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THE ECOLOGY OF BRITISH SPECIES OF *ENSIS*

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(Text-figs. 1–5)

CONTENTS

INTRODUCTION

In a recent paper describing the distinguishing characters of British species of *Ensis* (Holme, 1951), it was concluded that three valid species occur in British waters: *E. siliqua* (L.), *E. arcuatus* (Jeffreys) and *E. ensis* (L.). This paper is an attempt to analyse the ecological factors controlling the distribution of these species, particular attention being paid to the effect of soil grade.

In addition to those acknowledged in a previous paper, I would like to thank the following for their assistance: Dr A. G. Lowndes, Mr L. Birkett, Mr C. Edwards, and Mr O. D. Hunt. Specimens of *E. minor* were kindly supplied by Dr R. Tucker Abbott, U.S. National Museum.

I am indebted to the Director and Staff of the Station Biologique at Roscoff for facilities provided during a visit to the Station. Dr P. N. J. Chipperfield kindly placed at my disposal the research launch of I.C.I. Paints Division, Brixham, from which the dredgings in Torbay were made. I am grateful to

the Director of the National Institute of Oceanography for facilities provided on R.R.S. *Discovery II*, from which the bottom-sampling station in Aberporth Bay was worked.

The Habitat of *Ensis*

Ensis is found burrowing in sand at low-water mark of spring tides, and also occurs in shallow water offshore. On the beach, it burrows nearly vertically in the sand by means of a powerful foot, but it does not seem to possess a permanent burrow. The short siphons project just above the surface of the sand, when covered by water, and draw in water from just above the bottom. When disturbed, *Ensis* burrows rapidly into the sand, often emitting a jet of water into the air as it starts to burrow. Along a beach at low tide, *Ensis* may be located by the presence of keyhole-shaped depressions in the sand, which become more evident when the surface water has drained away, and also by the jets of water produced when they start to dig. It is possible to survey quite long stretches of beach in this way, only digging when a burrow is seen.

On a number of occasions the animals have been seen to come right out of the sand at low tide, and lie on the surface. This habit is also shared by certain other lamellibranchs living in the same habitat (e.g. *Spisula*, *Donax* and spiny *Cardium*).

On wave-exposed beaches, *Ensis siliqua* may be the only lamellibranch present, but in more sheltered areas the smaller *E. ensis* may be found, together with such species as *Venus striatula* (da Costa), *Donax vittatus* (da Costa), *Tellina fabula* Gmelin, *Gari fervensis* (Gmelin), *Mactra corallina cinerea* Montagu, and *Lutraria lutraria* (L.). The burrowing crab, *Corystes cassivelaunus* (Pennant), and the heart-urchin *Echinocardium cordatum* (Pennant) also occur in these localities.

Ensis arcuatus, which inhabits a coarser grade of soil, may be found with *Dosinia exoleta* (L.), *Tellina donacina* L., and the heart-urchins *Spatangus purpureus* O. F. Müller and *Echinocardium pennatifidum* Norman.

One or other of the species of *Ensis* occurs on practically every beach where there is sand of a sufficient depth and some slight protection from wave action. There may, however, often be none in small patches of sand between rocks: such sands are often highly reducing (see p. 158). *Ensis* does not occur in water of reduced salinity, although its absence from estuaries may sometimes be due to the lack of deposits of a suitable grade. A list of sandy beaches in which *Ensis* has not been recorded is given in Table VII (Appendix).

Methods

In order to eliminate so far as possible the effect of characteristics peculiar to individual beaches, collections were made over as wide an area as possible. On the shore, collections have been made on most of the sandy beaches in S. Devon, S. Cornwall, and the Scilly Isles (Fig. 1). I have also received samples collected in various other parts of the British Isles. Additional samples have been obtained from certain beaches in Jersey and the north Finistère coast around Roscoff. A list of localities is given in Table VII (Appendix).

Grab or dredge collections are chiefly from Great West Bay (Holme, 1950), off Plymouth (some stations are in Holme, 1953), and in St Austell Bay off the Cornish coast (Fig. 5).

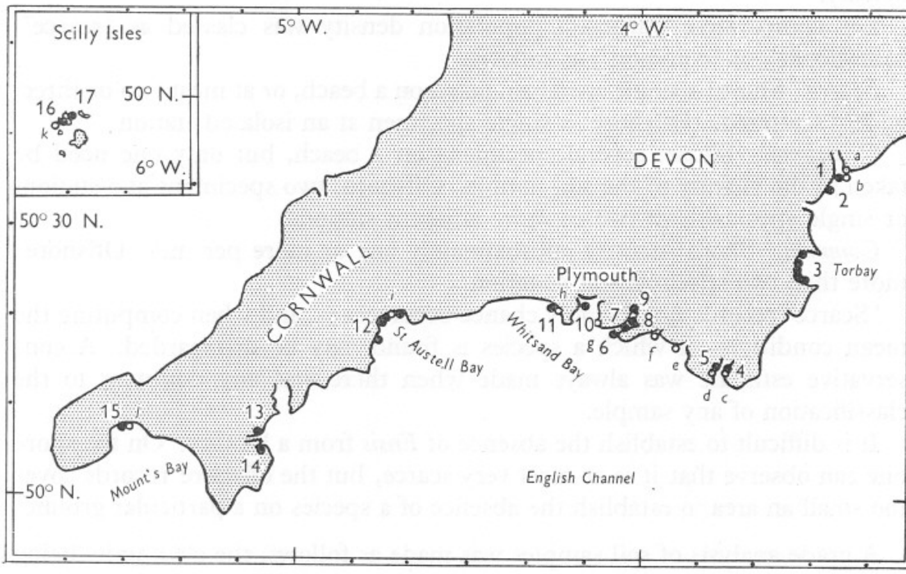

Fig. 1. Position of shore records (●) in Devon, Cornwall, and the Scilly Isles. Localities are numbered as follows: 1, Polesands; 2, Dawlish; 3, Torbay (see Fig. 5); 4, Salcombe, east; 5, Salcombe, west; 6, Cellars beach; 7, below Passage Wood; 8, Yealm sand bank; 9, Thorn Pt.; 10, Drake's Island; 11, Whitsand Bay; 12, St Austell Bay (see Fig. 5); 13, Helford; 14, Flushing Cove; 15, Marazion; 16, Tresco-Bryher channel; 17, Foreman's Island. Negative records (o): *a*, Maer Rocks, Exmouth; *b*, Polesands; *c*, south of Millbay, Salcombe; *d*, North Sands and South Sands, Salcombe; *e*, Borough Island; *f*, Mothecombe; *g*, Bovisand; *h*, Whitsand Bay; *i*, Charlestown (see Fig. 5); *j*, St Michael's Mount; *k*, Bryher.

At each locality a sample of the soil in which *Ensis* was living was taken for grade analysis. On the shore a sample from the top 5 cm. or so of soil was taken, all specimens taken within about a metre of the sample being considered to inhabit the same grade of soil. Samples were taken offshore either with the scoop-sampler (Holme, 1949*b*) or anchor-dredge (Forster, 1953). Where several hauls were made at a station, the soil sample was always taken from that in which *Ensis* was taken. There is little washing out of soil when the scoop-sampler is hauled up; but when using the dredge it was necessary to select a sample from an undisturbed portion of the dredge bag.

