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# MARINE MOLLUSCAN ASSEMBLAGES IN THE EARLY PLEISTOCENE OF SIDESTRAND, BRAMERTON AND THE ROYAL SOCIETY BOREHOLE AT LUDHAM, NORFOLK

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An account of a quantitative study of Mollusca from three East Anglian sites is given and from this work the author defines a series of molluscan Assemblage Zones and attempts to interpret the ecological and depositional environment in which they accumulated. The interpretations are thought to have local rather than regional significance. In the basal assemblage zone at Ludham (L.M. 1) and in zone L.M. 2 next above, the death-assemblages contain many Red Crag and Coralline Crag species, not recorded from Harmer's 'Icenian Stage' to which by his definition the Crag in the Ludham Borehole belongs. The L.M. 1 assemblage suggests deposition in sublittoral marine waters shallower than 50 m; the L.M. 2 assemblage suggests deposition at approximately 15 m. In zone L.M. 3 an association of mud-inhabiting bivalves dominated by *Abra alba* may have been *in situ.* Zone L.M. 4 is very poor in molluscs and the sediments are very silty. The zone L.M. 5 assemblage indicates deposition in less than 8 m of water; here the trend to shallower-water deposition of the assemblages culminates (the situation in zones L.M. 4 and L.M. 6 remaining obscure). The L.M. 5 and L.M. 6 assemblages, as regards their extant, intertidal species, resemble those of zones B.M. 1 and B.M. 2 (respectively) of the Bramerton Common sequence. This may indicate similar depositional conditions; yet each Ludham assemblage has proportionally more individuals of extant sublittoral species, which may indicate diachronism or changes of facies. At Sidestrand, the impoverished assemblage is interpreted as littorally deposited; it permits no analogy with the Bramerton and Ludham assemblages.

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Inferences about climatic change based on evidence from pollen and foraminiferal sequences are compared with inferences from the molluscan assemblages. The former indicate a succession of warm ('interglacial') and cold (almost 'glacial') phases but the molluscs show no such clear variation, those with 'interglacial' affinity being present at all levels.

It is shown that Harmer's subdivisions of the Icenian in East Anglia (based mostly on surface exposures) are not capable of being fitted to the succession now known.

## 1. INTRODUCTION

Table 1 summarizes the stratigraphy of the East Anglian Crags. The stratigraphical work of Harmer (1898, 1900, 1902, 1920) on the molluscs of the Crags of East Anglia has recently been confirmed in its application to the Red Crag but found to be inadequate in its application to the Icenian by complementary work on the Foraminifera (Funnell 1961 *a*, *b*) and the pollen (West 1961).

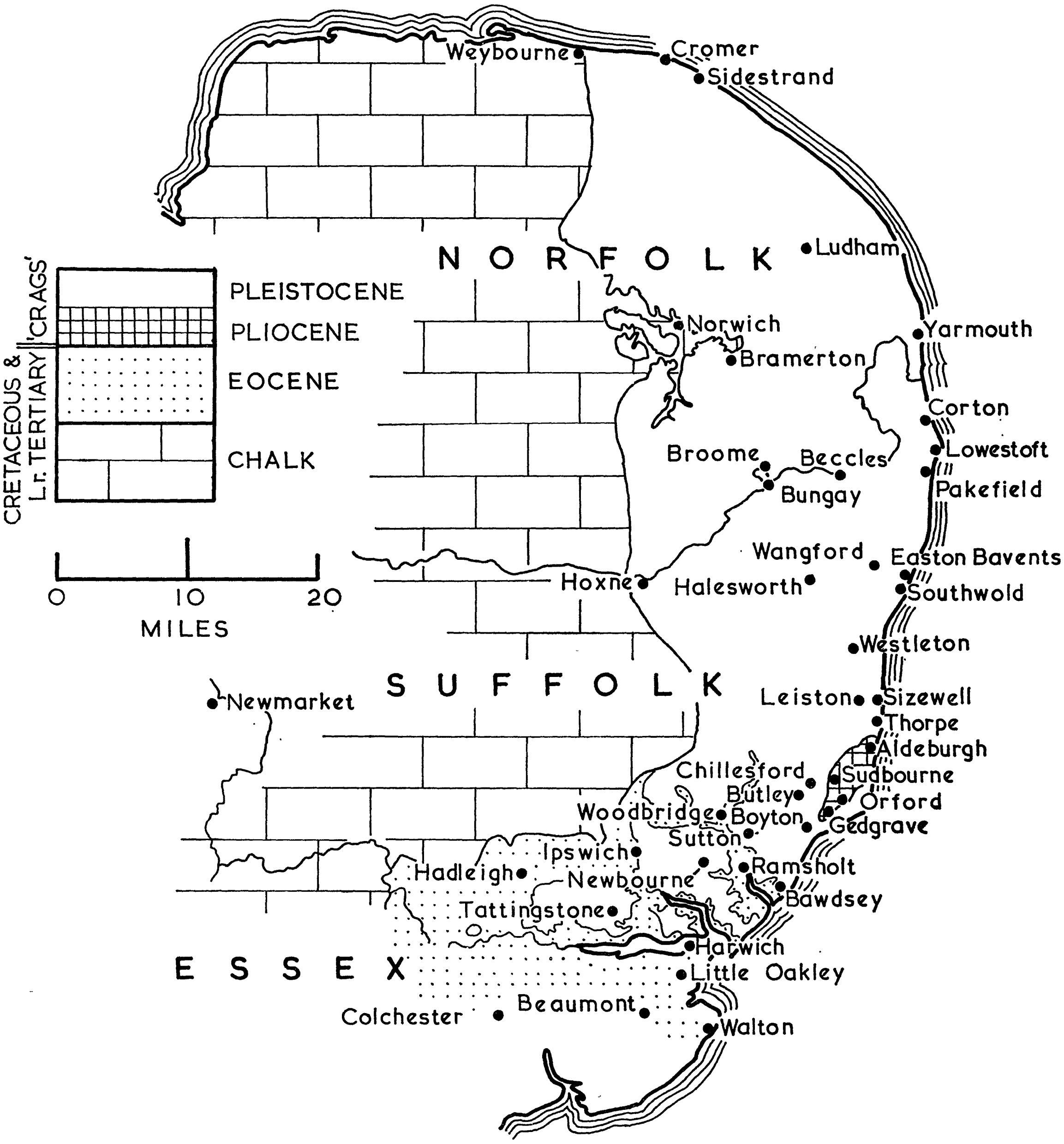

FIGURE 1. Map of East Anglia showing the Crags.

TABLE 1. STRATIGRAPHY OF THE EAST ANGLIAN 'CRAGS' UP TO 1950

| Charlesworth 1836 | | 1836–1898 | | Harmer (1920) | | International Geological Congress 1948 |
|---|---|---|---|---|---|---|
| Upper Crag | Mammaliferous Crag (called Norwich Crag by Lyell 1839) | Cromer Forest Bed series (Reid 1890) | | Cromerian | | PLEISTOCENE |
| | | Weybourne and Bure Valley Crag (Wood & Harmer 1868)<br>Chillesford Clay (overlies Red and Norwich Crags)<br>Upper Norwich Crag (equivalent to Chillesford sands: includes Weybourne Crag—Prestwich 1871)<br>Lower Norwich Crag (= Fluviomarine Crag) equivalent to the Lower Division, Red Crag (Prestwich 1871) | | Weybourne Horizon<br>Chillesford Horizon<br>Norwich Horizon | Icenian | |
| | Red Crag | Red Crag | Upper division (= *Scrobicularia* Crag of Wood 1866) and Unproductive Sands of Prestwich (1871)<br>Lower division (of Prestwich 1871) forms 3 regions: (Wood 1866)<br>Butley, Chillesford and Sudbourne beds<br>Beds between Stour and Deben<br>Walton-on-Naze stage | Butleyan<br>Newbournian<br>Waltonian | Red Crag | |
| Coralline Crag (Lower Crag) | | Coralline Crag | | Gedgravian | | PLIOCENE |

### (*a*) *The Icenian according to Harmer*

Harmer considered that the Icenian basin of deposition was separated from that of the Waltonian, Newbournian and Butleyan by a barrier of Coralline Crag (Gedgravian). The Icenian deposits succeed the Butleyan ones northwards and are nowhere superposed upon them.

The Icenian deposits stretch from the ridge of Coralline Crag at Aldeburgh in Suffolk (figure 1) to the north coast of Norfolk. They are underlain by Coralline Crag immediately to the north of Aldeburgh; then the Coralline Crag goes down below sea level and is not found at depth below Leiston. Harmer considered the Icenian sea less saline than the Red Crag sea, conjecturing that the Icenian basin was dammed by Scandinavian ice to the north (the 'Dover Strait' having closed in Red Crag times) and its sea diluted by rivers pouring in from the south. The Icenian deposits comprise three horizons.

The Norwich Horizon was envisaged by Harmer (1920, pp. 498, 499) as the deposit of a 'shallow and widespread brackish sea', in which 'subsidence seems to have gone on *pari passu* with the deposition of sediment'. Little of Harmer's evidence was drawn from boreholes but he examined that at Southwold, for example, where through '150 ft. the Mollusca maintain the same recent and shallow-water character throughout'.

The Chillesford Horizon at its type site occurs above Butleyan Red Crag deposits. It consists of Chillesford Sands (only at Chillesford) and succeeding micaceous clays whose 'sinuous course' was mapped by Harmer (1902, fig. 76) who conjectured that they represented an ancient, wandering and estuarine course of the Rhine which established itself following an uplifting of the basin at the end of Norwich Horizon times. Correlation of the *Chillesford* clay with clay layers at other Icenian localities has been much criticized (e.g. Woodward 1881, p. 34) and remains unproved. Mollusca are found in the deposits only at Chillesford.

The Weybourne Horizon rests directly on the Chalk at the north Norfolk coast. Harmer supposed it to be the deposit of a locally transgressive sea, younger than the Chillesford Horizon. There is an impoverished fauna with *Macoma balthica* (the first record of this species in the Pleistocene of the southern North Sea: see Spaink & Norton 1967). The exact lateral and vertical relationships of the Weybourne Horizon are obscure.

Characteristic Mollusca of the 'Icenian Stage' are listed by Harmer (1900, p. 723; 1902, p. 446; 1920, p. 449). From these sources a list of the molluscs can be compiled, bearing in mind that some of the species, which Harmer's lists of 1900 and 1902 had contained, are absent from his 1920 list, which in turn contains names not listed in 1900 and 1902. Often, the species are listed elsewhere as characteristic of other stages; e.g. Waltonian (Harmer 1900, p. 712), Newbournian (Harmer 1902, p. 442) and Butleyan (Harmer 1920, p. 490).

### (*b*) *The Icenian in the light of recent research*

#### (i) *In East Anglia*

The pollen and Foraminifera of certain Icenian sites have recently been investigated by West (1961), Funnell (1961 *a*, *b*) and Funnell & West (1962). Quantitative studies have revealed that a series of assemblage zones occurs. A series of climatic oscillations from warm to cold is indicated, not the progressive refrigeration of which Harmer (e.g. 1900,

p. 725) wrote. The micropaleontological zonation has been observed at Ludham (pollen from the Royal Society Borehole, Foraminifera from the Ludham Pilot Borehole 87 ft. to the west). Parts of it have been recognized also in surface exposures at Sidestrand and Bramerton in Norfolk and Easton Bavents in Suffolk. Stage names for each period of the vegetational succession (except for one final part recognized only in the Ludham Borehole which West—in West & Wilson (1966)—correlates with the Pastonian of the Cromer Forest Bed Series) have been proposed by West. They refer to the terrestrial sequence. The zones recognized on the basis of foraminifers, which display the concomitant sequence of marine events, have not been made the basis of a series of marine stages. The sequence of zones is given in table 8 (which contains the summarized results of the mollusc analyses).

### (ii) *The 'Icenian' in the Netherlands*

West (1961, table 2) and Zagwijn (unpublished) have suggested correlations between the East Anglian non-marine stages and those of the Netherlands non-marine succession, as follows:

| | | | Netherlands (Nomenclature from Zagwijn 1957) | | |
|---|---|---|---|---|---|
| | East Anglia | | West | | Zagwijn |
| Icenian | Baventian (cold) | | Menapian (cold) | | Eburonian (cold) |
| | Antian (warm) | | Waalian (warm) | | Tiglian TC-5-6 (warm) |
| | Thurnian (cool) | | Eburonian | 'Icenian' | Tiglian TC-4*c* (cool) |
| | Ludhamian (warm) | 'Icenian' | Tiglian | | Tiglian TC-1–4*b* (warm) |

## 2. The sites studied

### (*a*) *The Royal Society Borehole, Ludham*

This boring was made with the aid of a Royal Society grant in 1959. It was sunk between Ludham (figure 1) and Catfield at Grid Reference TG 385199. The location, method of coring and lithology of the borehole are described by West (1961). The lithology is summarized as follows:

| depth O.D. | lithology |
|---|---|
| +20 (surface) to –25 ft. | soil, drift, etc. |
| –25 to –45 ft. | closely alternating bands of sand and clay with no shells |
| –45 to –63 ft. | shelly sediments with sand and clay |
| –63 to –85½ ft. | clay with no shells |
| –85½ to –163 ft. | series of shelly sands, varying amounts of clay usually in seams. |
| | Basement Bed of large flints, up to 3 in. in diameter |
| –163 ft. | brown Clay (London Clay) |

The surface of the London Clay here descends below its normal level of –90 ft. to –100 ft. O.D. as a depression which deepens eastward and is one of several depressions and closed hollows on the Crag base. The Ludham Pilot Boring from which Funnell took samples for his foraminiferal work was 87 ft. away to the west.

From –25 ft O.D. downwards in the Royal Society Boring the sediments clearly belong to the Crag Series. The series of samples which was obtained was well located and almost complete. Two cores only were lost; one at –48½ ft. to –55 ft. O.D. (at the pollen zone

L 3/L 4 boundary) and another at –57 ft. to –61 ft. O.D. (towards the base of zone L 3). Mollusca from the same depth as the first missing core were obtained from 752 g of material, recorded in the Bore Log as '20 cm of contamination from core above', lying on top of the –55 ft. O.D. core. Mollusca from the region of the second lost core were obtained from a sample retained by the $\frac{1}{20}$ in. mesh of the drilling mud sieve. No evidence of contamination of samples was seen during the work on pollen or Mollusca. The levels at which samples for Mollusca were taken are shown in table 2 (p. 182–187) and figure 2.

*Previous studies*

Zonations based on pollen (West 1961) and Foraminifera (Funnell 1961 *b*) are summarized in table 8 (p. 180).

### (*b*) *Bramerton Common*

The 'type' exposure of the Norwich Crag on Bramerton Common was excavated by Funnell in 1958. The site is on a tree-covered bluff of the River Yare, a few yards after the last house on the road from Bramerton, at Grid Reference TG 297060. Funnell took two series of samples, one from which he investigated the Foraminifera (Funnell 1961 *b*) and another which has been used for the mollusc analyses. The mollusc sample series included samples at the same levels as Funnell's foraminiferal series and the positions at which they were taken are shown in table 3 (p. 189–191) and figure 3.

The sequence is summarized as follows:

| depth below soil surface (cm) | lithology |
|---|---|
| 0 to 260 | upper deposits with silty clay, occasional pebbles and a thick band of yellow sand (115 to 255 cm) |
| 260 to 405 | brown-grey clay |
| 405 to 485 | upper shell bed: occasional clay bands |
| 590 to 980 | sands with occasional clay streaks and a few shell fragments throughout |
| 980 to 1220 | lower shell bed: occasional clay bands: basement bed below |
| 1230 cm (11 ft. O.D.) | chalk |

*Previous studies*

Many of Harmer's records of Mollusca were taken from J. Reeve's collection, now in the Norwich Castle Museum. Woodward (1881) listed Mollusca, giving estimates of frequency; his list distinguished between the fauna of the upper and lower shell beds.

The foraminifers of the Bramerton sequence have been described by Funnell (1961 *b*); the zonation is summarized in table 8 (p. 180).

### (*c*) *Sidestrand*

A series of samples (as shown in table 4, p. 193 and figure 4) was obtained from an exposure of Weybourne Crag between Overstrand and Sidestrand, south-eastward from the end of the Overstrand promenade (Grid Reference TG 252410); here the Crag forms part of a mass of displaced Crag and Chalk. The samples came from three exposures.

1. *Site SS/E*: at the base of the succession there is an organic layer containing pollen, the latter indicating warmer conditions than elsewhere in this Crag. Samples were taken here in 1958 and 1962 by Dr R. G. West.

2. *Site SS/B*: the succession here begins with a stone bed. The organic layer of SS/E is missing. Samples were taken here by Dr B. M. Funnell in 1958.

3. *Site SS/K*: the succession here begins in a stone bed also. A series of samples from 80 cm of shelly material, equivalent to the basal part of SS/B, was taken by me in 1961. The succession at SS/B was described by Funnell (1961 *a*, p. 309) and is as follows:

| height above base (cm) | lithology |
|---|---|
| 300 to 330 | grey, black and yellow clay |
| 280 to 300 | sand with regularly arranged clay bands |
| 265 to 280 | shelly sand with pebbles |
| 190 to 265 | reddish-brown sand with shells and a 1 cm thick clay band at 248 cm. |
| 139 to 190 | brown shelly sands with two thin clay layers (at 190 cm and 175 cm) |
| 85 to 139 | shelly sand with grey clay bands |
| base to 85 | sand, with mainly comminuted shells and scattered pebbles. Larger shells and more pebbles of chalk and quartz |
| Stone bed below this | |

Two foraminiferal samples from SS/B were investigated by Funnell (1961 *b*) who recognized a distinct zonal assemblage in them. Mollusca from an exposure at Sidestrand are listed by Reid (1882, p. 18), who shows the fauna of this part of the Weybourne Horizon to be comparatively poor.

## 3. METHOD OF INVESTIGATION

### (*a*) *Quantitative investigation of the Mollusca*

The procedure for the mollusc analyses was as follows:

1. Samples of about 300 g were used, but less in some cases as with a few, basal, Ludham samples where only small amounts had originally been preserved; and more where a great deal of coarse material was present (stone beds), or where there was a poor but potentially interesting fauna, such as at the base of the Sidestrand sequence. It was found that 300 g of material usually contained good numbers of molluscs and although the species lists from the samples cannot be complete check-lists of the Mollusca of the time, they contain the frequent species and are therefore adequate for paleoecological interpretation.

2. Clayey samples, in which it was difficult to separate the Mollusca, were treated with hydrogen peroxide solution.

3. The samples were wet-sieved on meshes of 5660, 2830, 900, 380, 270 and 165 $\mu$m. No determinable molluscs occurred in the size fraction below 165 $\mu$m.

4. The following criteria were used in counting the Mollusca (under a stereoscopic microscope):

(*a*) Any gastropod shell with an apex, or one lacking so little of an apex that the remainder could not have been identified alone, was counted as an individual.

(*b*) The number of plates of any polyplacophoran species found in a sample was divided by eight, to give the number of individuals represented. If the answer was a smaller fraction than one-half, the species was recorded as 'present but only as fragments' (see (*d*) below). Otherwise numbers were given to the next half-individual.

