

# THE ECOLOGY OF THE TAMAR ESTUARY

## IV. THE DISTRIBUTION OF THE FAUNA AND FLORA ON BUOYS

By A. Milne, M.A., B.Sc., Ph.D.

From the Plymouth Laboratory and Marischal College,  
Aberdeen University

(Text-figs. 1 and 2)

### CONTENTS

	PAGE
Introduction . . . . .	69
Material and Methods . . . . .	70
Horizontal Distribution in the Estuarine Gradient . . . . .	71
Environmental Conditions . . . . .	75
Fluctuation of Limits with Fluctuation of Environment . . . . .	76
Comparison with Previous Work . . . . .	77
Vertical Distribution . . . . .	78
Vertical Zonation of the Algae and Illumination . . . . .	80
Discussion . . . . .	82
Summary . . . . .	84
References . . . . .	85
Appendices . . . . .	86

### INTRODUCTION

In considering the fauna and flora of estuaries, particularly the question of penetration from the sea and zonation along the estuarine gradient, a study of the growth on floating buoys has a special significance. The buoys supply a habitat in which certain variables affecting the bottom fauna are eliminated. Not only is a substratum of a constant type provided, but because the buoys are floating the organisms attached to them are subjected to a constant degree of immersion, thus eliminating an important element in the fluctuation of the environment, due to the rise and fall of the tide, to which the fauna and flora of the shore is subjected. A series of buoys along an estuary, such as exists in Plymouth Sound and Hamoaze, virtually supplies an experimental series in which the only important environmental variables are *salinity conditions* and (to a much lesser degree) *turbidity* of the water.

According to Orton (1930), the black varnish coating of buoys provides more or less "innocuous surfaces". Buoys are primarily available only for sessile organisms such as barnacles, mussels, coelenterates, Bryozoa, ascidians and algae. But once the latter have settled, they collect among their crevices, byssi and holdfasts, quantities of silt and plant debris, and this in turn provides

a foothold and food for amphipods, and to a lesser extent, worms. Animals such as *Ligia*, *Orchestia* and *Jaera*, which have no pelagic stage in their development, have slender chances of reaching the buoys in mid-river; while certain species, such as *Littorina littorea*, even though they have pelagic larvae, cannot withstand constant immersion (Flattely & Walton, 1922, p. 207). Colonization must be affected by the time at which the buoys are laid down (see Appendix I, p. 86), for this may happen when one species is breeding and it may have established itself before another, which breeds later, is able to gain a foothold. How far the present distribution is influenced by this fact it is difficult to say, but the possibility must not be overlooked. The longer a floating structure is in the water, the richer and more varied its fauna tends to be (cf. Orton, 1930; Fraser, 1938).

#### MATERIAL AND METHODS

A series of buoys extending from open sea (Mewstone) to typical estuarine conditions (Neal Point) was chosen. Certain physical and chemical factors for this area have already been discussed (Cooper & Milne, 1938, 1939; Milne, 1938). The buoys varied to some extent in size and shape, but all had some flat, vertical surfaces from which collections could be taken and zonation measured; their immersed portions varied from one to a little over two metres in depth. Buoys lie at their moorings from 12 to 15 months (see Appendix I) and then are towed gently to the wharf a little above Cremyll where they are scraped and repainted. Those mentioned here were examined immediately after they were raised from the water. There are other buoys closely neighbouring, or at the same level in the estuarine gradient as, each of the buoys named in Fig. 1. With the exception of New Rock, Panther and H 1 buoys, one to three of these were examined in each case as a check.

The following buoys, not shown in the map in Part I, are situated in relation to buoy D 4 as follows (approximately): Mallard, 1 km. west; New Rock, 3.2 km. south-south-west; Panther, 3.3 km. south; and Mewstone, 6.5 km. south-south-east. The Mallard and D buoys lie inside the Sound; while the New Rock, Panther and Mewstone lie outside the Breakwater.

Collections were made separately from each of the three plant zones, and from three different points in each zone. The dimensions of the areas scraped were governed by the uniformity of the distribution in the zone and by the size of the zone. In Zone III, where most of the fauna is concentrated, three squares of 20 cm. side were scraped. The macrofauna and macroflora only were studied; microfauna like copepods and Protozoa, and microflora like coating diatoms were omitted.

## HORIZONTAL DISTRIBUTION IN THE ESTUARINE GRADIENT

The horizontal distribution on the buoys is given in Fig. 1. Neal Point is not necessarily the up-river limit of those organisms found on it, since no buoys were available for examination above this point. It seems reasonable to take the absence of species on Neal Point buoys which are present on H 15 as indicating their limit at H 15, even though there are no buoys above Neal Point, for the Hamoaze series (H 1-H 15 and Neal Point) was laid down and lifted about the same time.

The following have been omitted from Fig. 1; of these A-E are algae, the remainder animals:

## LIST I

A. The filamentous green algae, unidentified, which are abundant on all the buoys in the series.

B. Fucoids, young stages, present on H 1-H 11.

C. *Ascophyllum nodosum* Le Jol, present on H 7 and H 11, and almost full grown on the former; strangely absent on the seaward buoys.

D. *Hypoglossum woodwardii* Kylin, found only on H 11, rare.

E. *Chylocladia* sp., on H 1, rare.

F. *Anomia ephippium* L., on Mallard buoy, rare.

G. *Idotea granulosa* Rathke, on Mallard and H 4 buoys, rare.

H. *Limnoria lignorum* (Rathke), in wood baulks protecting the surface of H 7, and tunnels only on H 11, common.

I. *Cellepora costazii* Audouin, common on Mewstone and abundant on New Rock buoys.

J. *Schizoporella hyalina* (L.), on Panther buoy, present.

K and L. *Cirratulus cirratus* (O. F. Muller) and *Polyophthalmus pictus* (Dujardin), on Panther buoy, present.

M. *Ophiothrix fragilis* (Abildgaard), on Mewstone, common but young, disk 3-5 mm.

N to R. *Gonothyrea loveni* Ellis & Sollander, *Opercularella lacerta* (Johnston), *Calycella* sp., *Campanulina repens* Allman, *Coryne* vel *Syncoryne* sp., all present but rare on H 7 and H 11 buoys, possibly present on others—but method of collection inefficient (see Appendix II).

S. *Tubularia larynx* Ellis & Sollander, similarly, but noticed in abundance on Panther and Mallard, and common on H 4, while adult stalks were present on Neal Point buoy. *Tubularia* dies off in winter.