No accurate estimates of population density have been made. It is difficult to compare populations on different beaches, as tidal levels have to be taken into consideration. One is only sampling the fringe of the *Ensis* zone when collecting on the beach, and numbers are likely to change considerably over quite short vertical distances, so that the observed density may be much affected by the distance the tide recedes on a particular day. Offshore, the size of the sample, usually 0·5 $m.^2$ or less, is too small for an assessment of density.

For comparative purposes, population density was classed as 'scarce', 'occasional', or 'common', as follows:

Scarce. Shore: a single specimen taken on a beach, or at most two or three, widely scattered. Offshore: a single specimen at an isolated station.

Occasional. Shore: several specimens on a beach, but only one need be taken in the vicinity of the soil sample. Offshore: two specimens at a station, or single specimens at two or more adjacent stations.

Common. Shore: density approximately one or more per $m.^2$. Offshore: more than two specimens at a station.

'Scarce' records may be only chance occurrences, and when computing the mean conditions in which a species is found may be disregarded. A conservative estimate was always made when there was any doubt as to the classification of any sample.

It is difficult to establish the absence of *Ensis* from a locality. On the shore one can observe that it is at most very scarce, but the offshore records cover too small an area to establish the absence of a species on a particular ground.

A grade analysis of soil samples was made as follows, the class units being based on the Wentworth system (2, 1, $\frac{1}{2}$, $\frac{1}{4}$ mm. etc.). The methods used and reliability of the results are described by Krumbein & Pettijohn (1938).

Samples were dried before storage, and for analysis were 'broken down' to a convenient size by dividing a flattened-out pile into quarters and taking opposite quarters. This operation was repeated until a sample of about 20 g. was obtained.

This was then treated with 20 vol. hydrogen peroxide on a hot plate for $\frac{1}{2}$ hr. to oxidize organic matter and break up aggregates, and then washed through a B.S.S. gauze sieve, with 0·124 mm. apertures.

The residue on the sieve was dried and screened through a set of B.S.S. sieves of the following apertures: 2·057, 1·003, 0·500, 0·251, 0·210, and 0·124 mm. (dimensions quoted by the manufacturers). The sieves were shaken mechanically by a machine which imparted a short but rapid to-and-fro motion, at the same time tilting them through a small angle to the horizontal by a slowly rotating eccentric. After 10 min. shaking a fairly accurate separation was obtained, and the fraction on each sieve was then weighed.

Material washed through the fine sieve after peroxide treatment was placed in a wide measuring cylinder having two marks, one 10 cm. above the other. Distilled water was added up to the top mark, and the material stirred into suspension. After allowing to settle for 1 min. 56 sec. (at 20° C.) the suspension was siphoned off down to the lower mark, the siphon having an upturned end so as not to disturb material which had settled. Distilled water was added up to the top mark, and the operation repeated until the siphoned-off material was almost clear. By this means a separation of particles over and under $\frac{1}{32}$ mm. was obtained. The residue in the cylinder was dried and added to that passing the finest of the sieves in the shaker. To the siphoned-off suspension was added a little alum solution and a few drops of acetic acid, to flocculate the particles. After a day or two this was filtered through a weighed filter-paper, washed, dried, and the weight of solid determined.

A separation was thus made at the following approximate particle diameters: 2, 1, $\frac{1}{2}$, $\frac{1}{4}$, $\frac{1}{5}$, $\frac{1}{8}$ and $\frac{1}{32}$ mm. Large particles, over about 10 mm., were taken out of the sample before analysis, and were not reckoned with when calculating the percentage grade composition of the soil. Besides inorganic particles, the analysis includes shell and other calcareous material.

When more than one sample with the same species was taken from a beach, it was sometimes necessary to reduce the records to a single one to avoid bias to the mean from all collecting grounds in favour of a well-worked beach. When two or more samples did not differ by as much as 10% in any one grade, all but one sample was eliminated. The sample taken last on any one day was usually retained, as this was generally at the lowest level on the beach, and therefore more representative of the typical habitat, which often extends below low-water mark.

The results of mechanical analysis are conveniently expressed as a cumulative curve (Fig. 3, p. 156), with grade size on a logarithmic scale. The cumulative curve for any soil is independent of the class units, provided these are sufficiently closely spaced, and is therefore a more satisfactory method of representation than a histogram, in which the shape of the figure is dependent on the class units employed.

A convenient term for comparing sands which may differ particularly in the percentage of coarser particles is the arithmetic mean (see Krumbein & Pettijohn, 1938, p. 240). The mean of the upper and lower limits of each class is multiplied by the percentage weight in that class. The total of the products is divided by 100 to obtain the arithmetic mean. The method of calculation is shown below:

Grade size (mm.)	Mean grade (mm.)	Percentage in sample	Product
(4)–2	3·0	14·24	42·72
2–1	1·5	10·84	16·26
1–$\frac{1}{2}$	0·75	10·51	7·88
$\frac{1}{2}$–$\frac{1}{4}$	0·375	29·81	11·18
$\frac{1}{4}$–$\frac{1}{5}$	0·225	7·72	1·74
$\frac{1}{5}$–$\frac{1}{8}$	0·1625	16·90	2·75
$\frac{1}{8}$–$\frac{1}{32}$	0·0781	8·38	0·65
$\frac{1}{32}$–0	0·0156	1·60	0·02
		100·00	83·20

Mean = 83·20/100 = 0·832 mm.

The value of the arithmetic mean is clearly more affected by changes in the percentages in the coarser grades than in the finer ones.

Geographical Distribution

Many previous identifications have been incorrect, owing to failure to distinguish *E. arcuatus* as a separate species, and the following notes are therefore based almost entirely on specimens which I have seen. (The records in Ford, 1923, are known to be correct, as I have been able to confirm identifications from specimens in Mr Ford's shell collection.) All three specimens are generally distributed on the Atlantic coast of Europe, and *E. siliqua* and *E. ensis*, at least, occur in the Mediterranean. A list of localities is given below, and a more detailed list of places where living specimens have been taken is given in Table VII (Appendix).

E. siliqua

England: S. Cornwall; S. Devon; Swanage Bay, Dorset[1]; Studland Bay, Dorset[1]. **Scotland**: Aberdeen[1]; Fairlie, Ayrshire. **Isle of Man**: Port Erin Bay. **Wales**: Criccieth, Caernarvonshire[1]; Dale, Pembrokeshire; Tenby, Pembrokeshire[1]. **Ireland**: Benderg Bay, Co. Down. **France**: Grève de S. Michel, Finistère. **Italy**: Naples (from specimen department).

E. arcuatus

England: Scilly Isles; S. Cornwall; S. Devon; Swanage Bay, Dorset[1]; Pevensey Bay, Sussex[1]; Newton Haven, Northumberland. **Scotland**: Millport, Firth of Clyde (from specimen department). **Isle of Man**: Derbyhaven. **Wales**: Benllech, Anglesey[1]. **Ireland**: Portaferry and Benderg Bay, Co. Down. **Channel Isles**: Bordeaux Harbour, Guernsey; Jersey. **France**: Finistère.