(*c*) A bivalve fragment with a hinge, or so much of a hinge that the rest could not have been identified alone, was reckoned as half an individual. To give the total number of individuals present, the count for each species was halved (except for *Anomia squamula* of which no right valve was ever seen, so the number of *Anomia* individuals was held to equal the number of valves).

(*d*) Unless a hinge, apex, or more than two polyplacophoran plates were found, the symbol '×', to mean 'species present, but only as fragments' was placed in the tables (2, 3, 4, pp. 182–187, 189–191, 193) of results.

5. Percentage frequencies for each species were then calculated except where less than 40 individuals occurred in a sample. These percentages and in the case of samples with less than 40 individuals, the actual numbers of individuals (italicized) are given in tables 2 to 4.

### (*b*) *Relation of fauna to sediment*

In order to consider the relation of the death-assemblages to the sediment, mechanical analyses (by wet sieving) were carried out. Certain species found in the assemblages have an infaunal mode of life at the present day. Their ecology (as regards the types of sea bed in which they now live) was considered against the particle-size composition of the sediments in which their shells had been deposited. This attempt to discriminate species which could have lived in a sediment from those which must have been brought in from elsewhere, during deposition, has three limitations to be borne in mind when any hypothesis is made.

(i) The disturbance caused by depositional processes, coring (disturbed samples were usual in these investigations) and sampling, make it unlikely that a true picture of the original sediment as a habitat for molluscs is being obtained. For example, detritus forming a topmost layer of the seabed is important in the life of deposit-feeding species and will, in the samples here dealt with, have been lost or redistributed.

(ii) Since all molluscs in the samples are fossils, it is impossible to say to what extent 'already dead' shells in the sediments influenced the nature of the ancient sea bed as a possible habitat for 'living' molluscs.

(iii) In any case, even were it possible to identify a sediment as having been suitable for colonization by an infaunal species, it would remain unknown whether its fossils in that sediment had in fact been *in situ*, unless the sediment was undisturbed by coring and sampling and the fossils could be examined to see if the shells were in the life-position or had the valves together.

## 4. The molluscan assemblage zones at Ludham, Bramerton and Sidestrand

The molluscan death-assemblages, used below to characterize zones in which the zonal assemblage has individual ecological and depositional significance, are 'accidental'. Generally, they have obviously been produced by the sweeping together after death of species which, on the basis of their known ecology, occupied very different habitats on the sea bed.

Another characteristic of the Norfolk assemblages is the presence together in the samples of species whose ranges do not overlap at present. One such pair are *Calyptraea chinensis* (present northern limit at the Dover Strait) and *Serripes groenlandicus* (present southern limit at East Finmark and Iceland). The feature occurs commonly in the Ludham sequence and it is further discussed on pp. 177 to 178.

A description of the series of assemblage zones which has been distinguished, and is shown in tables 2 to 4 (pp. 182–187, 189–191, 193) and figures 2 to 4, follows and possible inferences about environment are given. Climatic interpretation is dealt with separately on p. 176–179.

### (*a*) *The Ludham zonation*

Beginning at the base of the Ludham succession, the following zonation is distinguished.

*Zone L.M.* 1. –163 ft. to –131 ft. O.D.: zone of *Rissoa curticostata*, *Anomia squamula*, *Calyptraea chinensis*, *Hiatella arctica*, *Abra alba*, *Cingula semicostata semicostata*: also important but with fewer individuals are *Nucella lapillus vulgaris*, *Venus ovata*, *Caecum glabrum* and *Mytilus edulis*. Sediment chiefly composed of coarse to medium sand, coarser above –148 ft. O.D. The fauna is varied, usually with more than 35% of individuals of extinct species; the individuals of recent species being almost exclusively sublittoral at the present and dominated by those of mud-inhabiting bivalves and epifaunal forms. Many species are not characteristic of the Icenian (see below). The molluscan assemblages fall into two subzones which do not correspond with marked changes in lithology.

*L.M.* 1*a*. –163 ft. to –155 ft. O.D. Except at –155½ ft. O.D. there are fewer individuals of species now extinct: those of *Rissoa curticostata* are the most frequent but they do not dominate the assemblages.

The majority of individuals in this subzone belong to extant species: the sublittoral epifaunal *Hiatella arctica*, *Anomia squamula* and (less common) *Calyptraea chinensis*, the intertidal epifaunal species *Mytilus edulis* (a few specimens). The other ecological groups are less important; subtidal mud-bivalve species living at the present day are *Macoma calcarea* and *Serripes groenlandicus* (the latter is today characteristic of clay bottoms in arctic seas).

Some attempts were made (they are considered with subzone L.M. 1*b*) to determine the depth of water in which the assemblages might have been deposited; here it is suggested in anticipation that the two subzones seem to have been deposited in water of about the same depth. The small percentages of epifaunal intertidal species, not found above –155 ft. O.D., may have been brought into the L.M. 1*a* deposits by incorporation of littoral deposits during transgression of the Crag sea.

*L.M.* 1*b*, –155 ft. to –131 ft. O.D. The frequency of individuals of extinct species is higher in this subzone than in L.M. 1*a*, indeed than elsewhere in the boring. *Rissoa curticostata* is the most frequent fossil in the assemblage, *Nucella lapillus vulgaris* and *Cingula semicostata semicostata* are also common. The (extant) subtidal epifaunal species (the most frequent being *Calyptraea chinensis*) form the next most important group. Subtidal mud-bivalves, especially *Abra alba*, are also common, indeed more so than in subzone L.M. 1*a*.

In attempting to estimate the depth at which the L.M. 1 assemblages were accumulated, two lines of evidence are considered. First, apart from a few shells of *Mytilus edulis* in the subzone L.M. 1*a* assemblage, there are very few individuals of present-day intertidal species in zone L.M. 1. It is inferred that deposition of the assemblage was taking place at a depth on the sea bed too great for intertidal shells to be transported there, that is, well below the 'belt of movement' (of Johansen 1901, quoted by Sorgenfrei 1958). Using Johansen's figure (of which we may remain critical) for the extent of this belt, we may argue that deposition took place in water more than 15 m deep. Secondly, in subzone L.M. 1 *b* substantial numbers of *Abra alba* occur. Records (mainly by Ford (1923, especially p. 182); also Petersen 1913; Eisma 1966) indicate that an *Abra alba* association occurs at 8 to 40 m in boreal seas (Ford, Petersen) though a smaller minimum depth would satisfy Spärck (1935). It occurs infaunally, in sea beds with more than 50% of material smaller than 500 μm and about 20% or more of silt and clay (smaller than 60 μm or Allen Grade VIII of Ford), though *A. alba* itself is stated by Eisma to live where silt-clay percentages are above 5% and probably where sand is predominantly fine. We see in figure 2 that such sediment conditions as the former are not represented in zone L.M. 1 and it is inferred that the *A. alba* individuals were not in their environment here but had been moved into the deposits after their death. If the water was more than '15 m' deep (as suggested above) then the *A. alba* shells must have been transported laterally or from shallower water, the latter being unlikely because it seems from Johansen's findings that too little transport to account for the abundance of *A. alba* would occur below 40 m (suggested lower limit for the *A. alba* association). These features of the assemblage are taken (using the limited available knowledge of depositional processes and molluscan ecology) to indicate that water depth was perhaps between 15 m (Johansen's figure) and 40 m—in the light of Spärck's observation quoted above a depth closer to 15 m may be preferred—at the position where the zone L.M. 1 assemblage was deposited.

Leaving this topic, another feature of both subzones and of the next assemblage zone (L.M. 2) is analysed in table 5, whence it can be seen that there is in zones L.M. 1 and L.M. 2 a group of species (some known living) whose recorded distribution in the Crags stops short in the Red Crag or Coralline Crag and does not continue into the Icenian (see Harmer 1900, p. 722 and 1914–25; Wood 1848–82). Funnell (1961 *b*) makes the same remark about the Foraminifera in his zones L. I and L. II. However, zones L.M. 1 and L.M. 2 cannot be said to be Red Crag deposits. They contain many of the characteristic Icenian species listed by Harmer (references on p. 164), but typical Red Crag forms (Harmer 1920, pp. 495, 496) are lacking.

*Zone L.M.* 2 −131 ft. to −96 ft. O.D. Zone of *Abra alba*, *Calyptraea chinensis*, *Caecum glabrum*, *Rissoa curticostata*, *Anomia squamula*, *Turritella triplicata triplicata*, *Mytilus edulis*, *Chrysallida spiralis* and *Hiatella arctica*: *Spisula triangulata* and *Diplodonta astartea* are important but less abundant. A varied assemblage with many different ecological groups. The recent species principally deepwater in habitat, dominated at first by mud-bivalves, epifaunal molluscs and mixed-substratum infaunal molluscs in combination; the last category increases in importance later.

The following features distinguish L.M. 1 from L.M. 2:

(*a*) at the top of zone L.M. 1 (−131 ft. O.D.) there is a rapid increase in the amount of medium-sand in the samples. Above −107·5 ft. O.D., there is an increase in fine-sand, silt and clay until at the top of the zone the samples have more than 30% of the fines.

(*b*) just above the base of L.M. 2, there is a fall in the percentages of individuals of extinct species in the samples to a general level of about 25%. *Rissoa curticostata* remains the most frequent of the extinct species, but is not as important as in L.M. 1. *Spisula*

Table 5. Frequencies of certain species in the Ludham Borehole, which have not previously been found in the East Anglian Early Pleistocene deposits later than the Red Crag

| | | frequencies of species restricted to: | | | |
|---|---|---|---|---|---|
| zone | sample depth in feet below O.D. | Red Crag and Coralline Crag (%) | Coralline Crag (%) | Red Crag (%) | total (%) |
| L.M. 6 | 45½ to 48½ | 2·3* | ... | ... | 2·3 |
| | 48½ to 55 | × | 3·3† | ... | 3·3 |
| | 55 to 57 | 0·3 | 0·9 | ... | 1·2 |
| L.M. 5 | 57 to 61 | ... | ... | ... | nil |
| | 61 to 63 | ... | 0·3 | ... | 0·3 |
| | 66 and 69 | ... | ... | ... | nil |
| (at –67) | 80 | *1* | ... | ... | *1* |
| L.M. 4 | 85 | *2* | ... | ... | *2* |
| L.M. 3 | 85½ to 86½ | 1·1 | 0·1 | 0·1 | 1·3 |
| | 88 to 91 | 1·2 | ... | ... | 1·2 |
| | 91 to 94 | × | 0·8 | ... | 0·8 |
| | 94 to 94½ | 2·6 | 4·0 | ... | 6·6 |
| L.M. 2 | 97 to 99 | 5·4 | 0·1 | ... | 5·5 |
| | 101½ to 106¾ | 3·3 | 2·3 | ... | 5·6 |
| | 106¾ to 108½ | 3·2 | 0·2 | 0·4 | 3·8 |
| | 108½ to 110 | 2·4 | 2·7 | ... | 5·1 |
| | 111½ to 113¾ | 2·7 | 2·7 | ... | 5·4 |
| | 115¼ to 116¾ | 2·4 | 4·3 | ... | 6·7 |
| | 117¼ to 118¼ | 3·8 | 1·6 | ... | 5·4 |
| | 120¼ to 121¾ | 5·8 | 0·2 | ... | 6·0 |
| | 123¼ to 124¾ | 9·5 | 2·9 | ... | 12·4 |
| | 126¾ to 128¼ | 26·7 | 2·4 | ... | 29·1 |
| | 129¼ to 130¾ | 3·8 | ... | ... | 3·8 |
| | 132½ to 133½ | 7·7 | 1·0 | 0·3 | 9·0 |
| *a* | 135¾ to 136¾ | 2·5 | 1·4 | ... | 3·9 |
| | 143 to 144 | 3·3 | 0·8 | ... | 4·1 |
| | 146 to 147 | 1·7 | 0·4 | ... | 2·1 |
| | 148 to 149 | × | 0·6 | ... | 0·6 |
| | 152 to 153 | 2·6 | 0·9 | ... | 3·5 |
| L.M. 1 | 155½ | 13·6 | 0·2 | ... | 13·8 |
| | 157 to 158½ | 2·0 | 0·6 | ... | 2·6 |
| *b* | 161 | 1·9 | 5·1 | 0·4 | 7·4 |
| | 161¾ | 3·9 | 2·6 | ... | 6·5 |
| | 162½ | 1·5 | 3·3 | ... | 4·8 |
| | 163 | *0·5* | ... | ... | *0·5* |

*Notes*: ... indicates no individuals in this category. * One individual of *Solariella maculata*. † Includes 3·5 individuals of *Astarte incerta*. For other conventions see table 2, p. 182.

Species previously recorded only in the Red Crag and Coralline Crag are: *Caecum glabrum*, *C. mammillatum*, *Calliostoma zizyphinum*, *Chrysallida obtusa*, *Odostomia conoidea*, *Rissoa obsoleta*, *Solariella maculata*, *Tornus pulchralis*, *Astarte basterotii*, *A. digitaria*, *Diplodonta rotundata*, *Ensis ensis*, *Limopsis anomala* and *Nucula nucleus*.

Species recorded previously in the Coralline Crag only are: *Cingula proxima*, *Rissoa inconspicua*, *Astarte incerta*, *A. parvula*, *Callista chione*, *Laevicardium decorticatum*.

Species recorded previously in the Red Crag only are: *Acmaea rubella*, *Calliostoma noduliferens*, *Mangelia ambigua* and *Nassarius elegans*.

*triangulata* and *Diplodonta astartea* are other frequent extinct species, but they are less important than any of the recent ones.

(*c*) in L.M. 1 the most frequent group among the recent deepwater species in the assemblage is the epifaunal molluscs, but in L.M. 2 there are equal frequencies of mud-bivalves, mixed-substratum (coarse, muddy bottom) infaunal molluscs and deepwater epifaunal ones. The mud-bivalve group continues to consist of *Abra alba*, which is the most frequent species in the assemblage, and *Macoma calcarea* which occurs once. *Caecum glabrum* is the main member of the mixed-substratum infauna group. The most frequent deepwater epifauna species is *Calyptraea chinensis*.

Higher in zone L.M. 2, the mixed-substratum infauna group decreases in importance in the assemblage and there is an increase in the frequency of the tidal-zone epifaunal molluscs (particularly *Mytilus edulis*) from about –114 ft. O.D. upwards and of the intermediate-depth commensal and parasitic species from –119 ft. O.D. upwards, the commonest species in this group being an ectoparasite of the polychaete *Sabellaria*, namely *Chrysallida spiralis*. These higher percentages of tidal-zone and intermediate-depth species, especially above –119 ft. O.D., may indicate that the assemblages were deposited in shallower water than previously, at a depth to which shells were transported from intertidal communities, i.e. within Johansen's 'belt of movement' or not far below (at about 15 m—Johansen's figure—or less).

In this zone, as in L.M. 1, species not characteristic of the Icenian occur; this has been commented on in the text (p. 170) and in table 5.

*Zone L.M.* 3 –96 ft. to –85½ ft. O.D. Zone of *Abra alba*, *Rissoa curticostata*, *Calyptraea chinensis*, *Anomia squamula*, *Mytilus edulis*, *Chrysallida spiralis*, *Nucella lapillus vulgaris*, *Cingula semicostata semicostata* and *Hydrobia ulvae*. Sediment mainly composed of fine sand, silt and clay, the silt-clay fraction being more than 25% by weight of the total.

In this zone, there is a great increase in the numbers of *Abra alba*. Presuming (from p. 170) that a seabottom sediment with more than 50% by weight of particles smaller than 500 μm and with more than 20% of silt-clay, forms a suitable substratum for colonization by the *A. alba* association at suitable depths, then it is permissible to conclude that the *A. alba* association could have colonized the zone L.M. 3 sediments. Although there is no real diminution in the number of species found in each sample, there are fewer ecological groups in the assemblages than in zone L.M. 2. Sublittoral epifaunal species are the only group apart from *A. alba* to be well represented as far as the extant species are concerned. There is little change in the frequency of intermediate-depth forms or that of intertidal species (*Hydrobia ulvae* appears here for the first time).

It is suggested that here we find an *Abra alba* association which, if not *in situ*, is deposited in sediments which it could have colonized in life. The quantities of shells from intertidal habitats which are found in the L.M. 3 assemblage prompt the suggestion that deposition took place in the shallower part of the *A. alba* association's range, which at the present extends upward to about 8 m, or following Spärck (1935), 5 m depth. Often at the present the *Abra* association occupies shallow and protected waters of an estuarine character and we may therefore suggest the existence of such conditions during the deposition of L.M. 3.

Table 5 shows that at –94 ft. O.D. there is a fall in the frequency of species whose occurrence is thought to be restricted to the Red Crag and Coralline Crag (some are known living). It has been mentioned that Funnell (1961*b*, p. 349) refers to a change in the foraminiferal fauna at about −91½ ft. O.D. in the Ludham Pilot Boring, from a 'Ludham Crag' to an Icenian type.

*Zone L.M.* 4 −85¼ ft. to −64 ft. O.D. Very few Mollusca present, nine species in all and very few individuals. Sediments silt and clay.

The molluscs disappear with remarkable suddenness above −85¼ ft. O.D. and in two samples none were seen at all. The Foraminifera show that sedimentation was occurring in very shallow water according to Funnell (1961*b*, p. 350). West (1961, p. 445) states that the land surface was covered by a subarctic park-landscape vegetation and interprets the climate as having been almost glacial in nature. The absence of molluscan deposition in the sediments is not explainable, nor can interpretations about other features of the environment be derived from the very few molluscs recorded in this zone.

*Zone L.M.* 5 −67 ft. to −55 ft. O.D. Zone of *Lepton nitidum*, *Spisula subtruncata*, *Mytilus edulis*, *Hydrobia ulvae*, *Macoma obliqua*, *Littorina littorea*, *Abra alba*, *Cardium edule* and *Clathrus clathratulus minutus*.

As compared with zones L.M. 3 and L.M. 4, several features of the molluscan assemblage should be commented on.

(*a*) Individuals belonging to extinct species are less common, forming not more than 20% of the assemblages. *Rissoa curticostata* is absent.

(*b*) The part of the assemblage made up of present-day intertidal species increases greatly in numbers of individuals (e.g. of *Mytilus edulis*, *Hydrobia ulvae*, *Littorina littorea* and *Cardium edule*), reaching greater frequencies than in any previous zone. The four species mentioned tolerate low salinities. The freshwater species *Planorbis leucostoma* also occurs. Fossils of members of the present-day *Ensis* association are also present in the death-assemblage; these species are normally now found on sheltered shores.

(*c*) Species today living around and below the low-water mark (intermediate-depth species) and sublittorally in mud show a sharp decrease in frequency. There are increased frequencies of sandy-mud and coarse-substratum infaunal molluscs (the commonest are *Spisula subtruncata* and *Lepton nitidum* respectively) and decreased frequencies of individuals of subtidal epifaunal species, to give a varied agglomeration of subtidal ecological groups within the assemblage, dominated by a group which at present inhabits clean shell-gravel.