T. *Thalassomyia frauenfeldii* Zett and *Clunio marinus* Hal, insect larvae (see Fig. 1), and possibly others, since investigation was not exhaustive.

In Fig. 1 the data for Mewstone buoy are also not included because there is a possibility that one or two species were missed, since the collection was made several hours after the buoy had been taken from the water. The species are listed below. Several of the marine species present on other open sea buoys are absent but Mewstone is more out of the zone affected by estuarine waters.

## LIST II. Mewstone Buoy

Filamentous green algae, a.; *Ulva linza* var. *lanceolata* (Kütz), a.; *U. lactuca* var. *latissima* (D.C.), c.; *Laminaria digitata* Lamour, a.; *L. saccharina* Lamour, c.; *Mytilus edulis* L., c.; *Jassa falcata* (Montagu), a.; *Stenothoe monoculoides* (Montagu), c.; *Balanus*

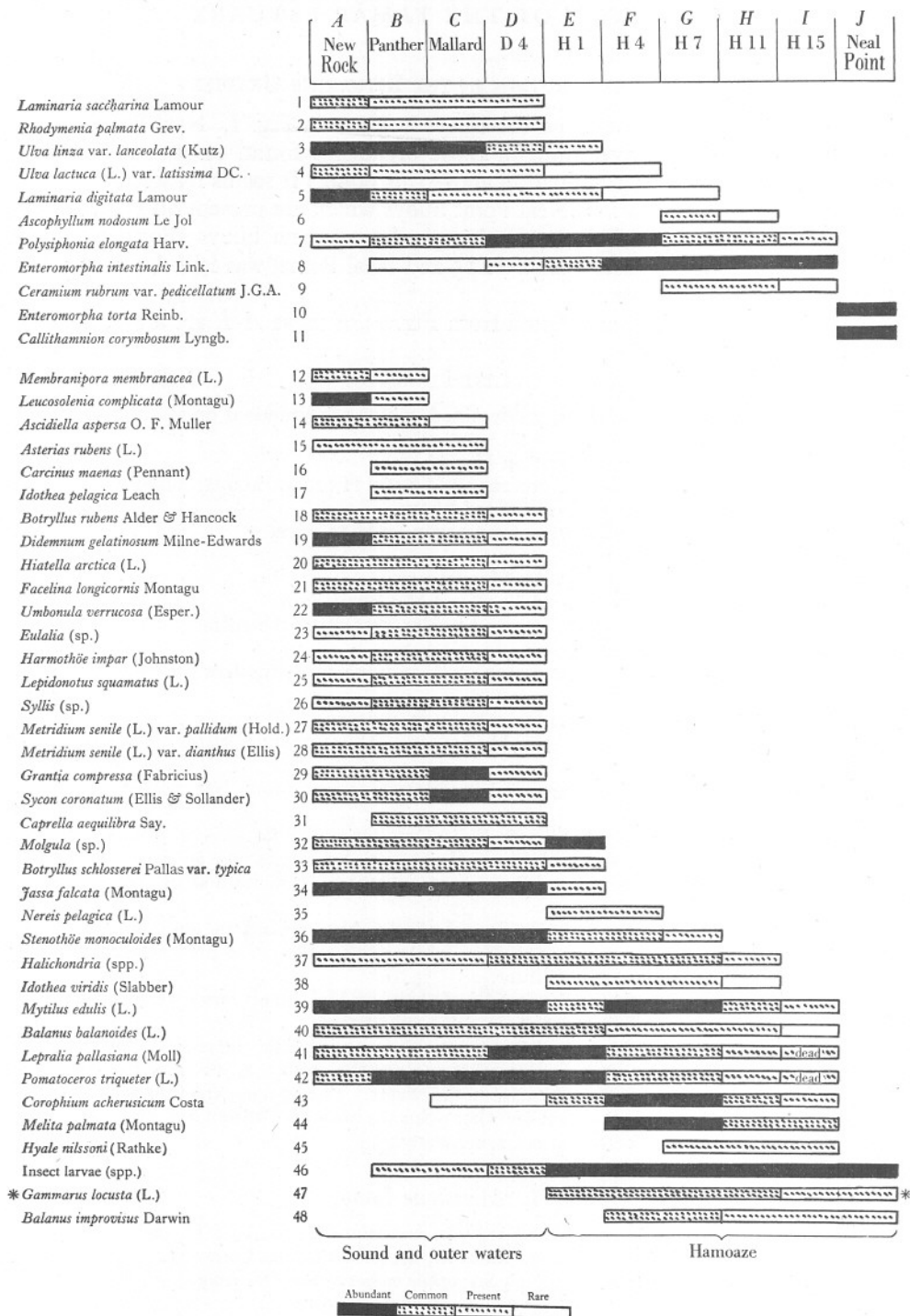


Fig. 1. Quantitative horizontal distribution showing limits on buoys in the Tamar Estuary, Plymouth Sound and outside.

\* Later found that at Neal Point buoy (only) this was a var. of *Gammarus zaddachi* Sexton.

*balanoides* (L.), c.; *Lepralia pallasiana* (Moll), c.; *Cellepora costazii* Audouin, c.; *Pomatoceros triqueter* (L.), c.; *Ophiothrix fragilis* (Abildgaard), p.

(a. abundant; c. common; p. present.)

As in the Tees (Alexander, etc., 1935) it was found "that the range of species even of the same phylum differed greatly". A considerable difference is also evident in the resistance, i.e. penetrative power of two species of the same genus (cf. *Enteromorpha*, *Ulva*, *Laminaria*, *Idotea* and *Botryllus*). Since the Hamoaze series, H 1 to H 15 and Neal Point, were all laid during November–December 1935 and examined during February–March 1937, there were at least thirty species available for colonization of these buoys (see Fig. 1). This is the total species on all the buoys of the Hamoaze series. But the number of species present on each buoy was as follows (A, B, N–S in list I, and insect larvae are omitted.)

H 1	H 4	H 7	H 11	H 15	Neal Point
19	17	19	18	10	4

Moreover, there is not one species which is present on all the Hamoaze series, though five—*Polysiphonia elongata*, *Enteromorpha intestinalis*, *Mytilus edulis*, *Balanus balanoides*, *Corophium acherusicum*—are present on H 1 to H 15.