E. ensis

England: S. Cornwall; S. Devon; Swanage Bay, Dorset[1]; Pevensey Bay, Sussex[1]; North Sea (52° 45′ N., 02° 44′ E.); off Cumberland coast (approx. 54° 23′ N., 03° 35′ W.). **Isle of Man**: Port Erin Bay. **Wales**: Aberporth, Cardiganshire. **Channel Isles**: Jersey. **France**: Finistère.

The Mediterranean form of *E. siliqua* is apparently smaller than the Atlantic form (Bucquoy, Dautzenberg & Dollfus, 1887–98, as var. *minor*), but specimens from Naples agree with the Atlantic form in the form of the fourth aperture papillae described by Holme (1951). The same authors give a photograph of *E. ensis* from Roussillon, on the French Mediterranean coast (pl. 73, fig. 5, as *E. ensis* var. *minor*; fig. 4 may be a small *E. arcuatus*).

There is insufficient data to fix the northern and southern limits of the three species, but they are not recorded from Iceland by Madsen (1949).

Four[2] species or forms of *Ensis* have been recorded from N. America: *E. directus* Conrad, *E. minor* Dall, *E. californicus* Dall (all listed in Dall, 1900), and the recently described *E. minor megistus* Pilsbry & McGinty (1943).

[1] Empty shells.

[2] A fifth species has recently been described by Stillman Berry (1953).

E. directus resembles *E. arcuatus*, but the shell of the former is broader and more arcuate. In addition, Bloomer (1905) notes that the fourth aperture is bordered by several rows of papillae, whereas in *E. arcuatus* there is only a single row on each side. Pilsbry & McGinty have illustrations of both *E. minor* and *E. minor megistus*. The former closely resembles *E. ensis* in shell form, and may well be the same species. *E. minor megistus* is more slender and parallel-sided than either *E. minor* or *E. ensis*, and the anterior end is obliquely truncated, not rounded as in *E. ensis*. *E. minor megistus* does not correspond with any European species.

I have not been able to see specimens or figures of *E. californicus*.

Apart from the possibility that *E. minor* Dall is the same as *E. ensis*, I have no records of the British species from outside European waters (including the Mediterranean).

Environmental Factors

The distribution of any organism is controlled by a complex of factors, each of which may act at a different point in the life history of the individual. Some factors may be too subtle to be detected by the methods employed, but an analysis of the more readily measurable factors should provide clues to the presence or nature of these other factors.

Any one factor interacts both with the organism and with its environment, and it is often difficult to distinguish whether the action of a factor is direct or indirect. Soil grade, for example, may influence distribution directly (see below), but it also has an indirect effect on the slope and stability of the beach, so affecting tolerance of wave action (see p. 158).

Soil Grade

Analyses of soil grade for the three species are given in Tables I–III. In these tables the samples have been grouped according to population density as 'scarce , 'occasional' or 'common', as defined on p. 148. Fig. 2 shows the percentage in each grade in histogram form, and the distribution of arithmetic means is given in Fig. 4. The mean of 'occasional' and 'common' samples only is shown as a cumulative curve in Fig. 3.

E. siliqua occurs in sands of fairly fine grade, in which particles between 0·21 and 0·0313 mm. preponderate. This species is not confined to sands of any particular grade composition within these limits, but seems to avoid those in which particles over 0·5 mm. form more than about 5% of the total. The percentage of silt (< 0·0313 mm.) is always small, and is usually less than 1%. *E. siliqua* is thus characteristic of ordinary 'clean' beach sands.

E. ensis occurs in soils of a grade similar to that in which *E. siliqua* is found. The histograms showing percentage weights in the different grades are very similar (Fig. 2), as is the distribution of arithmetic means (Fig. 4). Only eight of the *E. ensis* samples also contain *E. siliqua*, so the coincidence of the

TABLE I. GRADE-COMPOSITION OF SOILS IN WHICH *ENSIS SILIQUA* OCCURS

	Sample no.	Arith. mean (mm.)	Grade (mm.) >2·0 (I)	2·0–1·0 (II)	1·0–0·5 (III)	0·5–0·25 (IV)	0·25–0·21 (V)	0·21–0·125 (VI)	0·125–0·0313 (fs)	<0·0313 (s)
SCARCE										
Polesands	*47*	0·236	0·4	1·0	1·3	15·2	14·9	64·8	2·3	0·05
Saltern Cove	*53*	0·245	0	0·2	2·1	33·1	11·9	40·6	11·9	0·22
Salcombe, E.	*63*	0·646	3·1	17·4	25·5	10·2	5·3	22·7	15·0	0·76
Drake's Is. (C)	*172*	0·620	7·9	15·9	7·2	5·1	3·3	21·1	37·5	1·95
Drake's Is. (B, C)	*175*	0·272	0·1	1·0	4·1	37·7	10·9	30·1	14·3	1·93
Drake's Is.	*176*	0·103	0·1	0·1	0·3	1·7	1·3	15·4	79·7	1·36
Whitsand Bay	*117*	0·276	0	0·1	1·0	44·2	22·2	31·0	1·5	0·07
Porthpean	*61*	0·701	11·1	10·6	5·8	21·5	12·1	34·7	4·0	0·31
Helford River (C)	*41*	0·268	3·3	1·1	0·9	5·3	5·9	58·9	22·5	2·20
Flushing Cove	*58*	0·110	0	0·1	0·5	6·0	1·8	10·2	78·1	3·35
Mean		0·348	2·6	4·8	4·9	18·0	9·0	33·0	26·7	1·22
OCCASIONAL										
Dawlish	*74*	0·304	5·0	0·6	0·3	1·2	1·3	75·4	15·9	0·33
Salcombe, E. (B)	*6*	0·254	0·1	0·8	2·7	28·8	16·2	40·8	10·4	0·25
Par	*66*	0·287	0·2	0·1	3·2	44·9	14·3	31·8	5·2	0·38
Pentewan	*136*	0·222	0	0·3	1·3	18·9	17·9	57·1	4·4	0·16
Helford River	*38*	0·183	1·1	0·2	0·2	2·1	3·5	70·8	20·5	1·63
Helford River (B, C)	*165*	0·208	0·8	1·2	0·8	6·0	8·6	66·4	15·0	1·34
Dale Flats	*25*	0·100	0·2	0·1	0·1	0·3	0·2	18·5	79·3	1·38
Grève de S. Michel	*155*	0·085	0	0	0·1	0·1	0·3	6·1	93·0	0·35
Torbay[1]	*169*	0·140	0·3	0·7	0·6	0·6	0·3	45·1	51·8	0·61
Mean		0·198	0·9	0·4	1·0	11·4	7·0	45·8	32·8	0·71
COMMON										
Torr Abbey Sands	*139*	0·102	0·2	0·1	0	0·2	0·3	19·1	79·4	0·64
"	*141*	0·200	2·7	0·4	0·3	0·5	0·5	38·4	56·3	0·80
Paignton	*10*	0·187	0	0·6	1·6	5·9	3·5	79·5	8·7	0·20
Goodrington	*59*	0·287	2·0	3·7	3·5	5·0	3·0	67·3	15·2	0·34
"	*60*	0·169	0	0	0·1	3·4	7·4	82·6	6·4	0·17
Broadsands (C)	*2*	0·110	0	0	0·3	0·3	0·3	34·2	64·4	0·47
Broadsands (C)	*11*	0·199	1·3	0·7	0·5	1·0	0·8	77·8	17·7	0·29
Elbury Cove (C)	*106*	0·117	0·3	0	0	0·8	0·7	33·9	63·5	0·83
Par	*68*	0·096	0	0	0·1	0·4	0·5	20·0	77·6	1·40
Duporth	*62*	0·211	0·5	1·5	1·2	7·2	6·3	68·2	14·5	0·60
Flushing Cove (C)	*55*	0·169	0	0·1	0·4	11·0	9·3	49·5	28·5	1·28
Marazion	*52*	0·110	0	0·1	0·1	0·1	0·1	34·8	64·5	0·28
Dale Flats	*73*	0·139	0·1	0·1	0·1	0·3	0·1	66·1	32·1	1·11
Fairlie Sands	*18*	0·278	0	0	0·6	49·2	15·1	33·3	1·8	0·20
Torbay[1] (C)	*167*	0·089	0	0·1	0·1	0·2	0·3	10·8	87·7	0·77
Plymouth[1]	*22*	0·193	1·8	0·3	0·3	2·7	2·1	55·1	36·2	1·61
Mean		0·166	0·6	0·5	0·6	5·5	3·1	48·2	40·9	0·69