Taking it as probable (for reasons considered on p. 170) that the *Abra alba* association would colonize the type of sediment found in zone L.M. 5 and seeing that the *Abra* shells are not more than 6% of the total of molluscs in any sample in this zone, it is apparent that, either, this possible habitat was unsuitable for some reason, or (maybe and) the shells were exhumed, transported and buried elsewhere after death. The high percentages of individuals of extant and intertidal species in this zone suggest that the water was too shallow for the *A. alba* association to colonize the bottom sediments or for its shells to outnumber the locally deposited intertidal shells; in such a case a water depth of 5 to 8 m or less (above the upper limit of the *Abra* association mentioned on p. 170) is postulated.

In the uppermost sample of the zone 3·3% of the individuals are not characteristic of the Icenian (table 5); this figure is higher than those otherwise found above zone L.M. 2 and mainly accrues from seven individuals (little worn though broken) of *Astarte incerta*.

*Zone L.M.* 6 –55 ft. to –40 ft. O.D. Zone of *Calyptraea chinensis*, *Astarte montagui*, *Macoma calcarea*, *Yoldia oblongoides*, *Nucella lapillus vulgaris*, *Venus ovata*, *Spisula subtruncata*, *Anomia squamula* and *Tellina praetenuis*. Sediment mainly medium sand and finer, at the top of the zone almost exclusively fine sand, silt and clay, and above it, silt and clay. No Mollusca occurred above this zone. Compared with zone L.M. 5 the molluscan assemblage shows several differences:

(*a*) Extinct species gain in frequency. *Tellina praetenuis* and *Macoma obliqua* are important here. Both are similar to the recent shallow-water form *M. balthica* and were perhaps elements of an Icenian intertidal fauna which is now unknown. *Yoldia oblongoides* is another important extinct form.

(*b*) Recent species characteristic of the intertidal region almost disappear in zone L.M. 6.

(*c*) Sediments in the zone would (on the basis of such criteria as those on p. 170) have been suitable for colonization by *Abra alba* which is uncommon. *Macoma calcarea*, which has a similar habitat but at the present a more northern range than *Albra alba*, is very frequent at –45½ to –48½ ft. O.D.

(*d*) The mixed-substratum infauna (*Astarte montagui* is the most frequent species) is common for the first time since zone L.M. 2 *Venus ovata* also increases in frequency in zone L.M. 6. Both belong to ecological groups associated with coarser substrata than those of L.M. 5 (and note the existence of such sediments in zone L.M. 6).

(*e*) *Lepton nitidum*, common in zone L.M. 5, is absent from zone L.M. 6.

(*f*) Subtidal species reach very high frequency.

The frequency relation between the intertidal and subtidal species appears to indicate deeper water deposition than that of the zone L.M. 5 assemblages. The reason for the lack of the abundant intertidal fauna of L.M. 5 is obscure and no interpretation of the changes that accompanied the final disappearance of the population is offered. The relation between the very clayey and silty deposits above this zone and those (zone L.M. 4) above L.M. 3 is that both contain pollen spectra which indicate cold conditions following warm ones (table 8).

### (*b*) *Molluscan assemblages at Bramerton*

Table 3 and figure 3 show that the Bramerton assemblages are much poorer in species and variety of ecological groups than the Ludham ones. In particular, the subtidal groups contain many fewer species and some groups are missing altogether. The intertidal groups contain fewer species. This paucity may be related to smaller water depth and lower salinity than at Ludham, and to deposition in an area of uniform seabottom. On the other hand, several species occur which are not found at Ludham: *Nucella lapillus lapillus*, *Patina pellucida*?, *Hydrobia minuta*, *Littorina littorea* var *carinata*.

*Zone B.M.* 1. Base of section (11 ft. O.D., levelled 1965), to 610 cm below top. Zone of *Hydrobia ulvae*, *Cardium edule*, *Abra alba*, *Hiatella arctica*, *Calyptraea chinensis*, *Mytilus edulis* and *Macoma calcarea*. Sediment principally sand.

The subtidal part of the molluscan assemblages is not varied (much less so than in any Ludham zone). The 1220 cm sample contains 45 % of *Abra alba* individuals, which could not be *in situ* in these sediments. The rest of the zone has a restricted fauna with few extinct forms. Intertidal species are the most frequent, especially *Hydrobia ulvae*, *Mytilus edulis* and *Cardium edule*, the only other common molluscs being members of the subtidal epifauna. Higher in the zone, the coarser sediments and higher percentages of intertidal and worn shells, with rather few subtidal ones, suggest shallow water deposition in the 'belt of movement', thus above 15 m according to Johansen. The increasing percentages of worn individuals appearing above 920 cm may be a reflexion of increasing wave action.

All the characteristic species of the assemblage tolerate low salinities (to a mean minimum of about 2%). It is suggested that the deposit represents very shallow waters in a low-salinity sea, with considerable turbulence. The intertidal part of the assemblage is similar to that of zone L.M. 5 at Ludham, though much more important in the fauna. Similar conditions of deposition may be indicated but it is not possible to say whether the two zones are synchronous.

*Zone B.M.* 2. 610 cm to 485 cm below top. Zone of *Macoma obliqua*, *Spisula subtruncata*, *Cardium edule*, *Macoma calcarea*, *Mya arenaria*, *Tellina praetenuis* and *Lepton nitidum*. Sediment principally medium sand, at 500 cm below top silt and clay occur and continue as the main component above the level (490 cm) at which Mollusca cease to occur.

There are larger percentages of extinct molluscs than in zone B.M. 1. The part of the assemblages belonging to species still living shows fewer examples of *Hydrobia ulvae*, and is dominated by the intertidal '*Macoma* community infauna' group and by subtidal bivalves of mud and sandy mud. More ecological types are present than in B.M. 1. Higher in the zone the numbers of intertidal forms diminish, rather in the same way as has been remarked for zone L.M. 6 at Ludham which occupies a similar position at the end of a period of mollusc deposition.

The B.M. 2 fauna is similar to that of L.M. 6 in other respects. *Macoma obliqua* and *Tellina praetenuis* are common in both. At both sites *Hydrobia ulvae* is less common in this zone than the next lower zone. At both places *Macoma calcarea* and *Spisula subtruncata* are frequent in the subtidal faunas. In zone B.M. 2, however, the subtidal epifauna species are infrequent. Although these similarities may indicate similar conditions of deposition, it is not possible to say whether or not the two zones are synchronous.

### (*c*) *Molluscan assemblages at Sidestrand*

Table 4 and figure 4 show that the fauna in the Weybourne Crag at Sidestrand is an extremely impoverished one, and the environmental conditions appear to have been more unfavourable to mollusca than those at Ludham or Bramerton. Three species were not found at Ludham or Bramerton: *Macoma balthica*, *Zirfaea crispata* and *Tornus supranitidus*?. The Sidestrand sequence forms one assemblage zone.

*Zone* of *Macoma balthica*, *Cardium edule* and *Mytilus edulis*, at *Sidestrand*. Sediments principally sand, but finer in the sample at the base of SS/E. Fauna is predominantly of recent and intertidal species, dominated by *Macoma balthica*. The other Tellinidae found at Ludham and Bramerton (*M. obliqua*, *M. calcarea* and *Tellina praetenuis*) are very rare. The species in this assemblage tolerate low salinities, except for *Donax vittatus*. Sorgenfrei (1958, table 11) deduces that this species will tolerate an average minimum salinity of 3·3% but the figure could be fortuitous—most tolerances in Sorgenfrei's table are assessed on the basis of range of the species in the Kattegat, whereas *D. vittatus* is recorded from the

North Sea coast of Denmark where it may be at the limit of its range locally. This tolerance of low salinities may just be a quality of the littoral habit of the species, a phenomenon already noted by Fischer (1948, p. 115) in the present-day faunas: but it is also possible that it demonstrates that they lived in a brackish sea. The almost exclusive occurrence of intertidal species in the assemblages suggests an extensive area of tidal water and deposition at only a few metres depth (if it were not intertidal), very few subtidal shells being cast on the shore.

There is no part of the Ludham and Bramerton successions with which this zone can be compared, and the near-disappearance of several Tellinidae and appearance of *Macoma balthica* sets the zone apart from those so far distinguished. It may belong to a geographically distinct theatre of deposition, or perhaps to a later time. Thus it remains to determine the relationship between Harmer's Weybourne Horizon (including the Bure Valley Beds and Weybourne Crag) and the Ludham and Bramerton sequences.

### (*d*) *The problem of climatic interpretation*

In studies of the Pleistocene the recognition of glacial and interglacial climatic episodes is important. Evidence for such climatic episodes has been based on studies of pollen and of Foraminifera. The question is whether it is possible to discriminate between glacial and interglacial conditions by means of marine Mollusca, and to determine this it is necessary to consider changes in molluscan faunas associated with late-glacial (late Weichselian) and post-glacial (Flandrian) climatic changes.

Fossil pollen, Foraminifera and Mollusca occur in the deposits laid down after the Weichselian late-glacial ice retreat in the Oslofjord and Bohuslän regions of Scandinavia. They have been studied by Brøgger (1900–1901, Mollusca), Brotzen (1951, Foraminifera),

TABLE 6. SOME SPECIES OF THE NORFOLK SITES AND THEIR TIME OF FIRST ARRIVAL IN THE OSLOFJORD AND BOHUSLÄN LATE AND POST-GLACIAL DEPOSITS

| | |
|---|---|
| *Hiatella arctica*<br>*Macoma balthica* | late-glacial arrival. Present in all later deposits |
| *Acmaea rubella*<br>*Buccinum undatum*<br>*Chrysallida obtusa*<br>*Abra alba*<br>*Cardium edule*<br>*Cyprina islandica*<br>*Modiolus modiolus*<br>*Mya truncata* | post-glacial group 1. Present in all later deposits |
| *Chrysallida spiralis*<br>*Hydrobia ulvae*<br>*Mysella bidentata*<br>*Venus ovata* | post-glacial 'general' group, time of first arrival not the same at both localities |
| *Caecum glabrum*<br>*Chrysallida indistincta*<br>*Cardium scabrum*<br>*Chlamys opercularis*<br>*Corbula gibba*<br>*Ensis ensis*<br>*Lepton nitidum*<br>*Spisula elliptica*<br>*S. subtruncata*<br>*Zirfea crispata* | post-glacial group 2. Arrive shortly before, or at, the climatic optimum time |

Feyling-Hanssen (1957, Foraminifera), Hafsten (1960, pollen) and Hessland (1946, a general survey of the Bohuslän fossils). As the climate improved after the retreat of the ice, species immigrated to the region. The order of arrival of the Mollusca, of which 97 species are common to the Oslofjord and the Bohuslän successions, is rather similar at the two sites. The molluscan immigration sequence can be related to the sequence of climatic changes demonstrated by the pollen and Foraminifera, and it is possible to discern groups of Mollusca which arrived for the first time in the late-glacial, the early post-glacial, the post-glacial as a whole, and the later post-glacial time around the climatic optimum, as shown in table 6. The groups in this table are established on the basis that the species had either arrived or not arrived in the Oslofjord and Bohuslän deposits at particular times of climatic importance in the sequence. It is probable that the succession of species in the Oslofjord-Bohuslän deposits is controlled in the main by climate, not by local bottom sediments, as the earliest-arriving species persist in the deposits thereafter, many specimens being in raised-beach and shell-bank deposits which one would expect to contain samples from many inshore bottom communities. This use of immigration-times in the late- and post-glacial sequence of Oslofjord and Bohuslän employs limits to the immigration phases that are as close as possible to those employed by Funnell (1961*a*) in his studies of the foraminiferal succession.

Twenty-five of the species concerned are present in the Norfolk sites and are listed in table 6. The percentage occurrence of the groups in table 6 was calculated for each level in the Ludham, Bramerton and Sidestrand deposits. It was found that species immigrating to the Oslofjord-Bohuslän deposits only at the post-glacial climatic optimum time occur in all the samples studied, with the exception of three very poorly populated samples in Bramerton zone B.M. 1. Accordingly it appears that conditions during the time of deposition at the three sites never deteriorated beyond these encountered during the postglacial climatic optimum in the low-boreal region of the North Sea (or shortly before it, allowing for some lag in immigration of molluscs behind the time at which conditions became warm enough for them).

This interpretation of climate does not agree with those made by Funnell (1961*b*) and West (1961) who recognize a series of temperate and cold alternating periods (table 8). During the coldest periods which have so far been recognized, the Thurnian and Baventian terrestrial stages, the Mollusca are mostly absent. Whether their absence was ultimately caused by low temperatures cannot be determined. Thus the molluscan populations do not vary with climate as sensitively as the pollen and Foraminifera.

The molluscan assemblages of the Norfolk sites suggest that during this part of the early Pleistocene, a different climatic regime, or thermal ecotypes of the molluscan species different from the modern ones, may have been present in the North Sea. For instance, the faunas contain species whose geographical ranges do not overlap today, shown in table 7. To name a single example, one pair which occurred in almost all the Ludham samples are *Serripes groenlandicus* and *Calyptraea chinensis*. The feature can also be discerned in the Bramerton samples, though it is not so well marked in the Sidestrand fauna. Baden-Powell (1956) has observed it in other East Anglian deposits.

Two explanations may be suggested for the presence together of species whose modern distributions do not overlap. First, it is possible that the marine temperature regime (or at least those features of it which controlled molluscan distribution) included mean annual values similar to those of the boreal seas of today, but that temperatures ranged higher and lower during the annual cycle, allowing species which are today distributed mainly north and south of the boreal region, to live side by side with the boreal species and each other. Sorgenfrei (1958) inferred an analogous marine temperature regime in the marine upper middle Miocene of Denmark though here the general temperatures were thought to be similar to those of the modern lusitanian region, with a greater annual range. Alternatively, it is possible that the 'anomalous' Mollusca (table 7), though conchologically the same as the modern forms, existed as different ecotypes as regards their temperature tolerance. It is known that many 'cosmopolitan' modern species such as *Hiatella arctica* and *Mytilus edulis* exist over their range as a series of climate-ecotypes adapted to different latitudinal temperature regimes. In this alternative it is not obligatory to suppose that the early Pleistocene North Sea temperatures differed from those of the present.

TABLE 7. LUDHAM BOREHOLE SPECIES WHOSE DISTRIBUTIONS DO NOT NOW OVERLAP

| species names | North (N) and south (S) points in the north-west Atlantic at which ranges begin and finish | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Franz-Josef Land | Spitsbergen | Murman Coast | E. Finmark | N. Iceland | Nordkapp | W. Finmark | Norway, *c.* 67° N | S-W Norway | Oslofjord | Shetland | Lewis | Dover | Arcachon | Lisbon | S. from Lisbon |
| *Serripes groenlandicus* | N | . | . | . | S | . | . | . | . | . | . | . | . | . | . | . |
| *Acmaea rubella* | N | . | . | . | . | S | . | . | . | . | . | . | . | . | . | . |
| *Macoma calcarea** | N | . | . | . | . | . | . | . | S | . | . | . | . | . | . | . |
| *Trophon clathratus* var. *gunneri* | N? | . | . | . | . | . | . | . | . | . | S | . | . | . | . | . |
| *Abra ovata* | . | . | . | . | . | . | . | . | . | . | . | . | N | . | . | S |
| *Astarte digitaria* | . | . | . | . | . | . | . | . | . | . | . | . | N | . | . | S |
| *Callista chione* | . | . | . | . | . | . | . | . | . | . | . | . | N | . | . | S |
| *Calyptraea chinensis* | . | . | . | . | . | . | . | . | . | . | . | . | N | . | . | S |
| *Diplodonta rotundata* | . | . | . | . | . | . | . | . | . | . | . | . | N? | . | . | S |
| *Turritella triplicata* | . | . | . | . | . | . | . | . | . | . | . | . | . | . | N | S |

* A relict population of *Macoma calcarea* exists in the Danish Belt Seas.

In considering the modern distribution pattern of the species of table 7 in relation to these suggestions, we must suppose that the changing events of the Pleistocene have extinguished either the extraordinary temperature regime, or the ancient molluscan ecotypes, so that the modern ranges of the species concerned have withdrawn northwards and southwards as the case may be.

Some molluscan populations which do not breed in their own locality are maintained by planktonic larvae from remote breeding populations, currents sweeping the veligers in over long distances (Thorson 1966). This will not explain the present case, since embryological information for three species in table 7 shows that development is non-pelagic in *Macoma calcarea*, *Trophon clathratus* var *gunneri* (Thorson 1947) and *Calyptraea chinensis* (Fretter & Graham 1962) and thus long-range transport of larvae is not a factor maintaining their populations.

In conclusion, it is clear that the solution of the problems raised must be the object of future research, in which methods such as oxygen-isotope-ratio measurements of temperature may be very important.

## 5. Discussion and conclusions

### (*a*) *Comparison with earlier malacological work*

*Ludham*

No comparison with earlier work can be made in the case of Ludham. However, some comments have been made on the occurrences of species previously found only in the Coralline and Red Crag (some are also known living); these are greatly more frequent in zones L.M. 1 and L.M. 2 than elsewhere. The following Mollusca, found in the Ludham samples, have not been recorded from the Crags before: *Chrysallida indistincta*, *C. spiralis*, *Gibbula* cf. *spastica*, *G.* cf. *nehalenniae*, *G.* cf. *pennanti*, *Odostomia scalaris*.

*Bramerton*

A list of the Mollusca from the 'Upper' and 'Lower' shell beds is given by Woodward (1881, pp. 42–53) on the authority of the collector James Reeve. The small samples used in my studies contained most of the species that Reeve had marked (subjectively) as 'very common' and 'common', as well as some other species which had escaped being classed in either of these categories because of small size and (or) fragility. The following (mainly small and fragile) Mollusca, listed in table 3, were not recorded from Bramerton by Reeve: *Patina pellucida?*, *Caecum glabrum*, *C. mammilatum*, *Cingula semicostata semicostata*, *Calyptraea chinensis*, *Tellimya pumila?*, *Mysella bidentata*.

*Sidestrand*

Harmer (1905) gave a complete list of Weybourne Crag Mollusca. Reid (1882) listed Mollusca, with assessments of frequency, from the Weybourne Crag at Sidestrand. Compared with my list in table 4, both Harmer's and Reid's lists contain many more species. Table 4 includes all the species (except *Astarte borealis*, now *semisculàta*) that Reid classed as 'very common', almost all the ones he classed as 'common' and one which he gave as 'rare'. It lists the following Mollusca for the first time in the Weybourne Crag: *Hydrobia ulvae*, *Spisula subtrunctata*, *Astarte montagui?*, *Tornus subcarinatus?*.

### (*b*) *Comparison with micropaleontological results*

The correlations between the assemblage zones recognized in these malacological studies and those recognized on micropaleontological grounds are summarized in table 8. The quantitative study of the fossil Mollusca has been perhaps more laborious than micropaleontological investigation, but it has yielded useful results of its own. The molluscs give an account of more localized conditions than the microfossils, and appear to be much more closely related to the local sediments. The technique may prove very useful later, to determine differences of marine depth at a level shown to be synchronous by micropaleontological methods.