In the Tamar there is a great deal of suspended silt and this increases up-river. It is sometimes suggested that animals with delicate ciliary or pore mechanisms (suspension feeders) will be limited by suspended silt. The sponges, Coelenterata, Polyzoa and tunicates, together with *Mytilus*, *Pomatoceros* and *Balanus* may be classed as suspension feeders. The numbers of suspension and non-suspension feeders on each buoy in the series were as follows:

Buoy	Suspension feeder	Non-suspension feeder
Panther	19	14
Mallard	15	16
D 4	14	11
H 1	7	7
H 4	6	8
H 7	6	8
H 11	6	6
H 15	3	5
Neal Point	1	2

Fig. 1.

*Buoys and their positions*

In the map in Part I, it will be seen that the mouth of the estuary (zero position) is taken as being Devil's Point. The position of the buoys relative to this are as follows:

Sound and Outer Waters	{	A. New Rock, 3.2 km. S.S.W. of D 4
		B. Panther, 3.3 km. South of D 4
		C. Mallard, 1.0 km. West of D 4
		D. D 4, Drake's Island, 1.9 km. from zero position
Hamoaze	{	E. H 1, 1.2 km. up river from zero position
		F. H 4, 2.25 km. " " " "
		G. H 7, 3.3 km. " " " "
		H. H 11, 4.9 km. " " " "
		I. H 15, 6.0 km. " " " "
		J. Neal Point, 9.25 km. " " " "

The five species of hydroid (*N-R*, List I) on H 7 and H 11 buoys, and *Tubularia larynx* on H 4, are omitted. Thus on the Tamar buoys, just as in the bottom fauna of the Tees, Tay and Tamar estuaries (Alexander, *et al.*, 1935) there is no marked difference between the penetration of the two groups.

Although the relative abundance as well as the range is shown in Fig. 1, it must be clearly understood that too much stress must not be laid on the former since no detailed counts were made. The figure is only intended to indicate trends in density. In any case, the size-composition would be necessary to show the degree of ecological success. Generally the organisms become less numerous and smaller towards the lower end of their salinity range, as very obviously shown without measurement by *Laminaria* and *Mytilus*. Where there is a tendency to lesser density, not size, towards the seaward end of the range, e.g. in *Polysiphonia*, *Halichondria*, *Lepralia*, *Pomatoceros* and *Corophium*, this must be partly due to competition for space. Those organisms which do penetrate the estuary have some of the space normally shared with those which do not, since fewer species come in than drop out. Thus (excluding *A*, *B* and *N-S* in List I, and insect larvae) it is found that of the 39 species present on the Panther buoy, only 34 penetrate to the Mallard (37), 30 to D 4 (31), 14 to H 1 (19), 10 to H 4 (17), 9 to H 7 (19), 7 to H 11 (17), 4 to H 15 (10), and 0 to Neal Point (4). (The figures in brackets represent the total number of species present on the buoys with the exceptions noted above.) For example *Polysiphonia elongata* becomes denser at D 4 where the other algae, *Laminaria digitata* and *L. saccharina*, accompanying it in Zone III are becoming scarce; *Halichondria* similarly at D 4, where *Sycon compressum* and *Grantia compressa* are beginning to fall away. Of course the competition is not necessarily within a phylum only. Numbers are also reduced when one species gives place to another with a certain amount of overlapping, especially where those species have similar habits: this occurs where *Fassa falcata* begins to give place to *Corophium acherusicum* at H 1 (both live in tubular galleries in silt); and to a lesser extent with the two species of barnacles. A very abrupt changeover with no overlapping is seen where, at H 15, *Polysiphonia* is completely replaced by *Callithamnion* in Zone III, and *Enteromorpha intestinalis* by *E. torta* in Zone II. Zonation, as pointed out by Elton (1927), is more clearly marked in plants than in animals.

The occurrence of *Nereis pelagica* at H 1 and H 4 only, and not seawards of this, is explained by the fact that on these buoys a few had got a foothold in empty nailholes in the protecting wood baulks. But the presence of such truly marine organisms as *Gammarus locusta*, *Ascophyllum nodosum* and fucoids on Hamoaze buoys and their absence on more seaward buoys is not so easily explained. Fig. 1 shows that *Molgula* is common on all seaward buoys but tends to decrease towards the Hamoaze; just inside however, at H 1 buoy, it suddenly attains an extraordinary abundance, to a large extent crowding out *Mytilus* and *Polysiphonia*. After H 1 it drops out abruptly on buoys, though it is found opposite H 4 in St John's Lake.

The following are the dominant forms grouped roughly in order of their importance:

In the Sound and Outer Waters:

- (i) *Mytilus*, *Jassa*, *Ulva*, *Polysiphonia*, filamentous green algae.
- (ii) *Laminaria*, worms and Bryozoa, *Tubularia*.

In the Hamoaze and up to Neal Point:

- (i) *Mytilus*, *Corophium*, *Enteromorpha*, *Polysiphonia* (replaced, as noted above, by *Callithamnion* at Neal Point).
- (ii) *Lepralia*, *Pomatoceros*, *Gammarus*.

Speaking generally for the whole series, the dominant forms are filamentous green algae, *Ulva*, *Enteromorpha*, *Polysiphonia*, *Mytilus* and amphipods. The mussel competes with the algae, chiefly *Polysiphonia*, with which it shares Zone III.

#### ENVIRONMENTAL CONDITIONS

Salinity, temperature and hydrogen-ion concentration are discussed more fully in Part III of this series (Milne, 1938). Current and wave action are similar on the H 1-H 15 series of buoys; a little more wave action might be expected at those buoys between Devil's Point and the Mallard, though the current is much the same; Panther, New Rock and Mewstone buoys are subject to the violence of the open sea. The current in the Hamoaze and Sound, reversing with the tide, varies from  $1\frac{1}{4}$ - $2\frac{3}{4}$  knots. Suspended matter, always present in greater quantity than in the sea, increases up-river and during winter or spate conditions (Cooper & Milne, 1938). The sides of the buoys are perpendicular so that silt will not easily be deposited. There are no industrial effluents in the Tamar and only a relatively small amount of crude sewage. The hydrogen-ion concentration seldom falls as low as pH 7.5 even at H 15. Diurnal fluctuation of the temperature of the water passing the buoys is small but the seasonal range increases up-river—at Saltash the extremes may be 2-4° C. higher or lower than those at the Breakwater. Organisms on the buoys are subject to constant immersion, and this, as noted before, excludes certain species. This condition, however, avoids desiccation and large fluctuations in temperature, but lays the organisms open to more protracted and greater salinity fluctuation than on an equivalent point on the shore. Various workers have shown that certain marine organisms can be accustomed to salinities steadily decreasing to that of freshwater, provided the process is sufficiently gradual. Rate as well as range of salinity fluctuation is therefore important. Part III shows how this varies from high to low water, daily, fortnightly and seasonally from the exceptionally rainy winter of 1936-7 to the rather dry summer of 1937, so that most contingencies are covered. There is a progressive increase in the range of fluctuation in an up-river direction. Differences such as 12.8‰ (9 atm. of osmotic pressure) at Saltash, and 5.5 and 5.2‰ (3.5 atm.) at Drake's Island and the Breakwater respectively may have to be withstood in 6 hr. (tide) at springs in winter;

while summer conditions are more stable, the corresponding figures being 1.8‰ (1.5 atm.) and 0.2 and 0.3‰. Maximum ranges within one tidal cycle were 33.7–7.6‰ at Saltash, 33.7–19.5‰ at Drake's Island, and 34.9–26.6‰ at the Breakwater.