[1] Offshore records. (B), with *E. arcuatus*; (C), with *E. ensis*.

TABLE II. GRADE-COMPOSITION OF SOILS IN WHICH *ENSIS ARCUATUS* OCCURS

	Sample no.	Arith. mean (mm.)	Grade (mm.) > 2·0 (I)	2·0–1·0 (II)	1·0–0·5 (III)	0·5–0·25 (IV)	0·25–0·21 (V)	0·21–0·125 (VI)	0·125–0·0313 (fs)	< 0·0313 (s)
SCARCE										
Salcombe, W.	*64*	0·739	14·4	9·6	3·1	8·8	11·4	47·7	4·5	0·58
,,	*65*	1·453	33·2	22·7	5·9	6·7	4·0	19·4	7·9	0·28
Yealm River	*69*	2·144	60·8	16·0	8·0	2·7	0·4	2·6	5·7	3·77
,,	*171*	0·772	15·2	3·5	5·8	47·0	9·8	11·4	5·8	1·67
Helford River	*164*	0·196	1·3	0·7	0·7	3·9	5·1	55·7	29·6	2·97
Helford River (A, C)	*165*	0·208	0·8	1·2	0·8	6·0	8·6	66·4	15·0	1·34
Flushing Cove	*56*	0·832	14·2	10·8	10·5	29·8	7·7	16·9	8·4	1·60
,,	*57*	0·188	0·2	0·2	0·8	15·0	11·2	42·2	28·7	1·71
St Aubin's Bay	*15*	0·407	5·1	5·7	4·3	13·7	6·0	25·0	40·0	0·31
Térénès (C)	*149*	0·245	0·8	1·1	1·1	15·5	17·3	60·0	3·8	0·46
Plymouth[1] (C)	*31*	0·177	0·1	0·4	1·1	6·1	8·6	63·7	19·8	0·22
Mean		0·669	13·3	6·5	3·8	14·1	8·2	37·4	15·4	1·36
OCCASIONAL										
Salcombe, E. (A)	*6*	0·254	0·1	0·8	2·7	28·8	16·2	40·8	10·4	0·25
Yealm River	*70*	0·597	10·6	3·3	2·9	29·9	18·4	32·8	2·0	0·26
,,	*71*	0·667	7·6	9·8	15·8	32·1	7·6	18·6	7·9	0·73
Drake's Is. (A, C)	*173*	0·433	0·7	2·2	8·0	81·8	4·4	1·8	0·7	0·45
Drake's Is.	*175*	0·272	0	1·0	4·1	37·7	10·9	30·1	14·3	1·93
Foreman's Is.	*128*	0·866	16·2	9·3	8·3	36·9	6·5	11·1	10·7	1·21
Grouville Bay (C)	*16*	0·215	0	0·4	3·3	13·0	12·7	61·8	8·7	0·18
Goulven	*157*	0·208	0·2	0·4	2·2	16·0	7·0	56·7	17·6	0·05
Perharidy	*159*	0·726	7·3	7·8	19·5	64·0	0·6	0·6	0·1	0·05
Mean		0·471	4·7	3·9	7·4	37·8	9·4	28·3	8·0	0·57
COMMON										
Salcombe, E.	*3*	0·545	0·3	5·0	45·6	21·4	4·3	14·8	8·3	0·35
Salcombe, E. (C)	*12*	0·482	1·0	13·2	19·4	8·7	4·0	31·0	21·4	1·25
Yealm River	*1*	1·307	25·2	19·0	19·7	29·3	1·7	2·2	1·7	1·19
Tresco	*50*	1·242	10·6	42·5	32·0	10·6	2·1	1·9	0·3	0
Tresco-Bryher channel	*120*	0·961	11·7	21·0	21·1	27·7	6·3	10·7	1·4	0·13
,,	*121*	1·267	25·7	16·0	15·9	30·9	5·0	5·5	0·8	0·19
,,	*122*	0·978	10·6	23·3	20·6	38·0	3·2	3·8	0·4	0·19
Foreman's Is.	*126*	1·020	20·5	9·1	11·0	41·7	7·6	8·1	1·7	0·40
,,	*127*	0·641	5·5	8·5	13·9	58·7	6·8	5·9	0·7	0·17
,,	*129*	0·964	13·9	15·5	21·2	36·3	4·5	4·8	2·4	1·50
Tresco-Bryher channel	*130*	1·138	19·1	16·8	23·3	34·0	3·5	2·4	0·6	0·27
,,	*131*	0·622	3·3	9·9	21·7	47·7	9·2	7·7	0·3	0·13
Newton Haven	*19*	0·195	1·1	0·6	1·2	3·3	1·5	64·7	27·3	0·25
Grouville Bay	*9*	0·314	0	0·3	6·3	48·4	17·1	25·2	2·7	0·12
Goulven	*158*	1·612	30·2	33·0	21·0	14·1	0·6	0·7	0·4	0·04
Mean		0·886	11·9	15·6	19·6	30·0	5·2	12·6	4·7	0·41

[1] Offshore records. (A), with *E. siliqua*; (C), with *E. ensis*.