Until better understanding of marine temperatures in the early Pleistocene North Sea exists, it is only possible to characterise climatic change by means of microfossils, and in this respect, the value of the malacological method is at present restricted.

(Depths given, unless otherwise stated, are referred to o.d.)

| Mollusc zones | | Ludham pollen zones (after West 1961; West & Wilson 1966) | Easton Bavents zonation (after Funnell & West 1962) | | Foraminiferal zones (after Funnell 1961 *b*) | | |
|---|---|---|---|---|---|---|---|
| | | | Pollen | Foraminifera | | | |
| Sidestrand (Weybourne Crag). Fauna with *Macoma balthica*, impoverished and predominantly intertidal: water probably very shallow. Relation to Bramerton and Ludham deposits not shown by the Mollusca | | L 5. Temperate. −22 ft. to −27 ft. Correlated with Pastonian (1966)<br>L 4 *c*. Baventian. Glacial. −27 ft. to −35 ft. A little warmer than L 4 *b* | no pollen | no foraminifera | Ludham | Bramerton | Sidestrand |
| | | | | | L VII −32½ ft. to −38½ ft. | B III 0–485 cm below top | |
| | | | | | Semi-glacial conditions. Correlation of these zones is suggested | | |
| Bramerton | Ludham | No pollen, −35 ft. to −44 ft. | | | Ludham | Bramerton | |
| B.M. 2. 485 to 610 cm below top | L.M. 6. −40 ft. to −55 ft. | L 4 *b*. Baventian. Glacial. −44 ft. to −52 ft. Oceanic open heath vegetation | L 4 *b*. Baventian. 100 cm to 180 cm below top<br>L 4 *a*. Baventian. Cold at 300 cm | E.B. II, 265 cm to 300 cm. Sea shallow, interglacial to glacial, tentative correlation with B. II | L VI. −38½ ft. to −54½ ft. Suggested correlation with B II | B II. 485 cm to 980 cm below top. Possible stagnant, bay-head sea with fresh-water influx | |
| Faunas are similar but it is not clear whether they are synchronous. Many extinct forms. No molluscs in either succession above this zone. Water depth hard to interpret. B.M. 2 appears to be a shallower-water deposit with an impoverished fauna | | | | | Definite cooling: semi-interglacial conditions | | |
| B.M. 1. 610 cm below top, to base (11¼ ft. o.d.). Shallow-water fauna with very few sub-tidal forms | L.M. 5. −55 ft. to −67 ft. Water depth perhaps less than 15 m, possibly only a few metres | L 3. Antian. Interglacial. −52 ft. to −62 ft. | L 3. Antian, 380 cm to 490 cm below top | | L V. −54½ ft. to −72½ ft. Definite enrichment of fauna. Open sea conditions | B I. 908 cm below top, to base (11¼ ft.) | |
| intertidal assemblages in these zones similar, though not clearly synchronous. L.M. 5 has more deepwater individuals than B.M. 1 | | temperate mixed coniferous forest with *Pterocarya* and *Tsuga*<br>Possible non-sequence at base (Royal Society Boring) | | | Full-interglacial climate. Correlation of L V and B I is suggested | | |
| Ludham: Royal Society Borehole | | L 2. Thurnian. Cold. −62 ft. to −85 ft. Cold oceanic climate with sub-arctic park landscape vegetation | | | Ludham: Pilot Borehole | | |
| L.M. 4. −67 ft. to −85 ft. Very few mollusca, probably as a result of silting (perhaps caused by coldness of climate reducing vegetation cover of land soils) | | | | | L IV. −72½ ft. to −82½ ft. Conditions cold, but perhaps not glacial: possible non-sequence at top | | |
| L.M. 3. −85 ft. to −96 ft. Water depth about 15 m or less. *Abra alba* assemblage *in situ*. Pre-Icenian element in the fauna greatly reduced, fewer ecological types present. May represent the beginning of true Icenian conditions | | L 1 *b*. Ludhamian. −85 ft. to −112 ft. Temperate oceanic climate, getting slightly colder above −97 ft. Forest remains prevalent. *Pterocarya* and *Tsuga* pollen | | | L. III. −82½ ft. to −91½ ft. The first ‘Icenian’ assemblages. Marked impoverishment in the fauna probably caused either by a very shallow estuarine or bay-head environment, or by closure of channel connecting North Sea Basin with Atlantic, southwestwards. Full-interglacial climate | | |
| | | | | | L II. −91½ ft. to −119½ ft. ‘Ludham Crag’. Continuing warm (though deteriorating) climate. Water perhaps less than 50 ft. deep. Pliocene-relict forms | | |
| L.M. 2. −96 ft. to −130 ft. Water shallower than in L.M. 1, possibly about 15 m deep finally. Greater percentage of Mollusca is recent; dominated by *Abra alba*, possibly not *in situ* except at very top. Intertidal forms begin to occur frequently in the deposits | | L 1 *a*. Ludhamian. −112 ft. to −132 ft. and at −137 ft. (no pollen below). Forest cover of coniferous trees with *Pterocarya* and *Tsuga*. Climate temperate | | | L I. −119½ ft. to −165½ ft. ‘Ludham Crag’. An abundant fauna similar to the Newbournian–Butleyan Red Crag but lacking evidence of marked cold. Warm climate. Shallow, sublittoral environment, water depth perhaps 50 ft. | | |
| L.M. 1. −131 ft. to −163 ft. In L.M. 1 *b* (above −155½ ft.) fauna is predominantly extinct. In L.M. 1 *a* (below −155½ ft.), fauna dominated by deepwater epifauna spp., with intertidal elements. Water depth throughout, perhaps 15–40 m | | | | | | | |

### (c) *Stratigraphical conclusions about the Icenian*

It is not possible to reconcile Harmer's stratigraphic subdivision of the East Anglian Icenian with the micropaleontological and malacological zonations now known. A new pre-Icenian 'Ludham Crag', which is not of the nature of the Red Crag, has been recognized on the basis of its content of Foraminifera and Mollusca, the position of the Chillesford Clay in the succession is obscured and the recently recognized boundaries in the sequence cannot be related to those between Harmer's horizons.

The Icenian (including the East Anglian and Netherlands series) remains ill-defined in a time-stratigraphic sense. The fauna is rather impoverished. Many characteristic extinct forms occur, such as *Rissoa curticostata*, *Nucella lapillus vulgaris*, *Tellina praetenuis*, *Macoma obliqua*, and *Yoldia oblongoides*. Species now absent from the North Sea occur, their present distribution being entirely to the northward or southward. The temperature conditions affecting the composition of the molluscan fauna may have differed from those of the modern North Sea, or many species in the faunas may have been represented by extinct ecotypes. Although the conditions in which the Icenian deposits accumulated may have continued in a modified form in the marine phases of the Cromer Forest Bed series, such conditions and their dependent molluscan fauna are singular and have not appeared again. It is therefore useful to retain the word 'Icenian' to denote this facies of deposition in the early Pleistocene North Sea basin, even though the Icenian deposition in East Anglia and the 'Icenian' deposition in the Netherlands appear not to have the same chronological extent (see Spaink & Norton 1967).

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Frequencies are as percentages, except where italicized to denote actual numbers. A dot indicates a nil result. An × indicates that fragments only were found.

| limits of assemblage zones suggested in the text | sampling depths in feet below ordnance datum | *Planorbis leucostoma* | *Littorina littorea* | *Calliostoma zizyphinum* | *Lepidochitona cinerea* | *Cardium edule* | *Mya arenaria* | *M.* cf. *arenaria* | *Hydrobia ulvae* | *Mytilus edulis* | *Retusa obtusa* | *Rissoa inconspicua* | *R.* cf. *inconspicua* | *Odostomia scalaris* | *O.* cf. *scalaris* | *Callista chione* | *Donax vittatus* | *Ensis ensis* | *E. siliqua* | *Tellina fabula* | *Mya truncata* | *Chrysallida indistincta* | *C. obtusa* | *C.* cf. *obtusa* | *C. spiralis* | *Montacuta ferruginosa* | *M.* cf. *ferruginosa* | *Turbonilla elegantissima* | *Buccinum undatum* | *Nassarius incrassatus* | *N.* cf. *incrassatus* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | freshwater | rocky shore | | | ‘*Macoma balthica* community’ | | | | | | | | | | clean sand at low tide | | | | | ? | parasites and commensals | | | | | | | predators | | |
| | | | tidal zone molluscs | | | | | | | | | | | | | | | | | | | intermediate-depth spp. (E.L.W.S. and below) | | | | | | | | | |
| L.M. 6 | 42 | . | . | . | . | . | . | . | . | × | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 45·5–48·5 | . | × | . | . | × | . | . | . | × | . | . | . | . | . | . | . | × | . | . | 2·3 | . | . | . | . | . | . | . | . | . | . |
| | 48·5–55 | . | × | . | . | × | . | . | 0·7 | 1·0 | . | . | . | . | . | . | . | . | 0·4 | . | . | . | . | . | . | . | . | . | . | . | . |
| L.M. 5 | 55–57 | 0·6 | 6·4 | . | . | 1·9 | . | . | 7·6 | 9·6 | . | . | . | . | . | . | 0·3 | . | 0·3 | . | . | . | . | . | . | . | . | . | . | . | . |
| | 57–61 | . | 3·3 | . | . | 3·1 | . | . | 1·3 | 4·3 | 0·3 | . | . | . | . | . | 0·2 | . | × | . | . | . | . | . | . | . | . | . | . | . | . |
| | 61–63 | × | 1·1 | . | . | 4·9 | . | 0·3 | 7·0 | 4·0 | . | . | . | . | . | . | × | . | . | 0·3 | . | . | . | . | . | 0·8 | . | . | . | . | . |
| L.M. 4 | 66 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 69 | . | . | . | . | . | . | . | . | *1* | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 73 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 76 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 80 | . | . | . | . | . | . | . | . | × | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 85 | . | . | . | . | . | . | . | . | × | . | . | . | . | . | . | . | . | . | . | 0·5 | . | . | . | . | . | . | . | . | . | . |
| L.M. 3 | 85·5–86·5 | . | 0·2 | . | . | × | 0·5 | . | . | 5·5 | 0·1 | . | . | . | 0·2 | . | . | . | . | . | . | 0·5 | . | . | 4·6 | . | . | 0·5 | . | . | . |
| | 88–91 | . | . | . | . | × | . | . | 1·2 | 2·2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 2·2 | . | . | 1·2 | . | . | . |
| | 91–94 | . | 1·6 | . | . | . | . | . | . | 2 | . | 0·3 | . | . | . | . | . | . | . | . | . | . | . | . | 2·4 | . | . | 0·8 | . | . | . |
| | 94–94·5 | . | . | . | . | 0·2 | . | . | 3·9 | 3·5 | . | 0·5 | . | . | . | . | . | . | . | . | . | . | . | . | 1·1 | 0·1 | . | . | . | . | . |
| L.M. 2 | 97–99 | . | . | . | . | 0·2 | . | . | . | 3·8 | . | . | . | . | . | . | . | . | . | . | 0·1 | . | . | 0·2 | 1·9 | . | . | . | 0·1 | . | . |
| | 101·5–106·75 | . | . | . | . | . | . | . | . | 6·2 | . | . | 0·3 | . | . | . | . | . | . | . | 0·1 | . | . | . | 4·8 | . | . | . | . | 0·3 | . |
| | 106·75–108·5 | . | . | . | . | 0·2 | . | . | . | 5·6 | . | . | . | 0·2 | . | . | 0·1 | . | . | . | . | . | . | . | 3·9 | . | . | . | . | . | 4·7 |
| | 108·5–110 | . | . | . | . | . | . | . | . | 2·7 | . | . | . | . | . | . | . | . | . | . | 0·6 | . | . | . | 1·8 | . | . | . | . | . | . |
| | 111·5–113·75 | . | . | . | . | . | . | . | . | 9·8 | . | . | . | . | . | . | . | . | . | . | 0·2 | . | . | . | 3·2 | . | . | 0·5 | . | . | . |
| | 115·75–116·75 | . | . | . | . | . | . | . | . | 1·0 | . | . | . | 0·4 | . | . | . | . | . | . | . | . | . | . | 4·9 | . | . | . | . | . | . |
| | 117·75–118·75 | . | . | . | . | . | . | 0·2 | . | 1·4 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 3·6 | . | 0·2 | 0·5 | . | . | . |
| | 120·75–121·75 | . | . | . | . | × | . | . | . | 1·6 | . | 0·2 | . | . | 0·2 | . | . | . | . | . | 0·1 | . | . | . | 2·2 | . | . | . | . | . | . |
| | 123·75–124·75 | . | . | . | 0·1 | . | . | . | . | 1·3 | . | . | . | . | . | . | . | . | . | . | 0·1 | . | . | . | 2·2 | . | . | 0·2 | . | . | . |
| | 126·75–128·75 | . | . | . | . | . | . | . | . | 1·7 | . | 0·5 | 1·3 | . | . | 0·1 | × | . | . | . | . | . | . | . | 0·2 | . | . | . | . | . | . |
| | 129·5 | . | . | . | . | . | . | . | . | 1·0 | . | . | . | 0·5 | . | . | . | . | . | . | . | . | . | . | 2·4 | . | . | . | . | . | . |
| L.M. 1*b* | 132·5–133·5 | . | . | . | . | . | . | . | . | 1·3 | . | . | . | 0·3 | . | . | . | . | . | . | . | 0·6 | 0·3 | . | 1·0 | . | . | . | . | . | . |
| | 135·75–136·75 | . | . | . | . | . | . | . | . | 0·2 | . | . | . | . | . | . | . | . | . | . | . | 0·4 | . | 0·4 | . | . | . | . | . | . | . |
| | 143–144 | . | . | . | . | 0·3 | . | . | . | 0·5 | . | . | . | . | . | . | . | . | . | . | . | 0·5 | . | . | . | . | . | . | . | . | . |
| | 146–147 | . | . | . | . | . | . | . | . | 0·9 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 148–149 | . | . | . | . | . | . | . | . | × | . | . | . | . | . | . | . | . | . | . | . | × | . | . | . | . | . | . | . | . | . |
| | 152–153 | . | . | . | . | . | . | . | . | 0·3 | . | . | . | 0·3 | . | . | . | . | . | . | . | × | . | . | . | . | . | . | . | . | . |
| L.M. 1*a* | 155·5 | . | . | 0·5 | . | . | . | . | . | 2·4 | . | . | . | . | . | . | . | . | × | . | . | 0·5 | . | . | . | . | . | . | . | . | . |
| | 157–158·5 | . | . | . | . | . | . | . | . | 1·5 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 161 | . | . | . | . | . | . | . | . | 3·4 | . | 0·4 | . | . | . | . | . | . | . | . | . | 0·4 | . | . | . | . | . | . | . | . | . |
| | 161·75 | . | . | . | . | . | . | . | . | 8·3 | . | . | . | . | . | . | . | . | . | . | 1·3 | . | . | . | . | . | . | . | . | . | . |
| | 162·5 | . | . | . | . | . | . | . | . | 3·6 | . | . | . | . | . | . | . | . | . | . | 0·3 | . | . | . | . | . | . | . | . | . | . |
| | 163 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |

| limits of assemblage zones suggested in the text | sampling depths in feet below ordnance datum | *Abra alba* | *A.* cf. *alba* | *Macoma calcarea* | *Spisula subtruncata* | *S.* cf. *subtruncata* | *Actaeon tornatilis* | *Cyprina islandica* | *Diplodonta astartea* | *Lucinoma borealis* | *Serripes groenlandicus* | *Cingula proxima* | *Astarte montagui* | *A.* cf. *montagui* | *Caecum glabrum* | *Corbula gibba* | *C.* cf. *gibba* | *Nucula nucleus* | *Venerupis* decussatus or pullastra | *Arcopagia crassa* | *Cardium scabrum* | *C.* cf. *scabrum* | *Gouldia minima* | *Lepton nitidum* | *L.* cf. *nitidum* | *Spisula elliptica* | *Venus fasciata* | *V. ovata* | *V.* cf. *ovata* | *Mysella bidentata* | *M.* cf. *bidentata* | *Odostomia conoidea* | *O.* cf. *conoidea* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| L.M. 6 | 42 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 45·5–48·5 | . | 1·1 | 12·4 | 2·3 | . | . | × | . | . | 2·3 | . | 7·9 | 2·3 | . | . | . | . | . | . | × | . | . | . | . | . | . | 1·1 | . | . | . | . | . |
| | 48·5–55 | 0·4 | . | . | 5·9 | . | . | . | . | . | . | . | . | 3·1 | . | 2·1 | . | . | . | . | . | 2·1 | . | . | . | . | . | 7·7 | . | . | . | . | . |
| L.M. 5 | 55–57 | 0·3 | . | . | 5·1 | 14·3 | . | × | . | 0·3 | . | 0·6 | 1·6 | 3·2 | . | . | . | . | . | . | 0·6 | . | . | 13·7 | . | . | . | 1·0 | . | . | . | . | . |
| | 57–61 | 5·5 | . | . | 8·6 | . | . | . | . | . | . | . | . | . | . | 0·2 | . | . | . | . | × | . | . | 5·9 | . | . | . | 2·2 | . | . | . | . | . |
| | 61–63 | 4·6 | . | . | 7·0 | . | . | × | . | 0·5 | 0·3 | . | . | . | . | . | . | . | . | . | 0·8 | . | . | 2·0 | . | . | . | 1·9 | . | . | . | . | . |
| L.M. 4 | 66 | *0·5* | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 69 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 73 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 76 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 80 | *1·5* | . | . | . | . | . | . | . | . | . | . | . | . | *1* | . | . | . | . | . | . | . | . | . | . | . | . | × | . | . | . | . | . |
| | 85 | *1* | . | . | . | . | . | . | . | . | . | . | . | . | *2* | . | . | . | . | . | × | . | . | . | . | . | . | . | . | . | . | . | . |
| L.M. 3 | 85·5–86·5 | 32·8 | . | 0·1 | . | . | × | . | . | 0·1 | 0·2 | . | . | . | . | . | . | . | . | . | 0·4 | . | . | 0·2 | . | . | . | 0·2 | . | . | 0·1 | . | 0·1 |
| | 88–91 | 51·4 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | × | . | . | . | . | . | . | × | . | . | . | . | . |
| | 91–94 | 49·8 | . | . | . | . | . | . | . | . | 0·4 | . | . | . | × | . | . | . | . | 0·4 | . | . | . | . | . | 0·4 | . | . | . | . | . | . | . |
| | 94–94·5 | 33·8 | . | 0·3 | 0·1 | . | . | . | . | . | 0·6 | . | 0·3 | . | 2·5 | 0·1 | . | . | . | . | 0·1 | . | . | . | . | 0·6 | . | 1·5 | . | . | . | . | . |
| L.M. 2 | 97–99 | 13·7 | . | . | . | . | . | . | 0·2 | . | 0·1 | . | 0·4 | 0·2 | 5·0 | 0·1 | . | . | . | 0·2 | 0·4 | . | . | . | . | 4·0 | . | 1·9 | . | 0·1 | . | . | . |
| | 101·5–106·75 | 21·8 | . | . | . | . | . | . | . | . | 0·4 | . | . | . | 3 | 0·1 | . | . | 0·1 | . | . | . | . | . | . | 0·4 | . | 0·5 | 0·5 | 0·1 | . | . | . |
| | 106·75–108·5 | 18·7 | . | . | . | . | . | . | . | . | 0·3 | . | . | . | 2·6 | . | 0·3 | . | . | 0·1 | 0·7 | . | . | . | . | 2·5 | . | 0·4 | 1·1 | . | . | . | 0·2 |
| | 108·5–110 | 12·4 | . | 0·3 | 1·2 | . | . | . | . | . | 2·7 | . | . | 0·9 | 0·6 | . | . | . | . | . | 0·3 | . | . | . | . | 0·6 | . | . | 0·3 | . | . | 1·2 | . |
| | 111·5–113·75 | 10·0 | . | . | . | . | . | . | . | . | 0·2 | . | . | . | 2·7 | 0·2 | . | . | . | . | 0·2 | . | . | . | . | 0·2 | . | . | . | . | . | . | . |
| | 115·75–116·75 | 8·2 | . | . | . | . | . | . | . | . | 0·2 | . | 0·2 | . | 2·4 | 0·2 | . | . | . | . | 0·8 | . | . | . | . | . | . | 0·2 | 0·8 | . | 0·8 | . | . |
| | 117·75–118·75 | 20·2 | . | . | . | . | . | . | . | . | 0·9 | . | . | . | 3·8 | . | . | . | . | . | 0·7 | . | . | . | . | . | . | 1·2 | . | . | . | . | . |
| | 120·75–121·75 | 16·2 | . | . | . | . | . | . | . | . | 0·2 | . | 0·1 | . | 5·6 | . | . | . | . | 0·1 | 0·7 | . | . | . | . | 0·5 | . | 0·4 | 0·5 | 0·1 | . | . | . |
| | 123·75–124·75 | 11·9 | . | . | . | . | . | . | . | . | 0·7 | . | 0·2 | . | 9·4 | . | . | . | . | . | 1·0 | . | . | . | . | 0·5 | 0·1 | . | 3·4 | . | . | . | . |
| | 126·75–128·75 | 11·0 | . | . | . | . | . | . | . | . | 1·6 | . | . | . | 26·1 | . | . | . | . | . | 0·4 | . | . | . | . | 1·5 | . | . | 0·3 | . | 0·1 | . | . |
| | 129·5 | 15·3 | . | . | . | . | . | . | . | . | 0·2 | . | . | . | 2·4 | . | . | . | . | . | 1·9 | . | . | . | . | . | . | . | 3·4 | . | . | . | . |
| L.M. 1*b* | 132·5–133·5 | 10·5 | . | 0·2 | . | . | . | . | . | . | 1·3 | . | . | . | 7·1 | . | . | . | . | . | . | . | . | . | . | 1·1 | . | . | 0·6 | . | . | . | . |
| | 135·75–136·75 | 12·2 | . | . | . | . | 0·5 | . | . | . | 0·5 | . | . | . | 1·4 | 0·2 | . | . | . | . | . | . | . | . | . | 0·2 | . | . | 0·7 | . | . | 0·7 | . |
| | 143–144 | 15·5 | . | . | . | . | . | . | . | . | × | . | 0·5 | . | 2·2 | . | . | . | . | . | 0·5 | . | . | . | . | . | . | . | 0·8 | . | . | 1·1 | . |
| | 146–147 | 10·9 | . | . | . | . | . | . | . | . | . | . | . | . | 1·7 | . | . | . | . | . | . | . | . | . | . | 0·9 | . | . | 2·2 | . | . | . | . |
| | 148–149 | 4·8 | . | . | . | . | . | . | . | . | . | . | . | . | × | . | . | . | . | . | . | . | . | . | . | . | . | . | 3·3 | . | . | . | . |
| | 152–153 | 6·3 | . | . | . | . | . | . | . | . | 0·6 | . | . | . | 2·3 | . | . | . | . | 0·3 | . | . | . | . | . | . | 0·3 | . | 2·6 | . | . | . | . |
| L.M. 1*a* | 155·5 | 3·6 | . | . | . | . | . | . | . | . | 3·4 | . | . | . | 10·6 | 0·7 | . | . | . | . | 0·2 | . | . | . | 0·2 | . | . | 0·5 | 7·7 | . | . | . | . |
| | 157–158·5 | 1·5 | . | 1·5 | . | . | . | . | . | . | 4·1 | . | . | 0·5 | . | 2·6 | . | . | . | . | . | . | 1·0 | . | . | 1·0 | . | 0·5 | 3·1 | . | . | 1·0 | . |
| | 161 | 1·1 | . | . | 0·4 | . | . | . | . | . | 1·1 | . | . | 0·2 | . | 1·1 | 0·2 | . | . | . | . | . | . | . | . | 0·4 | 0·2 | 0·4 | 0·9 | . | . | 0·4 | . |
| | 161·75 | 4·4 | . | 0·4 | . | . | . | . | . | . | 3·0 | . | . | 0·8 | . | 3·0 | . | . | . | . | . | . | . | . | . | 0·4 | . | 2·2 | . | . | . | 3·5 | . |
| | 162·5 | 2·1 | . | 1·5 | . | . | . | . | . | . | 2·7 | . | . | . | × | 0·6 | . | . | . | . | . | . | . | . | . | . | . | 0·6 | 1·8 | . | . | 1·5 | . |
| | 163 | *1* | . | . | . | . | . | . | . | . | *0·5* | . | . | . | . | . | . | *0·5* | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | | fine grade substratum | | | | | | | | | | mixed substratum (mud + coarse matter) | | | | | | | | coarse grade substratum | | | | | | | | | | wide tolerance | | commensals | | | |
| | | normally sublittoral molluscs | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |

| limits of assemblage zones suggested in the text | sampling depths in feet below ordnance datum | normally sublittoral molluscs | | | | | | | | | little information | | | | | | | incompletely determinable forms (worn or poorly preserved, etc.) | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | epifauna molluscs | | | | | | | scallop | predator | | | | | | | | | | | | | | | | | | | | |
| | | *Acmaea rubella* | *Hiatella arctica* | *Anomia squamula* | *A.* cf. *squamula* | *Chlamys tigerinus* | *Modiolus modiolus* | *Calyptraea chinensis* | *Chlamys opercularis* | *Neptunea antiqua* | *Abra ovata* | *Astarte digitaria* | *A.* cf. *digitaria* | *Limopsis aurita* | *L.* cf. *aurita* | *Trophon clathratus* var. *gunneri* | *Turritella triplicata* f. *triplicata* | *Actaeon* sp. | *Anomia* sp. | *Astarte* sp. | *Calliostoma* sp. | *Cardita* sp. | *Cardium* sp. | '*Chiton*' sp. | *Cingula* sp. | *Clathurella* sp. | *Diplodonta* sp. | ? *Dosinia* sp. | *Ensis* sp. | *Eulima* sp. | *Gastropod* sp. |
| L.M. 6 | 42 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 45·5–48·5 | . | 1·1 | . | . | . | . | . | × | . | . | . | . | . | . | . | . | . | . | 4·5 | . | . | 1·1 | . | . | . | 1·1 | . | . | . | 2·3 |
| | 48·5–55 | . | . | 7·0 | . | × | × | 29·2 | × | 0·7 | . | . | . | . | . | . | . | . | . | 0·7 | . | . | 0·4 | 0·4 | . | . | 1·0 | . | . | . | 2·8 |
| L.M. 5 | 55–57 | . | 1·3 | × | . | . | × | 0·6 | × | 0·6 | 0·3 | . | . | . | . | . | . | . | . | 1·9 | . | . | × | . | . | . | 0·3 | . | . | . | . |
| | 57–61 | . | . | 2·0 | . | . | . | 6·0 | × | . | 0·3 | . | . | . | . | 0·3 | . | . | . | 1·5 | . | . | 4·3 | 0·2 | . | . | . | . | . | . | 3·3 |
| | 61–63 | . | 2·4 | 3·2 | . | × | × | 1·6 | × | . | 1·1 | . | . | . | . | . | . | . | . | 1·9 | . | . | 2·7 | × | . | 0·5 | . | . | 0·3 | . | 1·6 |
| L.M. 4 | 66 | . | *1* | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 69 | . | *1* | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 73 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 76 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 80 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | × |
| | 85 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| L.M. 3 | 85·5–86·5 | . | 1·1 | 3·8 | . | . | . | 10·8 | 1·4 | 0·5 | . | . | . | . | . | . | 0·4 | . | . | 0·1 | . | . | 0·1 | . | . | . | . | . | . | . | 3·1 |
| | 88–91 | . | . | 1·2 | . | . | . | 7·7 | 1·7 | . | . | . | . | . | . | . | . | . | . | 2·2 | . | . | . | . | . | . | . | . | . | . | 4·4 |
| | 91–94 | . | 0·4 | . | . | . | . | 10·5 | 0·8 | . | . | . | . | . | . | . | 1·6 | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 94–94·5 | . | 0·9 | 7·8 | . | . | . | 12·6 | 0·7 | 0·9 | . | . | . | . | . | . | 3·7 | . | . | 2·1 | . | . | . | . | . | . | 0·3 | . | . | . | . |
| L.M. 2 | 97–99 | . | 1·2 | 8·1 | . | 0·2 | . | 13·5 | 1·9 | . | . | . | . | . | . | . | 4·4 | . | . | 0·7 | . | . | 0·2 | × | 1·0 | . | 0·1 | . | . | . | 4·7 |
| | 101·5–106·75 | . | 2·1 | . | . | . | . | 17·0 | 2·4 | × | . | . | . | . | . | . | 4·0 | . | 6·8 | 0·5 | . | . | 0·1 | . | . | . | . | . | . | . | . |
| | 106·75–108·5 | . | 2·4 | 0·7 | . | . | . | 7·6 | 2·4 | . | . | . | . | 0·1 | . | . | 3·9 | . | 6·7 | 1·3 | . | . | 0·1 | . | 0·2 | . | . | 0·1 | . | 0·2 | 0·7 |
| | 108·5–110 | . | 1·5 | 3 | . | . | . | 15·8 | 3·0 | × | . | . | . | . | . | . | 1·2 | . | 0·6 | . | . | . | . | . | . | . | . | . | . | . | . |
| | 111·5–113·75 | . | 2·3 | 1·3 | . | . | 0·2 | 13·6 | 4·6 | × | . | . | . | . | . | . | 6·4 | . | 0·5 | 0·2 | . | . | . | . | . | . | . | . | . | . | . |
| | 115·75–116·75 | . | 2·4 | 2·4 | . | . | . | 15·5 | 0·2 | . | . | . | . | . | . | . | 9·8 | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 117·75–118·75 | . | 2·1 | 0·5 | 1·4 | . | . | 23 | . | . | . | . | . | . | . | . | 1·4 | . | . | 1·2 | . | . | . | . | . | . | . | . | . | . | . |
| | 120·75–121·75 | . | 3·7 | 10·5 | . | . | . | 16·9 | 0·1 | . | . | . | . | . | . | . | 3·2 | . | . | 1·1 | . | . | . | . | . | . | . | . | . | . | 0·5 |
| | 123·75–124·75 | . | 2·9 | 7 | . | . | . | 10·6 | 0·1 | . | . | . | 0·1 | 0·1 | . | . | 1·2 | . | . | 2·2 | . | . | . | . | . | . | 0·2 | . | . | 0·5 | 3·0 |
| | 126·75–128·75 | . | 3·5 | 3·6 | . | 0·1 | . | 6·9 | . | . | . | . | 0·1 | . | . | . | 2·5 | . | . | 0·4 | . | . | × | × | 0·7 | . | . | . | . | . | 2·9 |
| | 129·5 | . | 4·1 | 12·5 | . | . | . | 6·2 | × | . | . | . | . | . | . | . | 1·9 | . | . | 3·1 | . | . | . | . | 2·9 | . | . | . | . | . | . |
| L.M. 1*b* | 132·5–133·5 | . | 1·9 | 9·6 | . | . | . | 6·4 | . | × | . | . | . | . | 0·2 | . | 1·0 | 0·6 | . | 0·6 | . | . | . | . | . | . | . | . | . | 0·3 | 0·6 |
| | 135.75–136·75 | . | 1·9 | 6·6 | . | . | . | 7·7 | . | × | . | . | . | . | . | . | . | . | . | 0·4 | . | . | . | . | . | . | . | . | . | . | 0·7 |
| | 143–144 | . | 3·5 | 7·6 | . | . | . | 13·0 | . | × | . | . | . | . | . | . | 0·5 | 0·5 | . | 1·4 | . | . | 0·3 | . | . | . | . | . | . | . | 1·4 |
| | 146–147 | . | 0·4 | 4·4 | . | . | . | 15·7 | . | 0·9 | . | . | . | . | . | . | 0·9 | . | . | 2·2 | . | . | . | . | . | . | . | . | . | . | . |
| | 148–149 | . | 0·3 | 22·2 | . | . | . | 18·3 | . | × | . | . | . | . | . | . | 0·6 | . | . | 1·8 | . | . | . | . | . | . | . | . | . | . | 3·0 |
| | 152–153 | . | 0·6 | 7·4 | . | . | . | 12·0 | × | × | . | . | . | . | . | . | 6·8 | . | . | 0·9 | 0·6 | . | . | . | . | . | . | . | . | . | 3·4 |
| L.M. 1*a* | 155·5 | . | 9·2 | 3·9 | . | . | . | 4·8 | . | × | . | . | . | . | . | . | 1·5 | . | . | 8·7 | 0·5 | . | . | × | 1 | . | . | . | . | . | 7·7 |
| | 157–158·5 | . | 9·8 | 8·2 | . | . | . | 6·2 | . | . | . | 0·5 | . | . | . | . | 1·0 | . | . | 9·2 | 0·5 | 0·5 | . | . | . | . | . | . | . | . | 8·2 |
| | 161 | 0·4 | 17·4 | 24·7 | . | . | . | 3·0 | 0·4 | . | . | . | . | 0·2 | . | . | 0·4 | . | . | 1·3 | 0·4 | 0·9 | . | × | . | . | . | . | . | . | 3·8 |
| | 161·75 | . | 2·0 | 14·8 | . | . | . | 2·2 | × | 1·2 | . | . | . | . | . | . | . | . | . | 7 | . | . | . | . | . | . | . | . | . | . | 0·9 |
| | 162·5 | . | 13·0 | 37·4 | . | . | . | 1·2 | . | . | . | . | . | . | . | . | × | . | . | 0·3 | . | . | . | . | . | . | . | . | . | . | . |
| | 163 | . | *1* | × | . | . | . | . | × | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |

TABLE 2 (*cont.*)