Fischer-Piette (1931 *et seq.*) has shown that salinity is by far the most important agency controlling estuarine distribution. He demonstrated that horizontal limits fluctuate according to rainfall (i.e. lowering of salinity) summer and winter and from year to year.

With the aid of Fig. 1 in the present paper and Table II in Part III, and the map in Part I, some idea of the resistance of certain species to salinity fluctuation may be formed.

#### FLUCTUATION OF LIMITS WITH FLUCTUATION OF ENVIRONMENT

There was an exceptionally high rainfall and therefore a correspondingly low salinity in the winter of 1936–7. Towards the end of this rainy period skeletons of *Pomatoceros* and *Lepralia* were present at H 15, while living specimens were found on H 11; similarly, *Limnoria* tunnels were found to be occupied at H 7 but empty at H 11. This withdrawal of limits is undoubtedly due to a steepening of the estuarine gradient at this time (Fischer-Piette, 1931). Crawford (1937, p. 651) in the years immediately preceding states "in 267 specimens counted at random from Neal Point Buoys there was found

<i>Corophium acherusicum</i>	259	<i>Gammarus zaddachi</i>	2
<i>C. insidiosum</i>	3	<i>Melita palmata</i>	1
<i>Jassa falcata</i>	2		

*Idotea viridis* and *Hyale* were also present." Of these, only *Gammarus zaddachi* was present when the buoys were examined in March 1937.

But this rainy winter did not cause the retreat of all organisms. Percival's (1929) lists of intertidal organisms were made during and after a dry summer,\* while after the wet winter (1936–7) the writer noted the intertidal penetration of seven of his species:

Species	Penetration in kilometres	
	1928	1937
<i>Molgula</i> sp.	2.0	2.0
<i>Mytilus edulis</i>	13.3	13.3
<i>Littorina littorea</i>	9.4	9.4
<i>L. rudis</i>	9.4	9.4
<i>Balanus balanoides</i>	13.3	11.0
<i>Halichondria</i> spp.	9.4	5.0
<i>Littorina obtusata</i>	9.4	11.0

Four species had maintained their position, two had retreated and one had actually advanced. With the exception of one retreating species, *Halichondria*,

\* Percival does not mention the rainfall of the preceding winter.



and one static species, *Molgula*, the remainder are all able to close up and possibly escape harm while awaiting the return of suitable conditions (see later).

#### COMPARISON WITH PREVIOUS WORK

Orton's (1930) list of the chief organisms growing on or in experimental material—floating rafts, and piles fixed at L.W.S.T.—in Cawsand Bay and Plymouth Sound differ from the present findings chiefly because some of the material was not subject to constant immersion, and most of his rafts were in the sea three times as long as the Admiralty buoys.

Percival's (1929) distribution of intertidal and bottom species in the Tamar are compared in Table I. There are differences both in numerical order of and extent of penetration. If salinity alone were the limiting factor then at least the numerical order of penetration would be the same. The distribution

TABLE I. COMPARISON OF EXTENT OF PENETRATION OF SPECIES COMMON TO THE STUDIES OF PERCIVAL (1929) AND THE PRESENT PAPER

Distances given in kilometres up-estuary (+) or down-estuary (-) from zero position at Devils' Point (see map in Part I).

(*Gammarus locusta* is omitted because Percival did not recognize *G. zaddachi* as a separate species.)

Intertidal and Bottom 1928	km.	Buoys 1937	km.
<i>Carcinus maenas</i>	+21.7	<i>Balanus balanoides</i>	+6.0
<i>Asciidiella aspersa</i>	+14.0	<i>Melita palmata</i>	+6.0
<i>Botryllus schlosserei</i>	+13.6	<i>Lepralia pallasiana</i>	+5.0
<i>Pomatoceros triqueter</i>	+13.6	<i>Pomatoceros triqueter</i>	+5.0
<i>Melita palmata</i>	+13.3	<i>Botryllus schlosserei</i>	+1.0
<i>Balanus balanoides</i>	+13.3	<i>Jassa falcata</i>	+1.0
<i>Lepralia pallasiana</i>	+11.0	<i>Harmothoe impar</i>	-2.0
<i>Jassa falcata</i>	+9.4	<i>Metridium senile</i>	-2.0
<i>Ophiothrix fragilis</i>	+9.4	<i>Asciidiella aspersa</i>	-3.0
<i>Harmothoe impar</i>	+9.4	<i>Carcinus maenas</i>	-3.0
<i>Metridium senile</i>	+7.7	<i>Cirratulus cirratus</i>	-5.3
<i>Cirratulus cirratus</i>	+5.4	<i>Ophiothrix fragilis</i>	-7.5

on buoys ought to be the best indicator of order of penetration, or resistance to the salinity gradient, of those animals able to live on buoys: for while the substratum of the shore is irregular in many ways, thus bringing other factors into play, that on the buoys is constant in texture and slope. Organisms on the shore generally penetrate farther than those on buoys (Table I). This is believed to be due chiefly to the greater and more protracted salinity fluctuation on the buoys than on a corresponding point on the intertidal area or bottom. Mussels were absent on the Neal Point buoys in spring 1937, while the richest bed in the Plymouth district lies directly beneath them on the bottom.

The effect of rainfall conditions on extent of penetration is discussed in the preceding section.