TABLE III. GRADE-COMPOSITION OF SOILS IN WHICH *ENSIS ENSIS* OCCURS

	Sample no.	Arith. mean (mm.)	Grade (mm.) >2·0 (I)	2·0–1·0 (II)	1·0–0·5 (III)	0·5–0·25 (IV)	0·25–0·21 (V)	0·21–0·125 (VI)	0·125–0·0313 (fs)	<0·0313 (s)
SCARCE										
Torr Abbey Sands	*140*	0·143	1·1	0·1	0·1	0·3	0·4	35·9	61·4	0·82
Elbury Cove	*105*	0·125	0	0	0	2·5	1·2	45·6	49·6	1·02
Elbury Cove (A)	*106*	0·117	0·3	0	0	0·8	0·7	33·9	63·5	0·83
Salcombe, W.	*163*	0·836	21·1	6·6	0·8	2·9	3·9	32·6	30·9	1·17
Yealm River	*72*	1·164	28·1	10·2	4·6	20·0	8·3	20·6	7·4	0·76
Drake's Is. (A)	*172*	0·620	7·9	15·9	7·2	5·1	3·3	21·1	37·5	1·95
Drake's Is.	*174*	0·225	2·3	1·6	1·1	4·9	4·3	34·9	49·1	1·87
Flushing Cove	*54*	0·142	0	0·3	1·2	7·9	3·3	29·2	55·7	2·45
Grouville Bay	*7*	0·168	0·3	0·1	0·1	2·0	3·3	82·7	11·4	0·12
Grouville Bay (B)	*16*	0·215	0	0·4	3·3	13·0	12·7	61·8	8·7	0·18
Térénès	*147*	0·267	1·3	3·7	3·1	6·1	3·5	64·8	16·7	0·82
Térénès (B)	*149*	0·245	0·8	1·1	1·1	15·5	17·3	60·0	3·8	0·46
Goulven	*156*	0·194	0	0·1	2·0	16·9	7·1	47·9	25·9	0·14
Plymouth[1]	*116*	0·185	0·1	0·1	0·6	9·2	17·4	57·1	13·8	1·80
Plymouth[1]	*113*	0·272	2·4	3·2	3·2	3·4	2·8	51·6	30·1	3·30
Plymouth[1]	*32*	0·158	0	0·2	0·7	2·9	4·8	69·6	19·8	2·12
Mean		0·317	4·1	2·7	1·8	7·1	5·9	46·8	30·3	1·24
OCCASIONAL										
Broadsands (A)	*2*	0·110	0	0	0·3	0·3	0·3	34·2	64·4	0·47
Broadsands (A)	*11*	0·199	1·3	0·7	0·5	1·0	0·8	77·8	17·7	0·29
Salcombe, E. (B)	*12*	0·482	1·0	13·2	19·4	8·7	4·0	31·0	21·4	1·25
Drake's Is. (A, B)	*175*	0·272	0	1·0	4·1	37·7	10·9	30·1	14·3	1·93
Helford River	*24*	0·094	0	0·3	0·1	0·4	0·6	22·0	60·6	16·00
,,	*36*	0·177	0·7	0·1	0·2	2·5	3·9	73·1	18·6	0·83
,,	*40*	0·226	2·7	1·2	1·2	2·7	1·8	45·1	40·3	5·17
Helford River (A)	*41*	0·268	3·3	1·1	0·9	5·3	5·9	58·9	22·5	2·20
Helford River (A, B)	*165*	0·208	0·8	1·2	0·8	6·0	8·6	66·4	15·0	1·34
Flushing Cove (A)	*55*	0·169	0	0·1	0·4	11·0	9·3	49·5	28·5	1·28
Flushing Cove	*162*	0·147	0	0·4	0·6	6·0	4·7	41·9	45·3	1·26
Penpoull	*145*	0·443	7·4	4·5	2·8	3·4	1·8	62·9	16·1	1·14
Great West Bay, St. 12[1]	*27*	0·161	0·2	0·2	0·7	3·4	1·4	69·0	24·8	0·40
Great West Bay, St. 17[1]	*28*	0·136	0·1	0·3	0·9	5·6	2·2	33·8	53·6	3·45
Great West Bay, St. 16[1]	*29*	0·157	0·1	0·2	0·9	7·4	3·9	48·2	38·8	0·54
Torbay, St. 9[1]	*167*	0·089	0	0·1	0·1	0·2	0·3	10·8	87·7	0·77
Torbay, St. X[1]	*170*	0·080	0	0	0·1	0·2	0·1	1·4	97·3	0·91
Plymouth[1] (B)	*31*	0·177	0·1	0·4	1·1	6·1	8·6	63·7	19·8	0·22
St Austell Bay, St. 3[1]	*33*	0·145	0	0·2	1·0	5·5	5·3	46·4	30·9	10·74
St Austell Bay, St. 4[1]	*34*	0·098	0	0·1	0·6	2·0	1·6	19·6	60·9	15·29
St Austell Bay, St. 6[1]	*35*	0·109	0	0·4	1·3	4·2	1·2	7·0	80·2	5·71
Irish Sea[1]	*14*	0·203	0	0·7	1·6	12·2	8·8	65·0	10·6	1·22
Mean		0·189	0·8	1·2	1·8	6·0	3·9	43·5	39·5	3·29
COMMON										
St Aubin's Bay	*21*	0·180	0·5	1·8	1·8	8·2	5·1	20·3	61·9	0·42
Great West Bay, St. 19[1]	*30*	0·313	1·8	1·7	5·5	26·7	8·3	37·4	14·0	4·63
Aberporth Bay[1]	*160*	0·300	0·5	0·3	0·6	53·4	21·6	12·8	7·4	3·33
Mean		0·264	0·9	1·3	2·6	29·4	11·7	23·5	27·8	2·79

[1] Offshore records. (A), with *E. siliqua*; (B), with *E. arcuatus*.

histograms is not due to both being made up of the same set of samples. *E. ensis* is able to tolerate a slightly higher percentage of coarse material over 0·5 mm., but typically occurs where there is 3% or less. *E. ensis* is found in