| limits of assemblage zones suggested in the text | sampling depths in feet below ordnance datum | incompletely determinable forms (worn or poorly preserved, etc.) | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *Gibbula* sp. | *Glycymeris* sp. | *Kellya* sp. | ? *Kellya* sp. | *Lamellibranch* sp. | *Lepton* sp. | *Limopsis* sp. | *Macoma* sp. | *Modiolus* sp. | *Montacuta* sp. | *Mya* sp. | *Mytilus* sp. | *Nassarius* sp. | cf. *Nassarius* sp. | *Natica* sp. | ? *Nucella* sp. | *Nuculoma* sp. | *Nucula* sp. | *Odostomia* sp. | *Pyramidellid* sp. | *Rissoa* sp. | *Rissoid* sp. | *Spisula* sp. | *Tellinid* sp. | *Trochid* sp. | *Turbonilla* sp. | *Turritella* sp. | *Venerid* sp. | *Venerupis* sp. | *Venus* sp. | *Yoldia* sp. |
| L.M. 6 | 42 | . | . | . | . | × | . | . | . | . | . | . | . | . | . | . | . | × | . | . | . | . | . | . | *0·5* | . | . | . | . | . | . | . |
| | 45·5–48·5 | . | . | . | . | . | . | . | . | . | . | 2·3 | . | . | . | 2·3 | . | . | . | . | . | . | . | 2·2 | 12·4 | . | . | . | . | . | . | 6·7 |
| | 48·5–55 | 9·1 | . | 0·4 | . | 3·8 | . | . | 1·7 | . | . | . | . | . | . | 7·0 | . | . | . | . | . | . | . | 4·2 | . | × | . | . | . | . | . | . |
| L.M. 5 | 55–57 | 1·9 | . | . | . | . | . | . | . | × | . | 0·6 | . | . | . | 1·3 | . | . | . | × | . | . | . | 1·3 | 2·2 | . | . | × | . | 1·3 | . | 1·0 |
| | 57–61 | 2·0 | . | . | . | 6·6 | . | . | . | . | . | 0·2 | . | . | . | 0·7 | . | . | × | . | . | . | . | 11·6 | 6·9 | . | . | . | . | 0·3 | 0·5 | 1·0 |
| | 61–63 | . | . | . | . | 7·3 | . | 0·3 | . | . | . | 0·3 | . | . | . | . | . | . | . | . | . | . | . | 6·2 | 8·6 | . | . | × | . | 0·5 | . | 0·5 |
| L.M. 4 | 66 | . | . | . | . | *0·5* | . | . | . | *1·5* | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 69 | . | . | . | . | *1* | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 73 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 76 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 80 | . | . | . | . | *0·5* | . | . | . | *0·5* | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 85 | . | . | . | . | . | . | . | . | × | . | . | *1* | . | . | . | . | . | . | . | . | *1* | . | . | . | . | . | . | . | . | . | × |
| L.M. 3 | 85·5–86·5 | 4·6 | . | . | . | 0·9 | . | . | . | 0·1 | . | 0·1 | . | . | . | 0·1 | . | . | . | . | . | 0·2 | . | 0·2 | 0·2 | . | 0·1 | 0·1 | . | . | . | 1·3 |
| | 88–91 | 2·2 | . | . | . | . | . | . | . | . | . | . | . | 1·2 | . | . | . | . | . | × | . | . | . | 1·7 | . | . | . | . | . | . | . | . |
| | 91–94 | 1·6 | . | . | . | 2·4 | . | . | . | . | . | . | . | . | . | 0·8 | . | . | . | . | 2·4 | . | . | 4·1 | . | . | . | . | . | 0·4 | . | . |
| | 94–94·5 | 1·6 | . | . | . | . | . | . | . | . | . | 0·1 | . | . | . | 1·4 | . | . | . | 0·5 | . | 0·2 | . | 8·7 | . | . | . | 0·2 | . | 0·5 | . | 0·5 |
| L.M. 2 | 97–99 | 2·7 | . | . | 0·1 | 0·3 | . | . | . | . | . | . | . | . | . | . | . | . | . | 0·3 | 2·9 | 3·6 | . | 12·7 | 0·1 | . | 0·3 | . | . | 0·4 | 0·1 | . |
| | 101·5–106·75 | 4·3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 0·8 | 0·8 | 4·8 | . | 7·8 | 0·6 | . | . | . | . | . | . | 1·3 |
| | 106·75–108·5 | 7·1 | . | . | . | 0·8 | . | . | . | . | . | . | . | 0·4 | . | 0·4 | . | . | . | 1·3 | . | 8·6 | . | 8·5 | . | . | . | . | . | 0·4 | 0·2 | . |
| | 108·5–110 | 5·5 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 1·2 | 8·5 | . | 5·5 | 0·3 | . | . | . | . | . | . | . |
| | 111·5–113·75 | 3·6 | . | . | . | . | . | . | . | . | . | . | . | 0·5 | . | 0·5 | 1·4 | . | . | . | 1·1 | . | 14·5 | 1·1 | . | . | . | . | . | . | 0·2 | . |
| | 115·75–116·75 | 4·5 | . | . | . | 0·6 | . | . | . | 0·6 | 0·6 | 0·2 | 0·2 | 2·0 | . | 0·8 | . | . | . | 1·2 | 2·9 | 12·2 | . | 2·7 | . | . | . | . | . | . | 0·4 | . |
| | 117·75–118·75 | 3·3 | . | . | . | . | . | . | . | . | . | . | . | 1·9 | . | . | . | . | . | 0·9 | 1·4 | 6·6 | . | 4·5 | . | . | . | . | . | . | 0·5 | . |
| | 120·75–121·75 | 2·0 | . | . | . | . | . | . | . | . | 0·1 | . | . | 2·7 | . | 1·0 | . | . | . | 1·7 | 1·5 | . | . | 5·1 | . | . | 0·2 | . | . | . | 0·4 | . |
| | 123·75–124·75 | 1·2 | . | . | . | 1·9 | . | 0·1 | . | 1·0 | . | 0·1 | . | 0·2 | . | . | . | . | . | 0·7 | 1·4 | 7·5 | . | 7·7 | . | . | . | . | 0·2 | 0·1 | . | . |
| | 126·75–128·75 | 1·4 | 0·2 | . | . | 1·1 | 0·1 | 0·1 | . | 1·4 | 0·2 | . | 0·1 | 0·4 | . | 0·4 | . | . | . | 1·6 | 3·3 | 5·8 | . | 7·2 | . | . | . | . | 0·2 | . | 3·3 | . |
| | 129·5 | 1·9 | . | . | . | 3·1 | . | 0·2 | . | 1·2 | . | 0·2 | 0·5 | . | . | . | . | . | . | 2·9 | 3·8 | 13·4 | . | 3·8 | . | . | 0·5 | . | . | . | . | . |
| L.M. 1 *b* | 132·5–133·5 | 1·9 | . | . | . | 0·2 | 0·3 | . | . | 0·2 | . | . | . | . | . | 3·4 | . | . | . | . | . | 10·6 | . | 3·4 | 0·5 | . | 1·0 | . | . | . | . | . |
| | 135·75–136·75 | 3·8 | . | . | . | 0·7 | . | . | . | . | 0·2 | . | . | . | . | 5·2 | . | . | . | 0·4 | . | 19·5 | . | 2·4 | . | . | 1·4 | . | . | 0·2 | . | . |
| | 143–144 | 2·2 | . | . | . | 0·5 | . | . | . | × | . | 0·3 | . | . | . | 0·5 | . | . | . | . | 1·1 | . | . | 3·5 | 0·3 | . | 0·5 | . | . | . | . | . |
| | 146–147 | 8·7 | . | . | . | 0·9 | . | . | . | 1·3 | . | . | . | . | . | 1·7 | . | . | . | . | 0·9 | . | . | 1·7 | 0·9 | . | . | . | . | . | . | 0·9 |
| | 148–149 | 3·6 | . | . | . | 0·6 | . | . | . | × | . | . | . | . | . | × | . | . | . | . | . | 1·2 | . | 1·8 | . | . | 0·5 | . | . | . | . | . |
| | 152–153 | 4·6 | . | . | . | 0·6 | . | . | . | 0·9 | 0·3 | . | . | . | . | 0·6 | . | . | . | × | . | . | . | 1·1 | . | . | . | . | . | 0·3 | . | 0·3 |
| L.M. 1 *a* | 155·5 | 3·4 | . | . | . | 4·6 | . | . | . | . | 0·5 | . | 7·7 | . | . | 1·0 | . | . | . | 0·5 | 1·5 | 1·5 | . | 4·6 | . | . | . | . | . | 0·5 | 0·5 | . |
| | 157–158·5 | 2·1 | . | . | . | 6·7 | . | . | . | . | . | . | 0·5 | . | 1·0 | 3·1 | 1·0 | . | . | 1·0 | . | . | . | 6·2 | 0·5 | . | 0·5 | . | . | . | . | 0·5 |
| | 161 | 1·3 | . | . | . | 2·8 | . | . | . | 0·2 | . | 0·2 | 0·2 | . | . | 0·9 | . | . | . | 0·9 | 1·7 | 4·3 | . | 5·5 | 0·4 | . | . | . | . | . | 0·9 | 0·2 |
| | 161·75 | 1·3 | . | . | . | 0·4 | . | . | . | . | . | . | . | . | . | . | 0·9 | . | . | . | . | 0·9 | . | 4·4 | 0·4 | . | . | . | . | 0·4 | 0·4 | 0·4 |
| | 162·5 | 1·2 | . | . | . | . | . | . | . | . | . | . | . | . | . | 0·6 | . | . | . | . | . | . | . | 3·9 | 0·3 | . | . | . | . | 0·3 | . | . |
| | 163 | . | . | . | . | . | . | . | . | × | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |

TABLE 2 (*cont.*)

| limits of assemblage zones suggested in the text | sampling depths in feet below ordnance datum | extinct species | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *Acmaea parvula* | *Astarte basterotii* | *A.* cf. *basterotii* | *A. incerta* | *A.* cf. *incerta* | *A. obliquata* | *A. parvula* | *Caecum mammilatum* | *Calliostoma nodulifferens* | *Cardita chamaeformis* | *C. orbicularis* | *C. scalaris* | *Cingula semicostata semicostata* | *Clathrus clathratulus minutis* | *Diplodonta astartea* | *Divaricella juttingae* | *Gibbula nehalenniae* | *G.* cf. *nehalenniae* | *G.* cf. *pennanti* | *G.* cf. *spastica* | *Glycymeris glycymeris variabilis* | *Laevicardium decorticatum* | *Limopsis anomala* | *Macoma obliqua* | *Mangelia ambigua* | *Nassarius consociatus* | *N.* cf. *consociatus* | *N. elegans* | *Nucella lapillus vulgaris* | *Nucula cobboldiae* |
| L.M. 6 | 42 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | × |
| | 45·5–48·5 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 1·1 | . | . | . | . | . | . | . | . | 3·4 | . | . | . | . | 9·0 | × |
| | 48·5–55 | . | . | . | 2·4 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | × | . | 0·7 | × |
| L.M. 5 | 55–57 | . | . | . | . | 0·3 | . | . | . | . | . | . | . | . | 2·6 | . | . | . | . | . | . | . | . | . | 13·1 | . | . | . | . | × | × |
| | 57–61 | . | . | . | . | . | . | . | . | 0·3 | . | . | . | . | 4 | . | 0·2 | . | . | . | . | . | . | . | 0·7 | . | 0·3 | . | . | 1·7 | . |
| | 61–63 | 0·5 | . | . | . | . | . | . | . | . | . | . | . | . | 1·1 | 4 | . | . | . | . | . | . | . | . | 0·3 | . | . | . | . | × | × |
| L.M. 4 | 66 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | *1* | . | . | . | . | . | . | . | . | . | . | . |
| | 69 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | *1* | . | . | . | . | . | . | . | . | . | . | . |
| | 73 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 76 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 80 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 85 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| L.M. 3 | 85·5–86·5 | . | . | . | . | . | . | . | . | . | . | . | . | 2·3 | . | . | . | 0·6 | 0·2 | . | . | . | 0·1 | . | . | 0·1 | . | . | . | 0·2 | . |
| | 88–91 | . | . | . | . | . | . | . | . | . | . | . | . | 2·2 | . | . | . | . | . | . | . | . | . | . | 0·6 | . | . | . | . | 1·2 | . |
| | 91–94 | . | . | . | . | . | . | . | . | . | . | . | . | 3·2 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | 1·6 | . |
| | 94–94·5 | . | 0·1 | . | . | . | . | . | . | . | . | . | . | 0·5 | . | 1·3 | . | . | 0·2 | . | . | . | . | . | . | . | . | . | . | 0·5 | . |
| L.M. 2 | 97–99 | . | . | . | . | . | . | . | . | . | . | . | . | 0·3 | . | 2·6 | . | 0·3 | . | . | . | . | . | . | 0·1 | . | . | . | . | 0·6 | . |
| | 101·5–106·75 | . | . | . | . | . | . | . | . | . | . | . | . | × | . | 1·9 | . | . | 0·3 | . | . | . | . | . | . | . | . | . | . | 0·3 | . |
| | 106·75–108·5 | . | . | . | . | . | . | . | . | . | . | . | . | 0·2 | . | 1·4 | . | . | 0·2 | . | . | . | . | . | . | . | . | . | 0·4 | . | . |
| | 108·5–110 | . | . | . | . | . | . | . | . | . | . | . | . | 2·4 | . | 1·2 | . | . | 1·8 | . | . | . | . | . | . | . | 0·6 | . | . | 0·6 | . |
| | 111·5–113·75 | . | . | . | . | . | . | . | . | . | . | . | . | 1·8 | . | 0·9 | . | . | 0·5 | 0·5 | . | . | . | . | . | . | . | 2·7 | . | 1·8 | . |
| | 115·75–116·75 | . | . | . | . | . | . | . | . | . | . | . | . | 1·6 | × | 1·0 | . | . | 1·2 | . | . | . | . | . | . | . | 0·4 | . | . | . | . |
| | 117·75–118·75 | . | . | . | . | . | . | . | . | . | . | . | . | 2·3 | . | 0·2 | . | . | 0·5 | . | . | . | . | . | . | . | . | . | . | . | . |
| | 120·75–121·75 | . | . | . | . | . | . | . | . | . | . | . | . | 0·7 | . | 1·2 | . | . | . | . | 0·2 | . | . | . | . | . | . | . | . | 0·7 | . |
| | 123·75–124·75 | . | . | . | . | . | . | . | . | . | 0·1 | . | . | 1·2 | . | 3·0 | . | . | . | . | 0·2 | . | . | . | . | . | . | . | . | 0·5 | . |
| | 126·75–128·75 | . | . | . | . | . | . | . | 0·5 | . | . | . | . | 0·2 | . | 1·4 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 129·5 | . | . | . | . | . | . | . | 1·4 | . | . | . | . | . | . | 1·7 | . | . | . | . | . | . | . | . | . | . | . | . | . | 0·5 | . |
| L.M. 1*b* | 132·5–133·5 | . | . | . | . | . | . | . | 0·3 | 0·3 | . | . | . | 2·9 | . | . | . | . | 0·3 | . | . | . | . | . | . | . | . | . | . | 5·2 | . |
| | 135·75–136·75 | . | . | . | . | . | . | . | . | . | . | . | . | 2·8 | . | 0·4 | . | 0·7 | . | . | . | . | . | . | . | . | . | . | . | 5·2 | . |
| | 143–144 | . | . | . | . | . | . | . | . | . | . | . | . | 6·5 | . | 0·3 | . | . | . | . | . | . | . | . | . | . | . | . | . | 2·2 | . |
| | 146–147 | . | . | . | . | . | . | . | . | . | . | . | . | 12·2 | . | 0·4 | . | . | . | . | . | . | . | . | . | . | . | . | . | 5·2 | . |
| | 148–149 | . | . | . | . | . | . | . | . | . | . | . | . | 13·8 | . | 0·9 | . | 0·6 | 0·6 | . | . | . | . | . | . | . | . | . | . | 4·8 | . |
| | 152–153 | . | 0·3 | . | . | . | . | . | . | . | . | . | . | 1·7 | . | 0·3 | . | . | 1·7 | . | . | . | . | . | . | . | . | . | . | 5·7 | . |
| L.M. 1*a* | 155·5 | . | . | 0·2 | . | . | 1·0 | . | 1·9 | . | . | 0·2 | . | . | . | 0·5 | . | . | . | . | . | 0·2 | . | 0·2 | . | . | . | . | . | 0·5 | . |
| | 157–158·5 | . | . | 0·5 | . | . | 0·5 | . | . | . | . | . | . | 1·0 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 161 | . | . | . | . | 0·2 | 0·2 | 0·6 | 0·4 | . | . | 0·2 | 0·9 | 0·9 | . | 0·2 | . | . | . | . | . | 0·6 | . | . | . | . | . | . | . | . | . |
| | 161·75 | . | 0·4 | . | 1·3 | . | . | 2·6 | . | . | . | . | 0·4 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| | 162·5 | . | . | . | 0·3 | . | 0·3 | 0·6 | . | . | . | . | . | 1·2 | . | . | . | . | . | . | . | 0·3 | . | . | . | . | . | . | . | 0·6 | . |
| | 163 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |

TABLE 2 (*cont.*)

| limits of assemblage zones suggested in the text | sampling depths in feet below ordnance datum | extinct species | | | | | | | | | | | | | | | % contribution from one individual | number of species in the samples | number of individuals in the samples |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *Potamides tricinctus icenicus* | *Rissoa curticostata* | *R.* cf. *curticostata* | *R.* cf. *obsoleta* | *Solariella maculata* | *Spisula triangulata* | *S.* cf. *triangulata* | *Tellina praetenuis* | *T.* cf. *praetenuis* | *Tornus pulchralis* | *Turbonilla internodula* | *Yoldia lanceolata* | *Y. oblongoides* | *Y.* cf. *oblongoides* | *Y. semistriata* | | | |
| L.M. 6 | 42 | . | . | . | . | . | . | . | *0·5* | . | . | . | . | . | . | . | no %'s found | 6 | 5 and 8 frgts |
| | 45·5–48·5 | . | . | . | . | 2·3 | 1·1 | . | 6·7 | . | . | . | . | 2·3 | 5·6 | . | 2·3 | 34 | 44·5 |
| | 48·5–55 | . | . | 1·4 | . | . | 0·9 | . | . | . | . | . | . | . | 3·1 | . | 0·7 | 37 | 143·5 |
| L.M. 5 | 55–57 | . | . | . | . | . | . | . | 0·6 | 0·3 | . | . | . | . | . | . | 0·6 | 44 | 157 |
| | 57–61 | . | . | . | 0·3 | . | . | . | 1·8 | . | . | . | . | . | . | . | 0·3 | 39 | 302·5 |
| | 61–63 | . | . | . | . | . | 0·3 | . | 1·1 | . | . | . | . | . | . | . | 0·5 | 47 | 188·5 |
| L.M. 4 | 66 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | no %'s found | 5 | 8 |
| | 69 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | do. | 4 | 6 |
| | 73 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | do. | 0 | 0 |
| | 76 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | do. | 0 | 0 |
| | 80 | . | . | . | . | . | . | . | . | . | . | . | × | . | . | . | do. | 9 | 6 |
| | 85 | . | *1* | . | . | . | . | . | . | . | . | . | . | . | . | . | do. | 9 | 5 |
| L.M. 3 | 85·5–86·5 | . | 18·8 | . | 1 | . | . | . | 0·2 | . | . | 0·6 | 0·1 | 0·2 | . | . | 0·1 | 50 | 813·5 |
| | 88–91 | . | 14·4 | . | 1·2 | . | . | . | 0·6 | . | . | . | . | . | . | . | 1·1 | 23 | 90·5 |
| | 91–94 | . | 10·5 | . | . | . | . | . | . | . | . | 0·8 | . | . | . | . | 0·8 | 24 | 123·5 |
| | 94–94·5 | . | 1·6 | . | . | . | 3·5 | . | 0·1 | . | . | 0·2 | . | 0·5 | . | . | 0·2 | 43 | 438 |
| L.M. 2 | 97–99 | . | 4·2 | . | . | . | . | . | . | . | . | × | . | . | . | 0·1 | 0·2 | 49 | 619 |
| | 101·5–106·75 | . | 3·3 | . | 0·3 | . | 2·0 | . | . | . | . | 0·5 | . | . | . | . | 0·2 | 39 | 400 |
| | 106·75–108·5 | . | 3·9 | . | 0·4 | . | 0·1 | . | 0·1 | . | . | 0·5 | . | 0·5 | . | . | 0·2 | 50 | 464 |
| | 108·5–110 | . | 15·8 | . | 0·6 | . | 2·7 | . | 0·3 | . | . | 1·8 | . | 0·3 | . | . | 0·6 | 36 | 165 |
| | 111·5–113·75 | . | 8·2 | . | . | . | 2·7 | . | . | . | . | 1·4 | . | 0·2 | . | . | 0·4 | 37 | 220 |
| | 115·75–116·75 | . | 10·6 | 0·8 | . | . | 4·3 | . | . | 0·2 | . | 0·4 | . | . | . | . | 0·4 | 40 | 245·5 |
| | 117·75–118·75 | . | 5·2 | 8·9 | . | . | 0·7 | 0·9 | . | . | . | . | . | . | . | . | 0·4 | 31 | 213·5 |
| | 120·75–121·75 | . | 8·6 | 6·1 | 0·2 | . | 2·3 | . | . | . | . | 0·2 | . | . | . | . | 0·2 | 38 | 410 |
| | 123·75–124·75 | . | 10·6 | . | . | . | 2·8 | . | . | . | . | 0·2 | . | . | . | . | 0·2 | 47 | 415·5 |
| | 126·75–128·75 | . | 0·4 | 4·7 | . | . | 0·5 | . | . | . | . | 0·2 | . | 0·1 | . | . | 0·2 | 49 | 554 |
| | 129·5 | . | 6·2 | . | . | . | . | . | . | . | . | 0·5 | . | . | . | . | 0·5 | 38 | 208·5 |
| L.M. 1*b* | 132·5–133·5 | . | 22·9 | . | . | . | 0·8 | . | . | . | . | 0·5 | . | . | . | . | 0·3 | 36 | 311 |
| | 135·75–136·75 | . | 21·3 | . | . | . | . | 1·4 | . | . | . | . | . | . | . | . | 0·3 | 31 | 286·5 |
| | 143–144 | . | 23·4 | 7·6 | . | . | 0·8 | . | . | . | . | . | . | . | . | . | 0·5 | 34 | 184 |
| | 146–147 | . | 23·5 | . | . | . | 0·4 | . | 0·4 | . | . | . | . | . | . | . | 0·9 | 25 | 115 |
| | 148–149 | . | 16·8 | . | . | . | 0·6 | . | . | . | . | . | . | . | . | . | 0·6 | 23 | 166·5 |
| | 152–153 | . | 37·0 | . | . | . | 0·9 | . | . | . | . | . | . | . | . | . | 0·6 | 33 | 175·5 |
| L.M. 1*a* | 155·5 | . | 1·0 | . | . | . | 0·2 | . | . | . | . | . | . | 0·2 | . | . | 0·5 | 45 | 207 |
| | 157–158·5 | . | 2·0 | 1·3 | . | . | . | . | . | . | . | . | . | . | . | . | 1·0 | 33 | 97·5 |
| | 161 | 0·4 | 2·6 | 5·5 | . | . | 1·7 | . | . | . | 0·9 | . | 0·2 | . | . | . | 0·4 | 51 | 235 |
| | 161·75 | . | . | 10·4 | . | . | 1·3 | . | . | . | . | . | . | . | . | . | 0·9 | 33 | 115 |
| | 162·5 | . | . | 19·3 | . | . | 2·4 | . | . | . | . | . | . | 0·6 | . | . | 0·6 | 28 | 165·5 |
| | 163 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | no %'s found | 7 | 2 and frgts |