Fraser (1938) investigated the fauna of buoys submerged for one year in the Mersey Estuary in a salinity gradient varying from sea conditions down to

27.4‰. This resembles salinity conditions in the Sound and Outer Waters at Plymouth. The fauna in the Mersey is poorer in number of species than the Tamar; sponges, polyzoa and *Carcinus maenas* are absent in the former. Throughout the range in the Mersey estuary, *Mytilus edulis*, *Harmothoe imbricata*, *Lepidonotus squamatus*, *Nereis pelagica*, *Podocerus variegatus* and *Asterias rubens* are common; *Metridium senile* and hydroids, *Balanus crenatus*, and ascidians are less common; *B. balanoides* is practically absent. *Fassa falcata* is common at the seaward end of the range (cf. Tamar). The density of *Asterias* and *Nereis* here contrasts with their paucity in the Tamar. Apart from geographical position, the pollution and possibly the silt suspension factors, the former of which is much greater in the Mersey, may largely account for the differences.

The various comparisons made illustrate the difficulty of attributing the limiting factor to salinity alone.

#### VERTICAL DISTRIBUTION

The flora of the buoys showed a particularly clean-cut vertical zonation. The dimensions of the various belts are given in Table II; the data are averages from 2 to 4 buoys (except for Panther where only one buoy was examined) and three measurements were made on each buoy.

TABLE II. WIDTH OF THE ALGAL ZONES ON THE BUOYS IN CENTIMETRES

Zone III was limited by the depth of the buoy.

Buoy	Zone I	Zone II	Zone III
Panther	0-17.8	17.8-35.6	35.6-127.0
Mallard	0-18.6	18.6-35.6	35.6-218.5
D 4	0-17.8	17.8-35.6	35.6-111.8
H 4	0-10.2	10.2-25.4	25.4-127.0
H 7	0-9.7	9.7-22.3	22.3-246.6
H 11	0-8.0	8.0-18.0	18.0-183.1

Uppermost was a narrow belt of filamentous green algae unidentified. This belt, termed Zone I, was present on all the buoys.

Just below was a slightly wider belt, Zone II, occupied by *Ulva* or *Enteromorpha*, or both. *Ulva* (2 spp.) was present from Mewstone to H 4 and *Enteromorpha* from Panther to Neal Point. *E. intestinalis* was completely replaced by *E. torta* at Neal Point buoys, while the two species of *Ulva* are present together for some part of their horizontal range, though *U. lactuca* finally outstrips *U. linza* in penetration of the estuary.

Below this again was a very much wider belt, Zone III, where *Polysiphonia elongata* was dominant. *Polysiphonia* was absent at Mewstone, present from New Rock to H 15, and completely replaced by *Callithamnion corymbosum* at Neal Point. A few brown algae—chiefly *Laminaria* spp., and other red algae—such as *Rhodymenia* and *Ceramium*, were present also in Zone III. Moreover,

on the seaward buoys, some fronds of *Ulva lactuca* tended to spread downwards a few centimetres and mingle with *Polysiphonia*, but the latter was by far the dominant.

Thus Zones I and II were occupied solely by green algae, while Zone III was occupied predominantly by red, and to a lesser extent by brown.

Both the size and density of fronds tended to increase a little downwards in each zone. Zone II was more luxuriant than Zone I, and Zone III than Zone II.

No macrofauna was present in Zone I; in Zone II a few species were present, especially *Stenothoe*, insect larvae, and occasionally *Idotea*; but the greater part of the fauna, including the species in Zone II, was confined to Zone III. The macrofauna increased in abundance with depth below the surface, reached its maximum at about 50 cm., and maintained that abundance to the bottom of the buoy.

Colman (1933, p. 454) and Orton (1929, p. 278) give the upper limits of certain algae in normal habitats in the Plymouth district. Below, these limits are compared with those on the buoys by giving the least distance in metres below E.H.W.S.T. at which they grow on the littoral; and regarding the surface mark on the buoys as E.H.W.S.T. Unfortunately, in their works only three species could be found which occur on the buoys but they are examples from the green, upper brown, and lower brown algal zones normal to the shore.

Species	Shore (Colman)	Shore (Orton)	Buoys
<i>Enteromorpha</i> sp.	..	0.34	< 0.08
<i>Ascophyllum nodosum</i>	1.61	1.56	0.18
<i>Laminaria digitata</i>	4.55	5.22*	0.22

\* Orton refers to *Laminaria* spp.

According to Newton (1931) *Polysiphonia elongata*, *Ceramium rubrum*, *Callithamnion corymbosum* and *Rhodomenia palmata* live in rock pools between tidemarks as well as below low water mark which is the usual habitat of "red" algae; but Hamel (1923) gives -25 m. Chart Datum as the depth at which *Rhodomenia palmata* has been found growing at St Malo. Nevertheless the table above shows that there is an extraordinary compression of zonation on the buoys.

This compression of the normal littoral algal zonation must be due chiefly to light conditions on the buoys and to a lesser extent to constant immersion. Since buoys float, waves have practically no uncovering action. Algae are influenced by emersion just as animals are (Fischer, 1928; Baker, 1910; and others). Brown algae such as *Ascophyllum* and fucoids, being intertidal, are at a disadvantage owing to constant immersion, while most of the reds, and to a lesser extent some of the browns such as the species of *Laminaria*, are naturally constantly immersed in their normal habitat. *Ascophyllum* and fucoids only appear on buoys in the Hamoaze to which the laminarians do not penetrate. Where other conditions are suitable, then, the laminarians must oust the other

algae which are not so fitted to withstand the constant immersion of Zone III. The compression of the zonation even in the open sea at Mewstone buoy emphasizes the importance of tidal action in controlling zonation on the shore.

#### VERTICAL ZONATION OF THE ALGAE AND ILLUMINATION

Børgesen (1908) states that sublittoral algae raise their vertical limit in caves where illumination is poorer than on the shore. In the estuary light penetration is much less than in the open sea (Cooper & Milne, 1938). On proceeding from the sea inwards, not only does the total amount of light penetrating become progressively less but its composition changes with depth. "In marked contrast to the open sea, red light penetrates as well or better than green, and blue is cut down most rapidly" (p. 526).

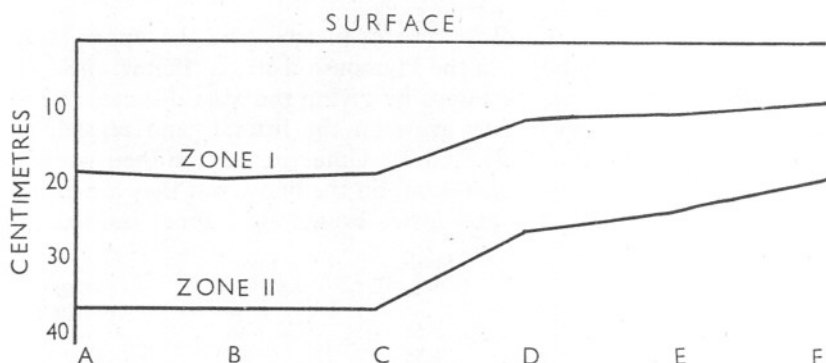


Fig. 2. Lower limits of upper algal zones on buoys. A, Panther; B, Mallard; C, Drake's Island D 4; D, H 4, Hamoaze; E, H 7, Hamoaze; F, H 11, Hamoaze.

