would seem that the somewhat lower intertidal position of *N. diversicolor* in the lower reaches of the Tamar Estuary reflects the general level of the suitable substrates. This situation may provide the incidental advantage that in the upper reaches of the estuary *N. diversicolor* is placed above the very low salinities of the ebb-tide, and in the marine-dominated lower reaches is exposed to favourably brackish water at low tide. It should be noted that if salinity stratification occurs in the middle or upper reaches of an estuary, as seems to happen in the Tamar, the upper intertidal and the lower intertidal zones are exposed longer to surface waters of low salinity than the mid-tidal levels, over which the rising or falling surface water passes most rapidly. That exposure at low tide is of direct advantage to *N. diversicolor* would seem unlikely except as it may reduce competition from less exposure-resistant forms. Submergence *per se* has not been shown to be deleterious to *N. diversicolor*, and this species must live permanently submerged in its habitat in the Baltic Sea. Only by considering the several factors of substratum, intertidal position, pattern and degree of daily and seasonal salinity variation, temperature, interspecific competition, and so forth, can the relation of a species to any one factor such as salinity be fully appreciated. The further problem of whether populations of a species in different parts of a wide geographical range are physiologically distinct in their responses to the factor in question should be viewed against the background of the ecology of the species. Certain information on the comparative physiology of *N. diversicolor* in response to low salinity will be presented in a later paper (Smith, 1955*c*).

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SUMMARY

The estuarine habitat of *Nereis diversicolor* in the River Tamar has been surveyed, and the distribution of this worm related to salinities in a 'normal' spring and a rainy autumn.

The method of evaluating the salinity at given points within an estuary by means of 'salinity profiles' of the interstitial water of the intertidal mud is put forward, and the results of the method shown to be informative and consistent with the results of previously used methods.

N. diversicolor is found to reach its maximum population density in that portion of the Tamar Estuary where the greatest salinity variation, both seasonally and with intertidal height, is the rule. At its up-stream limit it regularly endures salinities of less than 0·5‰.

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