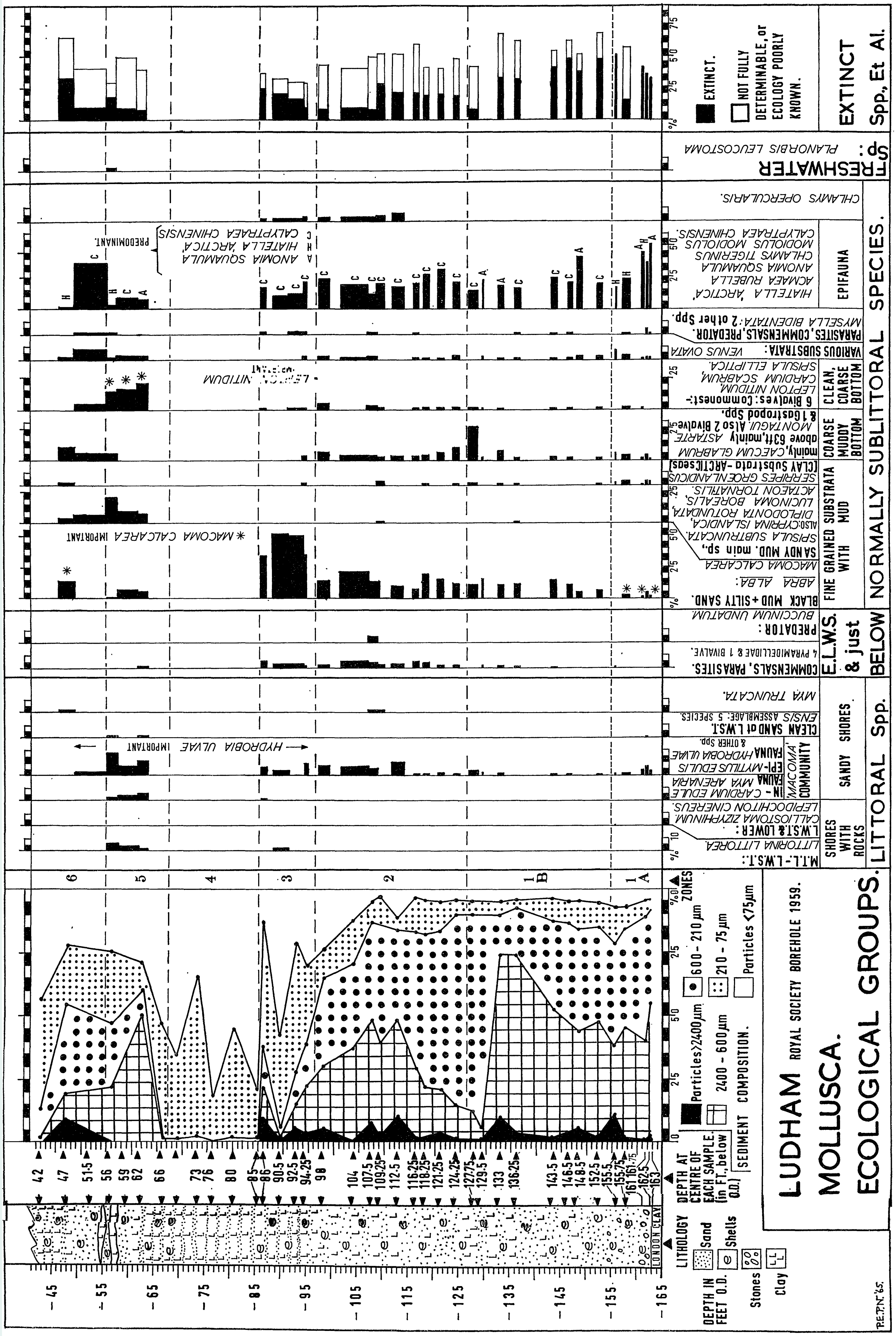

FIGURE 2. Ludham Mollusca (ecological groups) and granulometric analysis. Frequencies are shown to the nearest 1%.

### TABLE 3. BRAMERTON MOLLUSCA

Frequencies are given as percentages. A dot indicates a nil result. An × indicates that fragments only were found.

| sampling depths, in cm below top | tidal zone molluscs | | | | | | | | | | | normally subtidal species | | | | | | | | | | | | | | | | | little data | molluscan assemblage zones |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | rocky shores | | | 'macoma community' animals | | | | | | | ? | black mud and silty sand | | | sandy mud | | mud with coarse matter | | clean, coarse bottom | | | commensal | predator | epifauna | | | | scallop | | |
| | | | | infauna | | | epifauna | | | | | | | | | | | | | | | | | | | | | | | |
| | *Littorina littorea* | *Nucella lapillus* | ? *Patina pellucida* | *Cardium edule* | *C.* cf. *edule* | *Mya arenaria* | *Hydrobia ulvae* | ? *H. ulvae* | *Mytilus edulis* | *Retusa obtusa* | *Mya truncata* | *Abra alba* | *Macoma calcarea* | *M.* cf. *calcarea* | *Spisula subtruncata* | *S.* cf. *subtruncata* | *Astarte* cf. *montagui* | *Caecum glabrum* | *Cardium* cf. *scabrum* | *Venus* cf. *fasciata* | *Lepton nitidum* | *Mysella bidentata* | *Neptunea antiqua* | *Hiatella arctica* | *Anomia squamula* | *Calyptraea chinensis* | *C.* cf. *chinensis* | *Chlamys opercularis* | *Kellia pumila* | |
| 170 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | — |
| 290 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | |
| 440 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | |
| 500 | . | . | . | . | . | 3·3 | . | . | 1·7 | . | . | . | 1·7 | . | 20·0 | . | 1·7 | . | . | . | 5 | 1·7 | . | . | . | 3·3 | . | . | . | B.M. 2 |
| 580 | 0·4 | . | . | 15·6 | . | 4·8 | . | . | 2·8 | . | . | 0·2 | 12·6 | . | 4·4 | . | . | . | . | . | 1 | . | . | 4·2 | . | . | . | × | . | |
| 620 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | *1* | . | . | . | . | . | B.M. 1 |
| 710 | . | . | . | 3·2 | . | 1·0 | 1·6 | . | 0·4 | . | . | . | . | . | 0·4 | . | . | . | . | . | 0·4 | . | . | 17·5 | . | . | . | . | . | |
| 740 | 0·6′ | . | . | 15·4 | . | 0·3 | 12·7 | 0·9 | 1·2 | . | . | 0·9 | 3 | . | 0·6 | . | . | . | . | . | . | . | . | 2·7 | × | . | 1·2 | . | . | |
| 860 | . | . | . | 4·8 | . | 7·4 | 6·4 | 2·1 | × | . | . | 1·1 | 0·5 | 2·7 | . | . | . | . | . | . | . | . | . | 17·6 | × | . | . | . | 1·1 | |
| 920 | . | . | . | *1* | . | *2* | . | . | × | . | . | *0·5* | . | . | . | . | . | . | . | . | . | . | . | *6·5* | . | . | . | . | . | |
| 980 | 1·4 | 2·1 | . | 12·4 | . | 1·2 | 37·3 | 1·7 | 1·1 | 2·1 | 0·2 | 0·4 | 0·2 | . | 0·9 | . | . | . | . | . | . | . | . | 0·4 | . | . | . | . | . | |
| 1070 | 1·8 | 1·4 | 0·5 | 8·9 | . | 0·9 | 15·4 | 2·3 | 1·6 | . | . | 0·7 | 2·6 | . | 3·3 | . | . | . | . | . | 0·5 | . | . | 1·8 | . | . | . | . | . | |
| 1160 | × | . | . | 8·1 | 1·4 | 0·7 | 25·0 | . | 2·9 | . | . | 1·4 | . | . | . | . | . | . | . | . | 0·7 | × | . | 1·4 | . | . | . | . | . | |
| 1220 | 2·1 | . | . | 0·3 | . | . | 8·3 | . | 3·6 | . | 0·5 | 45.6 | 0·3 | . | 0·3 | 0·3 | . | × | × | 0·3 | . | . | × | 2·3 | . | 17·2 | . | 0·5 | . | |

TABLE 3 (*cont.*)

| sampling depths, in cm below top | incompletely determinable forms | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | molluscan assemblage zones |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *Abra* sp. | *Arca* sp. | cf. *Astarte* sp. | cf. *Calyptraea* sp. | *Cardium* sp. | *Cerithiopsid* sp. | *Cingula* sp. | cf. *Cingula* sp. | *Colus* sp. | *Diplodonta* sp. | *Gasteropod* sp. | *Gibbula* sp. | cf. *Hydrobia* sp. | *Lamellibranch* sp. | *Macoma calcarea* | *Modiolus* sp. | *Montacuta* sp. | *Mya* sp. | *Natica* sp. | ? *Natica* | *Nuculanid* sp. | *Odostomia* sp. | *Patellid* sp. | *Retusa* sp. | ? *Retusa* sp. | *Rissoa* sp. | *Spisula* sp. | *Tellinid* sp. | *Yoldia* sp. | ? *Yoldia* | *Venus* sp. | |
| 170 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | — |
| 290 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | |
| 440 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | |
| 500 | . | . | . | . | . | . | . | . | . | . | 3·3 | 3·3 | . | 1·5 | . | 1·7 | . | . | . | . | . | . | . | . | . | . | 1·7 | 13·3 | 1·7 | . | . | B.M. 2 |
| 580 | 0·2 | . | . | . | . | . | . | . | . | . | 7·2 | 0·8 | 0·4 | . | . | . | . | 1·6 | . | . | 0·4 | . | . | 1·6 | . | . | 0·4 | 23·2 | 1·6 | . | . | |
| 620 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | B.M. 1 |
| 710 | . | . | . | . | . | . | . | . | . | . | 21·5 | . | . | 16 | 2 | 0·4 | . | 2 | . | 0·8 | 1·2 | . | . | . | 0·8 | . | 4 | 14·7 | . | 0·8 | . | |
| 740 | . | . | . | . | 1·2 | . | 0·6 | . | . | . | 30·2 | 1·2 | . | 13·9 | . | . | . | 1·5 | . | . | . | . | 0·6 | . | . | . | 3·6 | 5·7 | . | . | . | |
| 860 | . | . | . | . | 11·1 | . | . | . | . | . | 20·2 | . | . | 8·5 | 0·5 | . | . | . | . | . | 2·7 | . | . | 1·1 | . | . | 3·2 | 6·4 | . | . | . | |
| 920 | . | . | . | . | . | . | . | . | . | . | *1* | . | . | *1·5* | . | . | . | . | . | . | × | . | . | . | . | . | . | *2* | . | . | . | |
| 980 | . | . | . | . | 2·1 | . | . | . | . | 0·2 | 0·7 | 0·7 | . | 0·5 | . | . | . | 0·4 | 1·4 | . | . | . | . | 1·8 | . | . | 1·2 | 7·8 | 0·4 | . | . | |
| 1070 | . | × | 0·2 | . | 3·3 | . | 0·5 | 1·4 | . | . | 3·7 | 1·8 | . | 19·3 | . | . | . | 1·2 | . | . | . | . | . | 0·5 | . | . | 2·8 | 10 | 4·4 | . | . | |
| 1160 | . | . | . | . | 0·7 | . | . | . | × | . | 14·7 | . | . | 1·4 | . | . | . | 1·4 | 1·4 | . | . | . | . | 2·9 | . | . | 0·7 | 2·5 | . | 6·6 | . | |
| 1220 | . | . | . | 0·5 | 1·3 | 0·5 | . | . | 1 | 0·5 | 2·6 | 0·5 | . | 3·1 | . | . | 0·3 | 1 | . | . | . | × | . | . | . | 0·5 | 1 | 1·6 | 0·3 | . | 0·3 | |

TABLE 3 (*cont.*)

| extinct species | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Caecum mammilatum* | *Cingula semicostata semicostata* | *Divaricella juttingae* | *Hydrobia minuta* | *Littorina littorea* var. *carinata* | *Macoma obliqua* | *M.* cf. *obliqua* | *Nucella lapillus vulgaris* | cf. *N. lapillus vulgaris* | *Potamides tricinctus icenicus* | *Rissoa curticostata* | *R. obsoleta* | *Yoldia oblongoides* | *Tellina praetenuis* | sampling depths in cm. below top | no. of individuals in the sample | no. of species/sample | % contribution per individual | molluscan assemblage zones |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | 170 | 0 | 0 | . | — |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | 290 | 0 | 0 | . | |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | 440 | 0 | 0 | . | |
| . | . | . | . | . | 2·0 | . | . | × | . | . | . | 1·7 | . | 500 | 30 | 17 | 3·33 | B.M. 2 |
| . | . | . | . | 0·4 | 8·6 | . | 0·4 | . | . | . | . | . | 7·4 | 580 | 249·5 | 24 | 0·4 | |
| . | . | . | . | . | . | . | . | . | . | . | . | . | . | 620 | 1 | 1 | %'s not found | B.M. 1 |
| . | . | . | . | . | . | . | . | . | . | . | . | . | 2·4 | 710 | 125·5 | 18 | 0·796 | |
| . | × | . | . | . | . | . | . | . | . | . | . | . | 1·8 | 740 | 165·5 | 22 | 0·6 | |
| . | . | . | . | . | . | 3·2 | . | . | . | . | . | . | . | 860 | 94 | 18 | 1·06 | |
| . | . | . | . | . | *0·5* | . | . | . | . | . | . | . | . | 920 | 15 | 10 | %'s not found | |
| 0·4 | . | . | 4·3 | . | 0·2 | . | . | . | . | . | . | . | 1·2 | 980 | 281·5 | 26 | 0·36 | |
| . | . | . | . | . | . | . | . | . | 0·5 | × | . | 0·7 | 7·9 | 1070 | 214·5 | 28 | 0·47 | |
| . | . | . | . | . | 2·9 | . | . | 1·4 | . | . | . | . | . | 1160 | 68 | 19 | 1·47 | |
| . | . | 0·3 | . | . | 1 | . | . | 1 | . | 0·5 | 0·5 | 0·3 | . | 1220 | 192 | 36 | 0·52 | |

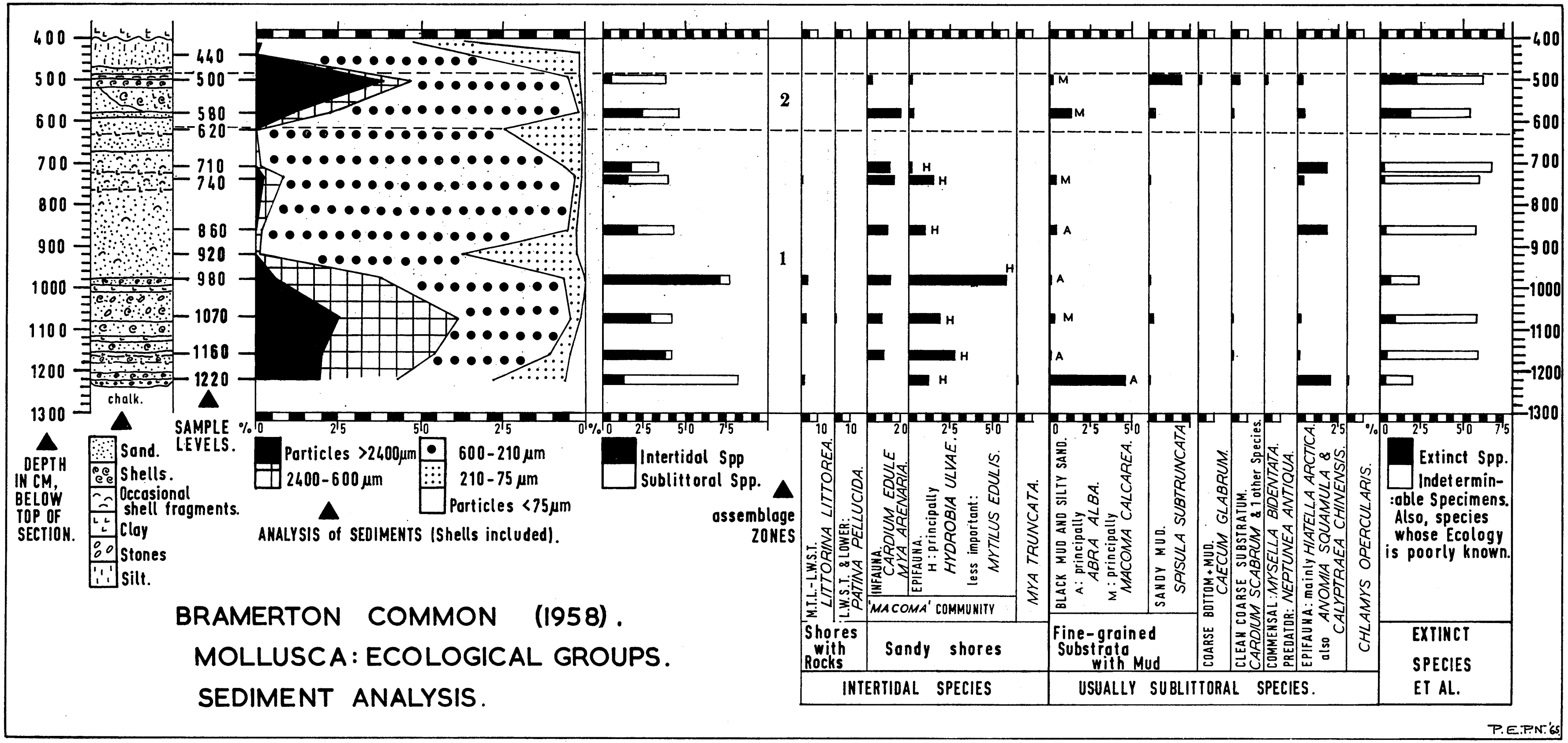

Figure 3. Bramerton Mollusca (ecological groups) and granulometric analysis. Frequencies are rounded to the nearest 1 %.