On the Mewstone buoy, where conditions are more or less those of the open sea, there is the typical triple zonation mentioned above, but Zone III contains no red algae, *Laminaria* only being present. The lesser penetration of light in the Sound possibly favours the (red) *Polysiphonia* and *Rhodomenia* so that in this situation they establish themselves and tend to oust *Laminaria* in Zone III. Light conditions are more or less uniform in the Sound but penetration decreases abruptly on entering the Hamoaze and continues to decrease up-river (at least to Neal Point buoy). The algal zonation follows the light conditions closely, for the bottom limits of Zones I and II are fairly constant in the Sound but rise abruptly on entering the Hamoaze and rise steadily on proceeding up the Hamoaze (Fig. 2 and Table II).

Daylight factors\* at the zonal boundaries found by the author on the buoys in Plymouth Sound and on Hamoaze No. 7 buoy were presented in our earlier papers (Cooper and Milne, 1938, 1939). They suggested forcibly that the

\* From here to the end of this section I am indebted to Dr L. H. N. Cooper for assistance.

depths of the boundaries are very largely conditioned by the daylight factors. Although we have zonal data for two other Hamoaze buoys, Nos. 4 and 11, we have light records only at Nos. 1, 7 and 15. Approximate extinction coefficients have been calculated for the water near buoys Nos. 4 and 11 on the assumption that the extinction coefficient for a given wave band varies linearly with the distance between two buoys, not too far apart. Thus

$$\mu_{\lambda(H4)} = \frac{\mu_{\lambda(H11)} + \mu_{\lambda(H7)}}{2}$$

and

$$\mu_{\lambda(H11)} = \mu_{\lambda(H7)} + \frac{1.5}{2.6} [\mu_{\lambda(H15)} - \mu_{\lambda(H7)}].$$

Using such values for the extinction coefficients, the daylight factor at each buoy and on each occasion,  $F$ , has been calculated from the equation

$$F = 100 \left( \frac{I_{\lambda_1} e^{-\mu_{\lambda_1} d} + I_{\lambda_2} e^{-\mu_{\lambda_2} d} + \dots + I_{\lambda_9} e^{-\mu_{\lambda_9} d}}{I_{\lambda_1} + I_{\lambda_2} + \dots + I_{\lambda_9}} \right),$$

where  $I_{\lambda_1}$ , etc., represent the spectral energy of a given wave-band in air, and  $I_{\lambda_1} + I_{\lambda_2} + \dots + I_{\lambda_9} = 1$ .

Since in 1937 the medium red filter, S 66, was not available, the rather large gap between the S 61 and S 72 filters has had to be closed by taking the mean values of the extinction coefficients as measured for those two filters ( $\mu_M$ ; see Cooper & Milne, 1938, p. 510) and adding 0.6 as an approximate distilled water correction factor at 660 m $\mu$  ( $\mu_{DW}$ ). The daylight factors so obtained are presented in Table III together with those from Plymouth Sound and Hamoaze No. 7 buoy. Both light transmission and zonation in Plymouth Sound were sufficiently uniform for us to amalgamate our results into one group, in itself evidence for our thesis.

TABLE III. DAYLIGHT FACTORS AT ZONAL BOUNDARIES ON BUOYS (1937)

	Plymouth Sound	Hamoaze			Weighted mean
		H 4	H 7	H 11	
Boundary of Zones I and II					
Depth in metres	...	0.180	0.102	0.097	0.080
June 17 (high water)	78.3	82.5	80.0	84.4	80
June 23 (low water)	76.4	79.4	77.8	76.9	77
February 18 (high water)	65.4	71.4	69.8	73.4	70
Boundary of Zones II and III					
Depth in metres	...	0.356	0.254	0.223	0.180
June 17 (high water)	62.3	62.2	61.8	72.9	64
June 23 (low water)	59.2	56.7	56.5	55.2	57
February 18 (high water)	43.7	45.0	45.0	50.1	45
Bottom of buoy (within Zone III) (Mallard)					
Depth in metres	...	2.19	1.27	2.47	1.83
June 17 (high water)	7.4	11.0	0.97	3.1	..
June 23 (low water)	5.5	6.8	0.35	0.29	..
February 18 (high water)	0.85	2.1	0.020	0.15	..

On June 17 1937, the estuary was optically almost uniform from Hamoaze No. 7 buoy as far up indeed as Neal Point buoy, a condition no doubt somewhat rare and accounting for the high daylight factors calculated for Hamoaze No. 11 buoy on that date. The rest of the additional data serves but to confirm our view that the zonation of algae on buoys in Hamoaze and Plymouth Sound is mainly, if not entirely, governed by the daylight factors.

The factors for the very turbid estuary at low water on February 16 1937, have not been calculated. Conditions must have been so adverse for photosynthesis that even quite considerable fluctuations in absolute light intensity may be safely ignored.

We may summarize the range of daylight factors found within the three zones, excepting times of winter spate, thus:

	Daylight factor %
Zone I	70-100
Zone II	45- 80
Zone III	> 1- 64

#### DISCUSSION

In an ecological study one is always confronted by the doubt that the environment has not been correctly assessed by merely choosing (of necessity) what are thought to be the most important factors. The relative importance of environmental factors ought therefore to be discussed.

The sea (tide) brings plankton and nutrient salts\* while the river brings detritus and possibly nutrient salts also. Thus detritus and plankton feeding animals apparently find no lack of their foods in the estuary, but for plants the opacity of the water must soon limit photosynthesis. Considering the relative bulks of sewage and water in the estuary basin together with the speedy rate of renewal of the latter by tide and river, sewage here is probably innocuous since it will be quickly diluted and swept away. Thus the Tamar has a relatively clean estuary and oxygen concentration probably never falls so low that it could be a significant factor alone. Sponges and Polyzoa are absent on Mersey buoys, and though present on seaward buoys are not generally exuberant in the Tamar. The latter estuary, though well oxygenated, contains a high silt content, and the Mersey, besides being polluted, seems to have a higher one still. The dominance of mussels in both estuaries may thus be explained, for, as Fischer-Piette notes (1935, p. 155), "the mud which accumulates between their shells and among their byssus threads soon eliminates animals which require clean water, like many sponges, Bryozoa, Hydrozoa, and compound ascidians".