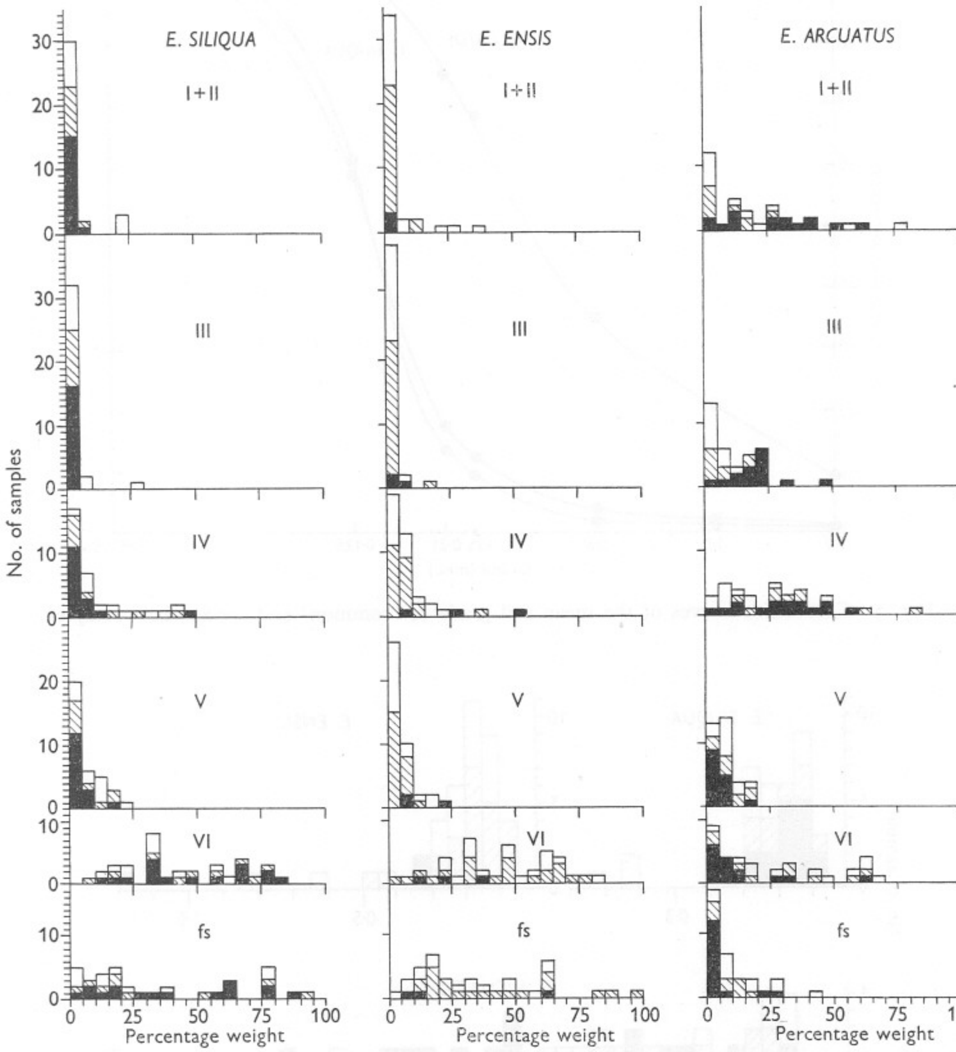

Fig. 2. Diagram summarizing the soil analyses given in Tables I–III. The percentage weights in each grade have been grouped in 5% units, and the number of samples in each 5% group are shown in histogram form. The silt grade has been omitted. Samples are represented thus: ■, common; ▨, occasional; □, scarce.

soils with a silt percentage ranging from 0·1 to 16%, the mean being about 3%. One might expect the mean silt percentage for this species to be rather higher than for *E. siliqua*, since most of the samples are from sheltered

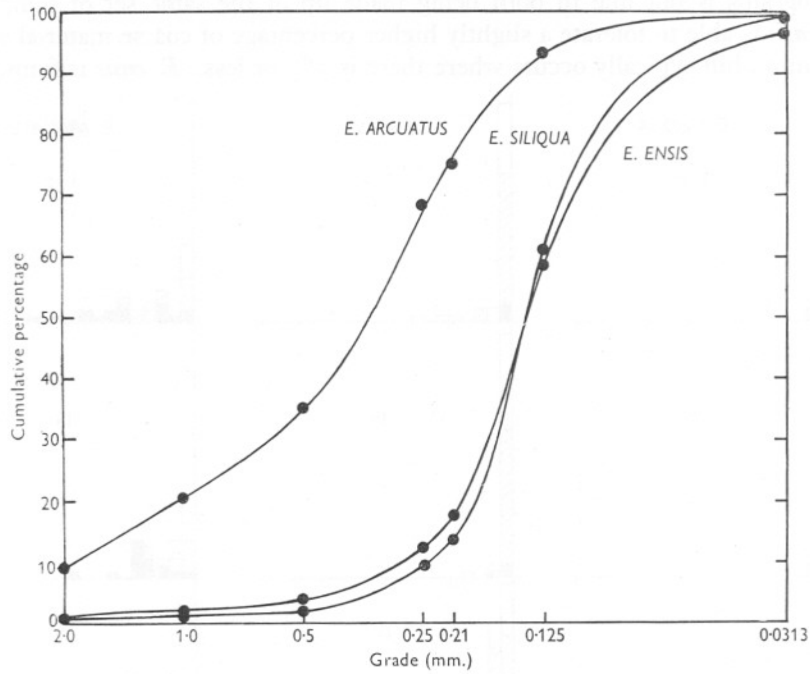

Fig. 3. Cumulative curves of the mean soil grade of 'common' and 'occasional' samples.

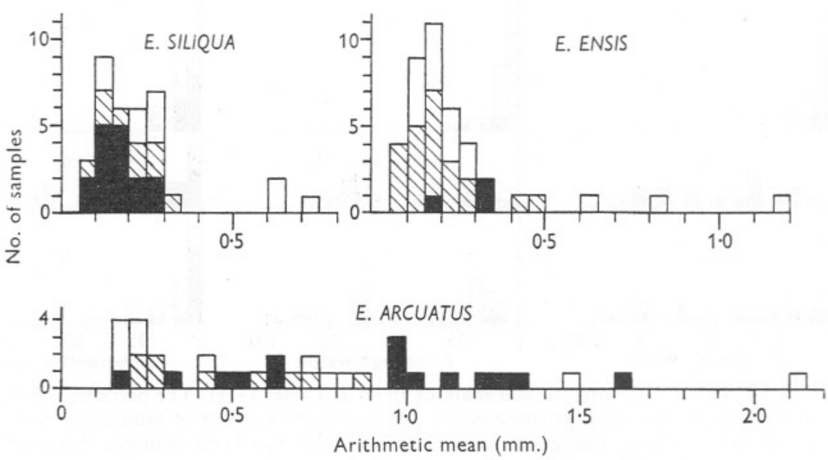

Fig. 4. The arithmetic mean of soils inhabited by the three species. The mean is grouped in units of 0·05 mm. Samples are represented thus: ■, common; ▧, occasional; □, scarce.

localities or from offshore, whereas the silt content is usually higher than on an open beach, but the occurrence of *E. ensis* in three samples containing over 10% silt indicates that it does have a greater silt tolerance.

E. arcuatus inhabits soils of a coarser grade than the other two species. The arithmetic mean of the soils ranges from less than 0·2 mm. to over 1·5 mm. In fine-grade soils its distribution overlaps that of *E. siliqua* and *E. ensis*, and it occurs with either or both of these species on certain beaches. Sands inhabited by *E. arcuatus* typically contain about 35% over 0·5 mm., and naturally show a correspondingly lower percentage in the finer grades. It is therefore not possible to say whether the distribution of this species is correlated with the presence of coarse or the relative scarcity of fine particles.

The density of *Ensis* populations is usually greater in sands approaching the 'mean' grade of the samples for that species. This is clear from an inspection of Figs. 2 and 4. In particular, population densities of *E. siliqua* and *E. ensis* are less in soils coarser than the mean. The densities on different beaches cannot readily be related to the grade of deposit, as so many other factors may be concerned. In St Austell Bay, however, there are a number of open beaches within a few miles of each other (Fig. 5), on which the populations of *E. siliqua* are very different. These differences may be correlated with the varying grade of beach deposit, but the effect could be an indirect one due to the greater disturbance by waves on beaches of coarse sand (see p. 158).

Beach	Arith. mean (mm.)	Population density
Porthpean	0·701	Scarce
Par (nr. Callyvador rocks)	0·287	Occasional
Pentewan	0·222	Occasional
Duporth	0·211	Common
Par (E. end beach)	0·096	Common

Nature of the Soil Particles

The sands in which *Ensis* occurs are usually predominantly of quartz grains, although the percentage of calcareous material is often high.