Table 4. Sidestrand Mollusca

Frequencies are given as percentages (method of calculation, see p. 168) except where figures in *italics* represent the actual number of individuals seen. A dot indicates a nil result.

| | species | SS/E base | SS/K 1 | SS/K 6 | S 12 (51) |
|---|---|---|---|---|---|
| intertidal species | *Littorina littorea* | × | × | . | . |
| | *Macoma balthica* | *4·5* | 39·7 | 39·8 | *5·5* |
| | *Cardium edule* | × | 3·8 | 3·1 | . |
| | *Mya arenaria* | . | 12·8 | . | . |
| | *Hydrobia ulvae* | *1* | 1·3 | . | . |
| | *Mytilus edulis* | *0·5* | 2·6 | 3·1 | *0·5* |
| | *Donax vittatus* | × | 1·9 | . | . |
| | *Zirfea crispata* | . | . | 0·8 | . |
| subtidal species | *Cyprina islandica* | *1* | 0·6 | 1·6 | *0·5* |
| | *Spisula subtruncata* | *1* | 0·6 | 7·8 | . |
| | *Astarte montagui* | . | 0·6 | . | . |
| | *Corbula gibba* | *1* | . | 6·2 | *1* |
| incompletely determinable forms | *Astarte* sp. | . | 0·6 | . | . |
| | *Cardium* sp. | . | . | 3·1 | . |
| | *Gastropod* sp. | *2* | 2·6 | 3·1 | *2* |
| | *Lamellibranch* sp. | *2·5* | 12·8 | 13·3 | *3·5* |
| | *Mya* sp. | . | . | 0·8 | . |
| | *Pholas* sp. | . | 1·9 | . | . |
| | *Spisula* sp. | . | 0·6 | 0·8 | . |
| | *Tellinid* sp. | *2·5* | 3·2 | 10·9 | *3* |
| | *Yoldia* sp. | *3* | 10·3 | 2·3 | *1·5* |
| extinct spp. | *Macoma obliqua* | *2* | . | . | . |
| | *Nucella lapillus vulgaris* | × | . | . | . |
| | *Nucula cobboldiae* | . | × | 0·8 | *0·5* |
| | *Yoldia* cf. *oblongoides* | *0·5* | . | . | . |
| | *Tornus supranitidus* ?? | . | 1·3 | . | . |
| | individuals | 20·0 | 78·0 | 64·5 | 18·0 |
| | species | 15 | 20 | 15 | 9 |
| | % contribution of 1 individual | — | 1·28 | 1·55 | — |

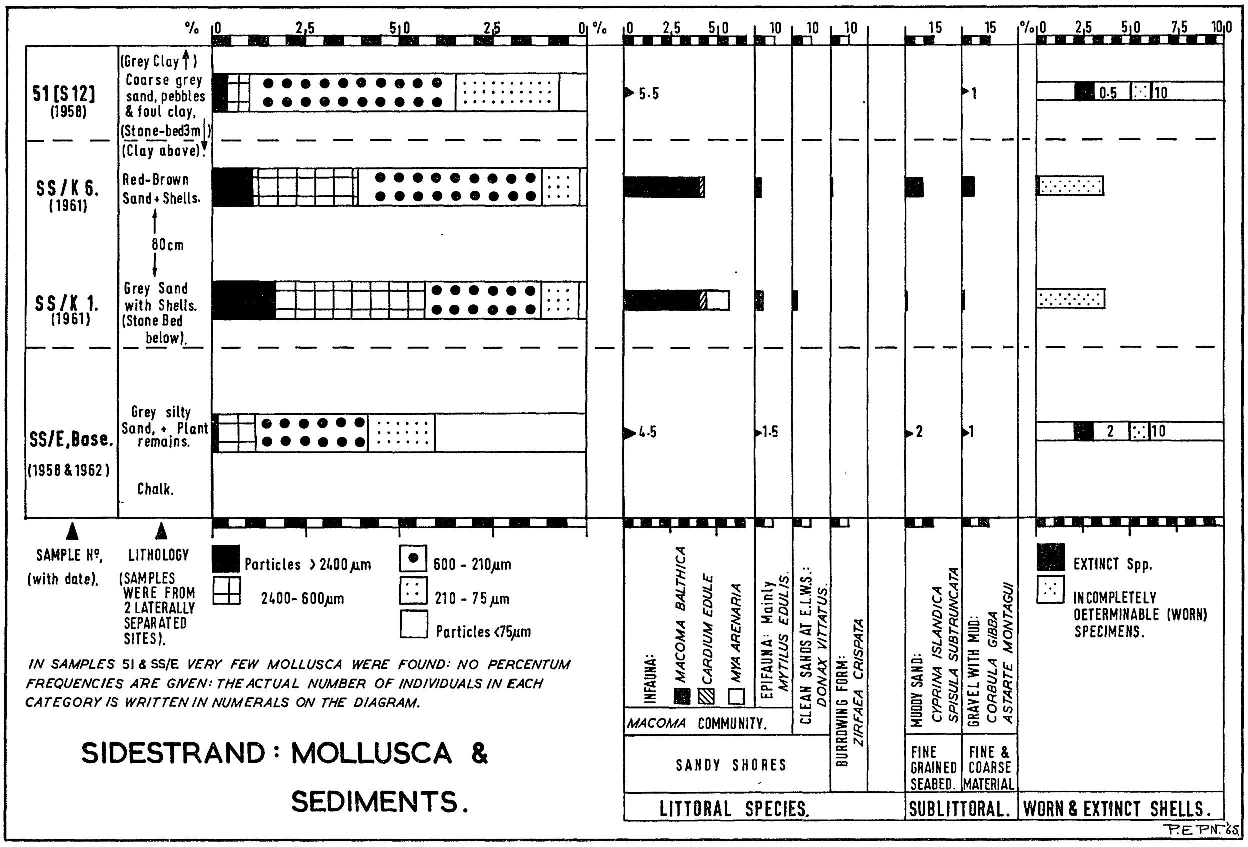

Figure 4. Sidestrand Mollusca (ecological groups) and granulometric analysis. Four samples from three horizontally separated localities are represented, see p. 166–167.

## APPENDIX. NOTES ON THE MOLLUSCA

This appendix supplements the lists at the foot of tables 2 to 4 by giving authorships and relevant notes. Extinct species are preceded by an asterisk and species whose determinations are uncertain have a query after the author's name. Nomenclature is based on Winckworth (1932, 1951), van Regteren Altena, Bloklander & Pouderoyen (1954, 1955, 1957, 1962), Thiele (1931–35) and Heering (1950). Of the material available for comparative study, much of S. V. Wood's is in the Paleontology Department of the British Museum (Natural History), the Ipswich Museum and the Castle Museum, Norwich. Harmer's material is distributed among the Ipswich Museum, the Sedgwick Museum at Cambridge and the Castle Museum at Norwich.

### CLASS AMPHINEURA

*Lepidochiton cinereus* (Linné, 1767)?.

### CLASS GASTROPODA

*Patina pellucida* (Linné, 1758)??.

**Acmaea parvula* (S. Woodward, 1833).

*A. rubella* (Fabricius, 1780).

**Solariella maculata* S. V. Wood, 1842.

**Calliostoma noduliferens* (S. V. Wood, 1872).

*C. zizyphinum* (Linné, 1758). Although the specimens were worn, it is not thought they belong to the extinct subspecies *C. zizyphinum simile* (J. Sowerby, 1818).

**Gibbula nehalenniae* van Regteren Altena, 1954?. Not previously recorded from the English Early Pleistocene. A paratype and topotype from Boring Haamstede, Schouwen, Netherlands (–96·60 to –103·30 m, Pliocene) was compared. van Regeteren Altena points out that Beets (1946, p. 29) referred young specimens of the present *G. nehalenniae* (c.f. the adults which he named '*Gibbula species 1*') to *G. pennanti* Philippi. The nearest resemblance of *G. pennanti* and *G. nehalenniae* to monographed species from the Crags is stated by van Regteren Altena to lie in the species *G. philberti* Recluz (Harmer 1923, p. 739, pl. 59, figs. 19–20) which has a smaller apical angle than my specimens, and *Margarites crassistriata* (R. Bell in S. V. Wood, 1882, p. 10, pl. 1, fig. 15) which has a thicker shell and less evenly rounded body whorl. Compare also with *G. beetsi* van Regteren Altena, 1954, which has a more pronounced ornament than *G. nehalenniae*.

**Gibbula* cf. *pennanti* (Philippi, 1851). Not previously recorded from the English Early Pleistocene. Determined from the description and figure in Spaink (1957).

**Gibbula* cf. *spastica* Beets, 1946. Not previously recorded from the English Early Pleistocene.

*Littorina littorea* (Linné, 1758).

*L. littorea* var *carinata* S. Woodward, 1833.

**Cingula semicostata semicostata* (Montagu, 1803). *Rissoa*, *Onoba striata* of Wood and Harmer. *O. striata* is given by Harmer (1920, p. 641) as living, in my opinion because he equated his specimens with Forbes & Hanley's (1850) figure of *Rissoa striata*, which I find to resemble *C. semicostata aculeus*, Gould, 1841 (living). Harmer's figure is of *C. semicostata semicostata* (extinct; see van Regteren Altena *et al.* 1954, p. 62, no. 35, pl. 4).

*C. proxima* (Alder MSS, Thompson, 1847).

**Rissoa curticostata*, S. Wood, 1848. The name *R. semicostata* Woodward, 1833, used by Wood and Harmer, is a *nomen nudum* and Wood's suggested name must be used (van Regteren Altena *et al.* 1954, p. 63).

**R. inconspicua* Alder, 1844.

**R. obsoleta* S. V. Wood, 1842.

**Hydrobia minuta* (S. Woodward, 1833). As *Paludestrina subumbilicata* (Montagu, 1803) in Wood (1848). Many accounts of *Hydrobia* species in the nineteenth-century literature give the impression that *H. minuta* is very common in the Norwich Crag. This may be due to the use of the name *Hydrobia minuta* Totten as a junior synonym of *H. ventrosa* (Montagu, 1803), although the specimens should often have been named *H. ulvae* in the first place, there having been erosion at the sutures, giving the whorls a spurious inflated appearance.

*H. ulvae* (Pennant, 1777).

*Caecum glabrum* (Montagu, 1803). During growth, the uncoiled, planar spiral shell of this species is broken off several times, the animal continuing to live in the larger part, the tube being closed by a calcareous septum posteriorly and the old portion discarded. When confronted with a number of fossil *Caecum* shells it is thus not easy to decide how many individuals are represented. The juvenile shell is coiled in a planar spiral, which Wood (1848, p. 117) called *Caecum*? *incurvatum*? Walker. Although Carpenter (1858, quoted by Wood 1872–4, p. 87) considered such individuals to be juveniles of *C. mammilatum*, I find this untrue. Both *C.* '*incurvatum*' and *C. glabrum* have a sculpture of minute growth lines only, forming a series of extremely fine close-set rings round the shell tube. *C. mammilatum* has more marked growth rings and the shell is more solid. The breaks which form in *C. mammilatum* at the formation of a new septum are oblique (and see Harmer 1923, p. 848), but in *C. glabrum* they are transverse and this is also true of *C.* '*incurvatum*'.

**C. mammilatum* S. V. Wood, 1842. (Jeffreys, in Prestwich 1871, gives it as living off Japan).

**Tornus pulchralis* (S. V. Wood, 1848).

**T. supranitidus* (S. V. Wood, 1842).??

*Turritella triplicata triplicata* (Brocchi, 1814). For a revision of nomenclature of certain *Turritella* species see van Regteren Altena *et al.* 1955, pp. 27, 28.

**Potamides tricinctus* var *icenica*, Harmer, 1918.

**Clathrus clathratulus minutus* (J. de C. Sowerby, 1823). In Wood (1848) as *Scalaria clathratula*; in Harmer as *Scala* (*Hyaloscala*) *minuta* Sowerby; in van Regteren Altena *et al.* as *Epitonium* (*Epitonium*) *clathratulum minutum*. The subspecies *C. clathratulus clathratulus* (Kanmacher, 1798) is living.

*Calyptraea chinensis* (Linné 1758).

*Trophon clathratus* var *gunneri* (Loven 1846)

**Nucella lapillus vulgaris* (S. V. Wood 1848).

*N. lapillus lapillus* (Linné, 1758). A few specimens from Bramerton appeared to have the less inflated whorls and less powerful sculpture of the extant subspecies; where the specimens are worn the separation of the subspecies is extremely difficult.

*Buccinum undatum* (Linné, 1758).

*Neptunea antiqua* (Linné, 1758).

**Nassarius consociatus* (S. V. Wood, 1848).

**N. elegans* (Leathes MSS, J. Sowerby, 1825).

*N. incrassatus* (Ström, 1768).

*Mangelia ambigua* (Brugnone, 1862)?.

*Actaeon tornatilis* (Linné, 1758).

*Retusa obtusa* (Montagu, 1803). In Wood (1848), as *Bulla regulbiensis* Adams, 1798; in Wood and Harmer later as *Bulla* or *Utriculus obtusus*; in Winckworth as *Retusa alba* Kanmacher, 1798.

*Chrysallida indistincta* (Montagu, 1803). Not previously recorded in the Crags.

*C. obtusa* (Brown, 1827). In Wood (1848) as *Odostomia pupa* (Dubois, 1831); in Wood and Harmer later as *Odostomia* or *Pyrgulina interstincta* (Montagu).

*C. spiralis* (Montagu, 1803). Harmer records this species from St Erth and Selsey but not from the Crags.

*Odostomia conoidea* (Brocchi, 1814). In Wood (1848) as *O. plicata* (Montagu). Sorgenfrei (1958, p. 313) found that the protoconch is usually hidden in the first adult whorl. In my specimens and those of the General Collection of British Pyramidellidae in the British Museum (Nat. Hist., Dept. of Zoology) the second and third and sometimes the first protoconch whorls were in part visible (this difference may be due to erosion).

*O. scalaris* Macgillivray, 1843. In Harmer (1920) as *O. risoides* Hanley, 1844. The fossil shells have a somewhat rugose exterior due to decay along transverse lines of growth, and are not translucent. Recorded by Harmer from St Erth but not the Crags. This species parasitises *Mytilus edulis* which was common in the samples.

*Turbonilla elegantissima* (Montagu, 1803). In Wood and Harmer as *Chemnitzia elegantior* or *Turbonilla lactea*.

**T. internodula* (S. V. Wood, 1848).

*Planorbis leucostoma* Millet. As *Planorbis spirorbis* Müller 1774 in Wood and Harmer. One apex and one fragment of the outermost whorl were found. This is a freshwater species.

### CLASS BIVALVIA

**Nucula cobboldiae* J. Sowerby, 1817.

*N. nucleus* (Linné, 1758).

**Yoldia lanceolata* (J. Sowerby, 1817).

**Y. oblongoides* (S. Wood, 1840). In Wood (1851–61) as *Leda myalis*. This is a frequent mistake in identification of Crag specimens and leads to confusion when the *Leda-myalis* bed of the Cromer Forest Bed Series (in which *L. myalis* really does occur) is spoken of.

**Y. semistriata* (S. V. Wood, 1840).

**Glycymeris glycymeris variabilis* (J. Sowerby, 1824). In Wood as *Pectunculus glycimeris*. More dorsoventrally elongated and less inflated than the extant *G. glycymeris glycymeris* which according to Heering (1950) is unknown in the Early Pleistocene.

**Limopsis anomala* (Eichwald, 1830). In Wood as *Limopsis pygmaea* (Philippi).

**L. aurita* (Brocchi, 1814).

*Modiolus* cf. *modiolus* (Linné, 1758).

*Mytilus edulis*, Linné, 1758.

*Chlamys opercularis* (Linné, 1758).

*C. tigerinus* (Müller, 1776).

*Anomia squamula* (Linné, 1758). The interesting growth forms which this species may attain through its habit of attaching by the right side to hard objects (other molluscs, stones, even corks; van Regteren Altena 1937) were unrepresented in the fossils. It was also impossible to use Winckworth's method of identification using the muscle scars (Winckworth 1922, p. 34) except in a few doubtful cases.

**Astarte basterotii* de la Jonkaire, 1823. Heering (1950) gives descriptions and plates which I found very helpful in determining the *Astarte* species.

*A. digitaria* (Linné, 1767).

**A. incerta* S. V. Wood, 1853.

*A. montagui* (Dillwyn, 1817). In Wood as *A. compressa*.

**A. obliquata* J. Sowerby, 1817.

**A.* cf. *parvula* S. V. Wood, 1840.

**Cardita chamaeformis* (Leathes MSS, J. Sowerby, 1826).

**C. orbicularis* (Leathes MSS, J. Sowerby, 1825).

**C. scalaris* (Leathes MSS, J. Sowerby, 1825).

*Cyprina islandica* (Linné, 1767).

**Diplodonta astartea* (Nyst, 1835).

*D. rotundata* (Montagu, 1803).

*Lucinoma borealis* (Linné, 1767).

*Divaricella divaricata* (Linné, 1758).

**D. juttingae* G. Spaink, 1965. This species is known only in the Pliocene and Early Pleistocene and is based partly on my specimens from Ludham (–57 to –61 ft. O.D.) and Bramerton (1220 cm below surface).

*Lepton nitidum*, Turton, 1822.

*Tellimya pumila*, S. Wood, 1840. This species is believed living on the basis of Jeffreys (in Prestwich 1871), and Thiele (1935), but I have no details of its ecology.

*Montacuta ferruginosa* (Montagu, 1808).

*Mysella bidentata* (Montagu, 1803).

**Laevicardium decorticatum* (S. V. Wood, 1840).

*Serripes groenlandicus* (Bruguière, 1789). In Wood as *Cardium groenlandicum* Chemnitz.

*C. edule* Linné, 1758.

**C. parkinsoni* J. Sowerby, 1814.

*C. scabrum* Philippi, 1844. In Wood as *C. nodosum*.

*Gouldia minima* (Montagu, 1803)

*Callista chione* (Linné, 1758).

*Venus c.f. fasciata* (Da Costa, 1778).

*V. ovata* (Pennant, 1777).

*Venerupis* spec., either *decussatus* or *pullastra*. The numerous specimens were hinge fragments with cardinal teeth but little else remaining.

*Spisula elliptica* (Brown, 1827). In Wood as *Mactra ovalis*. Determined with reference to van Urk (1959). The species is not easy to identify and probably many references from the past should be *S. solida*.

*S. subtruncata* (Da Costa, 1778).

**S. triangulata* (S. V. Wood, 1857).

*Donax vittatus* (Da Costa, 1778).

*Abra alba* (W. Wood, 1802).

*A. ovata* (Philippi, 1836). In Wood (1851–61) as *A. obovalis* S. Wood, 1840.

*A. obovalis* S. Wood, 1840.

*Arcopagia crassa* (Pennant, 1778).

*Macoma balthica* (Linné, 1758).

*M. calcarea* (Gmelin, 1791). In Wood as *Tellina lata*.

**Macoma obliqua* (J. Sowerby, 1817).

**Tellina praetenuis* Leathes MSS, Woodward, 1833.

*T. fabula* Gmelin, 1791.

*Ensis ensis* (Linné, 1758).

*E. siliqua* (Linné, 1758).

*Corbula gibba* (Olivi, 1792). In Wood as *C. striata*.

*Mya arenaria* Linné, 1758.

*Hiatella* '*arctica*' (Linné, 1767). In Wood as *Saxicava rugosa* (Pennant). Hunter (1949) gives characters for determination of *H. arctica* and *H. rugosa*.

*Zirfaea crispata* (Linné, 1758).

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