\* Generally speaking: "So far as nutrient salts are concerned conditions in Plymouth Sound are usually better than those of the open sea at the same season" (Dr L. H. N. Cooper).

Huntsman (1918) has shown that a combination of comparatively high temperature and low salinity influenced the vertical distribution of certain marine species, so that the temperature gradient in the Tamar may be more important than some factors. But undoubtedly salinity is the chief limiting agency, outweighing all others (see Fischer-Piette 1931). Yet all the other factors even though they may be thought harmless\* of themselves (because of their usually small range of variation and their apparently negligible difference from sea conditions) must help both singly and collectively to make salinity a greater or lesser limiting factor. It is well known that one physical or chemical factor may affect the action of another. This point is emphasized by a comparison of intertidal penetration of marine species in several estuaries of similar salinity gradient (Tees, Tay, Tamar and La Rance in France): there are broad similarities, but there are also striking differences both in extent of penetration and in the order in which the organisms drop out. These differences or at least the latter difference would be absent if salinity were the only limiting factor. Fischer-Piette's (1931) "salinity" is really rainfall which includes pH, temperature, current and suspended matter changes. In nature, then, one can only speak of a chief limiting factor. In a clean estuary the chief one is salinity.

*Mytilus* certainly (unpublished work) and *Balanus*, *Pomatoceros* and *Lepralia* possibly, can close up and wait for the return of suitable salinity conditions; but that amphipods, coelenterates and algae in the Tamar can withstand osmotic changes up to 9 atm. four times in 24 hr. and often for several days at a time without their tissues disrupting is remarkable. Atkins (1916, p. 179) has shown that *Ascophyllum nodosum* in seawater of osmotic pressure 22.6 had an osmotic pressure of 23.6 atm. after 24 hr. in the dark in the laboratory; on being placed in diluted sea water (10.7 atm.) the same thallus, after 3½ hr., was at 13.4 atm. Thus "alteration of the medium... leads to a very rapid readjustment of pressure through the diffusion outwards of salts". Atkins goes on to say that "injurious effects... are occasioned by fluctuations which are too rapid for the proper adjustment to be effected". Although the changes at Saltash (H 15) are large at certain times, they are never so abrupt as this (being spread gradually over 6 hr.) and never so large (9 atm. as opposed to 12).

The horizontal distribution of algae in the different zones may be partly affected by the spectral composition (as well as the daylight factor) of the penetrating light since this changes in the up-river direction. But probably the horizontal gradients in salinity and temperature have some influence as well as light in this connexion. While the zonal boundary curves of flora on buoys are undoubtedly a function of the light factor, it may be that these other factors also influence the *absolute* limit of vertical distribution for it is conceivable that salinity and temperature may affect the metabolism of the plant cell and thus its capacity for photosynthesis. Some of the invertebrate

\* (Cf. Fischer-Piette, 1931.)

population are possibly also limited in their distribution by that of the algae in which they dwell (cf. Russell, 1936, p. 6).

Owing to the limited time available, seasonal variations in distribution on the buoys could not be investigated, but the Tees Survey Report (Alexander, etc., 1935) states that "apart from the normal seasonal changes which occur in the abundance of various organisms, such as the dying away of hydroids in winter and the seasonal maxima of insect larvae, no seasonal changes were observed in the fauna and flora of the (Tees) estuary".

My thanks are due to the authorities of H.M. Dockyard, Devonport, for facilities afforded for the examination of the buoys; and also to the staff of Plymouth Laboratory, especially to Dr L. H. N. Cooper.

#### SUMMARY

Buoys differ from the intertidal area in that they are constantly immersed near the surface of the water and the slope and texture of their surface is constant. The horizontal and vertical distribution of the macrofauna and macroflora on a series of buoys stretching from the open sea up the Tamar estuary is given.

There are differences in estuarine penetration even among species belonging to the same genus. Distribution is likely to be affected by the time of laying the buoys and the period in the water. But the six buoys farthest from the sea were laid down and lifted at approximately the same time. For these, at least thirty species were available for colonization, but little more than half that number was found even on the most seaward; and the number decreased up-river.

Although there is more suspended silt in the estuary than in the sea and although this increases up-river, the penetration of suspension and non-suspension feeders is similar.

Generally organisms become less numerous and smaller towards the up-river end of their range. Where there is a tendency to lesser density (not size) in a species towards the seaward end of the range, this is largely due to competition for space. Those organisms which do penetrate the estuary have some (new species come in) of the space normally shared with those which do not. Density also decreases where one animal gives way with overlapping to another of similar habits. There is usually no overlapping and no density decrease where replacement occurs in plants.

Dominants on these buoys are filamentous green algae, *Ulva*, *Enteromorpha*, *Polysiphonia*, *Mytilus* and Amphipoda. *Mytilus* competes with the algae.

Salinity seems clearly to be the main limiting factor. Range of fluctuation alone may be less important than range plus rate of fluctuation. Average salinity decreases and range and rate of fluctuation increases in the up-river direction. Salinity data, however, do not suffice to explain all the observed



facts of distribution so that other chemical and physical factors must be taken into account in association with salinity. Organisms such as amphipods and algae, which cannot close up to await the return of suitable conditions like *Mytilus*, sometimes withstand 12 ‰ fluctuations (9 atm. of osmotic pressure) four times in 24 hr. at springs in winter.

Data are given which show the observed salinity-fluctuation-tolerance of certain organisms in the Tamar. After an exceptionally rainy winter, certain organisms on buoys withdrew their limits a little down-river. On the shore, though some had retreated, others maintained their position, while one had actually advanced from the position it occupied after a dry summer some years previously. With two exceptions all these could close down like *Mytilus*, though whether they could escape the bad conditions like the latter, is not known, for one, *Balanus balanoides*, had retreated.

Comparisons are made with other work in the Tamar. Differences in numerical order and extent of penetration on shore and buoys indicate that the salinity factor is conditioned by other factors which differ in the two habitats. The fact that organisms penetrate farther up-river on the shore arises largely from the greater and more protracted salinity fluctuation on the buoys compared with an equivalent point on the shore or bottom.

The vertical algal zonation normal to the shore is much compressed on the buoys. This is due mainly to light penetration and to a lesser extent to constant immersion. Light penetration decreases up-river and the zonal boundaries exhibit a corresponding approach to the surface in the up-river direction; this is shown to be mainly, if not entirely, governed by the daylight factor. Spectral composition also changes up-river but that the composition of the flora changes likewise may be due partly to salinity and temperature gradients.