Sandy beaches in Devon and Cornwall are usually discontinuous, being separated by rocky headlands, so that little movement of material along the coast can occur. The sand grains on any beach are probably formed largely from rocks in the vicinity, together with material washed in from offshore. The size, shape, and surface texture of the quartz grains will depend on the rocks from which they are derived (Hatch & Rastall, 1952, pp. 86–90), although some subsequent degree of rounding may be achieved on exposed beaches.

Between Paignton and Exmouth the cliffs are mainly of New Red Sandstone, which produces fine-grade quartz grains with some degree of rounding. Much of the coastline between Torbay and Mount's Bay is formed of Devonian slates and grits: these produce more angular grains, similar to the Polzeath sand figured by Wilson (1948, plate XVII). Grains derived from the chain of granite bosses extending through Devon and Cornwall are probably found in most of these sands. Where there are china clay workings, kaolin and mica may be carried down to the sea in large quantities, contributing both to littoral and offshore deposits. This is particularly noticeable in St Austell Bay. The granite of the Scilly Isles produces a coarse-grained quartz sand, in which *E. arcuatus* is abundant.

In Jersey and Brittany the local granite and metamorphic rocks produce quartz grains of a much smaller size than in Scilly. Pruvot (1897) has described the geology and deposits of the N. Brittany coast, and has shown that many of the beaches have a high calcium carbonate content.

There is no evidence that any species of *Ensis* is restricted to sand of a particular mineralogical character, degree of roundness, or surface texture. Wilson (1953) suggests that an organic coating on certain sands affects the settlement of *Ophelia* larvae. Most sands probably possess an organic coating of some sort, but this matter has not been investigated. Certain sands from the Scilly Isles have a conspicuous green coating on the grains, which may be of algal or fungal nature.

Reducing Conditions in the Sand

Ensis typically occurs in sands which are not black below the surface, indicative of reducing conditions. Where seaweed or other organic matter gets buried in and incorporated in the sand, resulting in a black layer containing ferrous sulphide, *Ensis* is absent. The absence of *Ensis* from beaches at Mothecombe and Bovisand, near Plymouth, is probably due to such conditions. *Ensis* can tolerate sands which are slightly reducing, in which there is a grey layer below the surface, however. Such conditions occur on beaches of firm fine sand in which the organic content is not high, but there is little circulation of water. *E. siliqua* has been found in 'grey' sands at Torr Abbey, Elbury, S. Michel, etc.

Wave Exposure

On exposed beaches where the sand is continually churned by waves, *Ensis* is absent. Such beaches are typically barren. *E. siliqua* is only found where there is at least slight shelter from wave action. Tolerance of wave action seems to be dependent on the stability of beach deposits. King (1951) has shown that on an exposed beach the depth of disturbance during storms is unlikely to exceed 20 cm., but if wholesale transport of material occurs the sand may be disturbed to a much greater depth. The depth of disturbance in a coarse sand is greater than in a fine one, on account of the steeper slope of beaches of coarse material.

Although *E. siliqua* is capable of rapid burrowing, it is sometimes washed inshore in large numbers after storms, as are the other species. In very exposed areas it is only able to live below low-water mark, where wave disturbance is less severe (e.g. in Bigbury Bay). Some of those washed on to an exposed beach after a storm may burrow into the sand and establish a temporary foothold until disturbed by the next storm. This may account for occasional specimens found on the beach at Whitsand, also on the Polesands, where wave action is not extreme, but the bank is too shifting for *Ensis* to persist. On the other hand, *E. siliqua* is found in large numbers on the exposed beach at Marazion, in Mount's Bay. Its occurrence may be due to the sand there being fine and gently sloping, so that the depth of disturbance is minimized. The arithmetic mean of a sample from Marazion was 0·110 mm., as against 0·276 mm. in Whitsand Bay.

E. arcuatus seldom occurs on open beaches in south-west England, and this may be due to the relatively greater depth of disturbance for a given wave height on beaches of the coarse sand which it inhabits. It is confined to sheltered harbours and estuaries where accumulations of coarse material occur. It is also found in relatively sheltered beaches between the islands in Scilly.

Although occurring in sands of a similar grade to those occupied by *E. siliqua*, *E. ensis* is absent from the more exposed beaches on which the former occurs. In such exposed areas, it may occur only below low-tide mark (e.g. St Austell Bay, Fig. 5). In Jersey and Finistère, however, it occurs on exposed beaches (see pp. 162–3).

It is difficult to obtain an objective estimate of the severity of wave action on a beach. On nearly all beaches on which *Ensis* occurs, wave action may at times be severe, and a comparison of beaches is perhaps best made in relation to the normal conditions which prevail, rather than to the extreme conditions when a storm is blowing from an unusual quarter. On the basis of the normal wave exposure, a tentative classification has been made as follows:

(1) Beaches fully exposed to prevailing wind and swell (from south-west).

(2) Beaches with some slight shelter from prevailing wind and swell.

(3) Beaches sheltered from prevailing wind and swell, but exposed to waves from another direction.

(4) Beaches in bays which are sheltered from prevailing wind and swell.

(5) Sheltered beaches in harbours and estuaries.

Such a classification cannot take into account individual differences due to submarine topography, etc., but in the absence of detailed observations is the nearest approximation which can be achieved.

The occurrence of species of *Ensis* in relation to wave-exposure is summarized in Table IV. *E. siliqua* is found in all five categories, but *E. ensis* and *E. arcuatus* are more or less confined to groups 4 and 5. Notable exceptions are the occurrence of these last two species on exposed beaches on the south side of the Channel.

The occurrence of *E. siliqua* and *E. ensis* in St Austell Bay and Torbay is shown in Fig. 5. St Austell Bay is sheltered from the west, but is open to the south and south-east. *E. siliqua*, only, occurs on the beaches there, exposure being too great for *E. ensis*, which occurs offshore. (*E. siliqua* has not been recorded offshore, where it no doubt occurs in shallow water.)

TABLE IV. OCCURRENCE OF *ENSIS* IN RELATION TO WAVE EXPOSURE

(Names in italics are of beaches on the south side of the Channel. +, 'common' or 'occasional' records; (+), 'scarce' records. Samples from certain areas (e.g. Scilly Isles) are lumped together. *, probably washed in from offshore.)

Exposure	Beach	*siliqua*	*arcuatus*	*ensis*
1	Whitsand	(+)*	–	–
	Marazion	+	–	–
2	*St Aubin's Bay*	–	(+)	+
	Goulven	–	+	(+)
3	Polesands	(+)*	–	–
	Dawlish	+	–	–
	Paignton	+	–	–
	Goodrington	+	–	–
	Saltern	(+)	–	–
	Par	+	–	–
	Duporth	+	–	–
	Porthpean	(+)	–	–
	Pentewan	+	–	–
	S. Michel	+	–	
	Perharidy	–	+	–
	Grouville	–	+	(+)
4	Torr Abbey	+	–	(+)
	Broadsands	+	–	+
	Elbury	+	–	(+)
	Cellars Beach	–	+	(+)
	Scilly Is.	–	+	–
	Dale	+	–	–
	Térénès	–	(+)	(+)
5	Salcombe	+	+	+
	Yealm (excl. Cellars Beach)	–	+	–
	Drake's Is.	(+)	+	+
	Helford	+	(+)	+
	Flushing	+	(+)	+
	Penpoull	–	–	+

Torbay is more sheltered, being open only to the east. *E. siliqua* occurs on all sandy beaches, and in shallow water offshore. *E. ensis* is absent from beaches in the middle of the bay, being found only at Torr Abbey Sands, in the north-west corner, and Broadsands and Elbury in the south-west corner. These beaches are probably a little more sheltered than those in the middle of the bay.