#### REFERENCES

- ALEXANDER, W. B., SOUTHGATE, B. A., and BASSINDALE, R., 1935. Survey of the River Tees. Part II. The Estuary—chemical and biological. *D.S.I.R. Water Pollution Research*, Tech. Paper No. 5, H.M. Stationery Office.
- ATKINS, W. R. G., 1916. *Some Recent Researches in Plant Physiology*. London, 1916.
- BAKER, S. M., 1910. On the causes of zoning of brown seaweeds on the seashore. II. *New Phytologist*, Vol. IX, pp. 54-7.
- BØRGESEN, F., 1908. The algal-vegetation of the Faroese coasts with remarks on the phyto-geography. *Botany of the Faroes*, Part III, pp. 683-834.
- COLMAN, J. S., 1933. The nature of the intertidal zonation of plants and animals. *Journ. Mar. Biol. Assoc.*, Vol. XVIII, pp. 435-76.
- COOPER, L. H. N. & MILNE, A., 1938. The ecology of the Tamar estuary. II. Under-water illumination. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 509-28.
- — — 1939. The ecology of the Tamar estuary. V. Under-water illumination. Revision of data for red light. *Journ. Mar. Biol. Assoc.* Vol. XXIII, pp. 391-96.
- CRAWFORD, G. I., 1937. The fauna of certain estuaries in West England and South Wales with special reference to the Tanaidacea, Isopoda and Amphipoda. *Journ. Mar. Biol. Assoc.*, Vol. XXI, pp. 647-62.
- ELTON, C., 1927. *Animal Ecology*. New edition, 1935. London: Sidgwick and Jackson.

- FISCHER, E., 1928. Recherches de bionomie et d'océanographie littorales sur la Rance et le littorale de la Manche. *Ann. Inst. Océanogr. Paris*. Tome I, v, fasc. 3, pp. 201-429.
- FISCHER-PIETTE, E., 1931. Sur la pénétration des diverses espèces marines sessiles dans les estuaires et sa limitation par l'eau douce. *Ann. Inst. Océanogr.* Tome x, fasc. 8. pp. 217-43.
- FISCHER-PIETTE, E., 1933. Nouvelles observations sur l'ordre d'euryhalinité des espèces littorales. *Bull. Inst. Océanogr.*, No. 619, pp. 1-16.
- 1934. Faune et flore de Saint-Servain en 1934. *Bull. Lab. Saint-Servain.*, fasc. 13, pp. 22-30.
- 1935. Histoire d'une moulière. Observations sur une phase de déséquilibre faunique. *Bull. Biol. Fr. Belg.*, Tome LXIX, fasc. 2, pp. 153-77.
- FLATTELY, F. W. & WALTON, C. L., 1922. *The Biology of the Seashore*. London: Sidgwick and Jackson.
- FRASER, J. H., 1938. The fauna of fixed and floating structures in the Mersey estuary and Liverpool Bay. *Proc. Trans. L'pool Biol. Soc.* Vol. LI, pp. 1-21.
- HAMEL, G., 1923. Sur la limite de la végétation dans la Manche d'après les dragages effectués par le "Pourquoi-Pas?" *C.R. Acad. Sci. Paris*, Tome 176, pp. 1568-70.
- HARTLEY, P. H. T. & SPOONER, G. M., 1938. The ecology of the Tamar estuary. I. Introduction. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 501-508.
- HUNTSMAN, A. G., 1918. The vertical distribution of certain intertidal animals. *Trans. Roy. Soc. Canada*, Sect. IV, p. 53.
- MARINE BIOLOGICAL ASSOCIATION. 1931. *Plymouth Marine Fauna*. 2nd edition.
- MILNE, A., 1938. The ecology of the Tamar estuary. III. Salinity and temperature conditions in the lower estuary. *Journ. Mar. Biol. Assoc.*, Vol. XXII, pp. 529-42.
- NEWTON, L., 1931. *A Handbook of the British Seaweeds*. British Museum, London.
- ORTON, J. H., 1929. Observations on *Patella vulgata*. Part III. Habitat and habits. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 277-88.
- 1930. Growth-inhibitive value of paints. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 373-452.
- PERCIVAL, E., 1929. A report on the fauna of the estuaries of the River Tamar and the River Lynher. *Journ. Mar. Biol. Assoc.*, Vol. XVI, pp. 81-108.
- RUSSELL, F. S., 1936. Submarine illumination in relation to animal life. *Rapp. Proc. Verb. Cons. Int. Expl. Mer.*, vol. CI, 2ème Partie, pp. 1-8.
- SERVENTY, D. L., 1935. Observations on *Gammarus zaddachi* Sexton, an estuarine amphipod. *Rev. Hydrob. Hydrog.* Bd XXXII.

## APPENDIX I. DATES OF LAYING AND EXAMINATION OF BUOYS

Name of buoy	Laid down	Examined
Mewstone	Jan. 1936	Feb. 11 1937
New Rock	Jan. 1936	May 4 1937
Panther	Jan. 1936	May 3 1937
Mallard	Apr. 1936	Apr. 23 1937
D 4	Apr. 1936	June 10 1937
H 1	Dec. 1935	Feb. 5 1937
H 4	Dec. 1935	Feb. 16 1937
H 7	Dec. 1935	Feb. 22 1937
H 11	Dec. 1935	Feb. 17 1937
H 15	Nov. 1935	Feb. 10 1937
Neal Point	Dec. 1935	Mar. 9 1937

## APPENDIX II. NOTES ON IDENTIFICATION

The species are as in the Plymouth Marine Fauna (1931), and *A Handbook of the British Seaweeds* (Newton, 1931). In some cases it was impossible to give more than the generic name either because the specimen was in a bad state of preservation (especially the smaller coelenterates) or the systematics are confusing (e.g. *Molgula* and *Halichondria*—of the latter, L. R. Crawshay of the Plymouth Laboratory holds that there may be several species at Plymouth all formerly called *H. panicea*). I am indebted to the following for aid in identification:

- E. W. Sexton, G. I. Crawford and G. M. Spooner—certain Crustacea.
- L. R. Crawshay—certain sponges.
- H. B. Moore—Balanids.
- D. P. Wilson—certain worms.
- Professor Stephenson—*Metridium* sp.
- W. J. Rees—small coelenterates.
- Professor Lily Newton—certain algae.
- Professor Theinemann—insect larvae.