Currents

On open beaches the effects of currents are negligible in comparison with the water movements produced by breaking waves. No correlation has been found between the occurrence of *Ensis* and the strength of currents, although these have an indirect effect by their action on the distribution of particles, particularly in sheltered waters.

Depth Distribution

On the shore all species occur from about MLWST downwards, often increasing in number toward extreme low-water mark.

E. siliqua extends seawards to a depth of *c.* 20 m. on suitable substrata. It seems to be most common at extreme low water and just below. Several specimens were taken in Bigbury Bay in 20 m., and it has also been taken in the anchor-dredge in Torbay in depths of 1·6–6·9 m., where it is common.

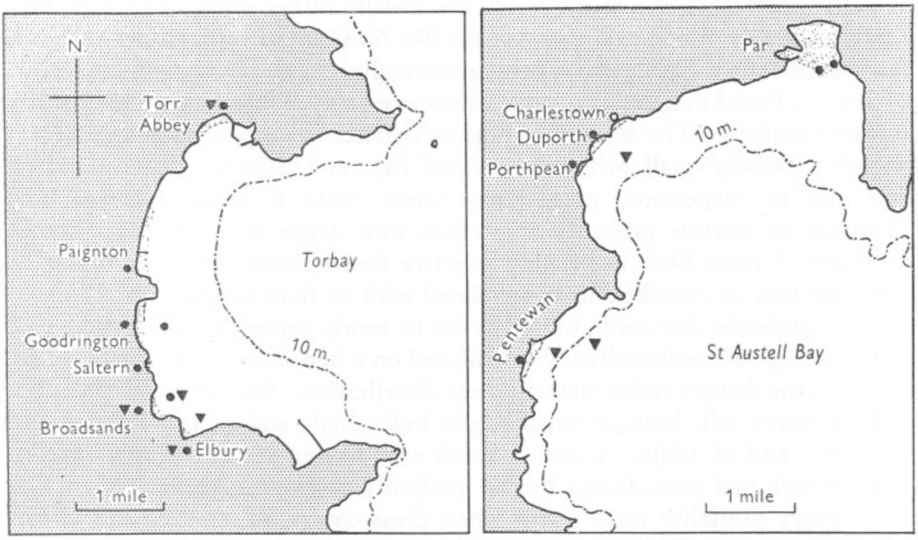

Fig. 5. Charts of Torbay and St Austell Bay, showing the distribution of *E. siliqua* (●) and *E. ensis* (▼). Beach samples are indicated on the land masses, offshore samples on the sea, the latter in their approximate positions. A negative record for Charlestown is also shown. Sandy beaches are stippled. The 10 m. depth contour is shown.

Other specimens have been taken in shallow water in Whitsand Bay and Plymouth Sound.

E. ensis occurs in small numbers at LWST in south-west England, but is much more common in depths of *c.* 10 m. (see Table VII, Appendix, and Ford, 1923). Single specimens have been taken in depths of 58·5 m. and 60 m. off Plymouth (Holme, 1953).

E. arcuatus occurs at LWST and has been recorded in 14·5 m. in Whitsand Bay. It is sometimes taken when dredging in the Eddystone shell gravel in *c.* 42 m. Ford (1923) records it from a number of stations in Plymouth Sound.

Moore (1936) has shown that *Echinocardium cordatum*, which lives in a similar habitat to *Ensis siliqua*, settles below low-water mark, and may subsequently migrate into the intertidal region. There is no evidence of a similar migration in *Ensis*. Although small specimens of *Ensis* were not often dug on the shore, they might easily have been missed since sieving methods were not employed. On those days when *Ensis* came out of the sand at low tide, small specimens of a size seldom taken when digging were sometimes seen. These would normally be missed because their burrows are inconspicuous, and they would rarely be taken during random digging. The only movements of populations so far recorded occur when *Ensis* are washed in during storms (p. 158).

Biotic Factors

The inhabitants of a sandy beach are usually rather sparse, and it is difficult to see that filter-feeding organisms like *Ensis* are in competition with one another for a food supply that is being continually renewed by water movements.

Ensis is found in habitats in which there are great differences in the quantity of food available. The amount of organic detritus in suspension over an open beach is usually small, while in enclosed bays and estuaries large quantities may be in suspension, particularly where there is much *Zostera*. The quantity of detritus probably also varies with depth of water and distance offshore. Unless *Ensis* is a highly selective feeder, there seems no reason to suppose that its distribution is correlated with its food supply.

It is probable that some toll of larvae or newly settled spat is inflicted by filter or deposit feeders already established on a beach, but this is more likely to affect the density rather than absolute distribution. Similarly, fish probably take a heavy toll, both of small whole individuals and of the siphons and posterior end of adults. I cannot recall ever having seen an empty shell of *Ensis* which had been drilled by the predatory gastropod *Natica*.

A heavy mortality must result when *Ensis* comes out of the sand at low tide (see p. 146). While some probably survive the exposure and burrow in again when the tide returns, many must be eaten by gulls.

Distribution on the Southern Side of the English Channel

The distribution and abundance of *Ensis* on beaches in Finistère and Jersey is rather different from that in south-west England. Although the grade of soil occupied by each of the three species is much the same as in England (Tables I–III), there are differences in tolerance of wave-exposure (Table IV).

In Jersey the tidal range is large, being 32·5 ft. (9·91 m.) at spring tides. The beaches are gently sloping in most places, so that the distance between high and low water may be as much as a kilometre or more. St Aubin's Bay and Grouville Bay are relatively exposed, but on such gently sloping beaches, mostly of firm fine sand, the depth of wave disturbance cannot be great (cf. King, 1951). In the middle of St Aubin's Bay (near Beach Rock), wave action is so severe as to exclude burrowing lamellibranchs, although small clumps of eel-grass (*Zostera*), indicating fairly stable conditions were found. Close to St Aubin's Fort, on the west side of the bay, where there is more shelter, *E. ensis* was found in some abundance, together with several *E. arcuatus*. This is the only beach on which *E. ensis* has been taken in any numbers. *Solen marginatus* Montagu also occurs, but at a slightly higher level on the beach.

In Grouville Bay, which is open to the east and only sheltered in this direction by isolated reefs, *E. arcuatus* and *E. ensis* were quite common near S. Etac, as was *Solen marginatus*.

These beaches differ from those in south-west England in the presence of *Ensis ensis* and *E. arcuatus* under more exposed conditions, in the absence or rarity of *E. siliqua* (none was found during 3 days' collecting), and in the abundance of *Solen marginatus*, which is restricted to sheltered conditions in muddy sand of estuaries, etc., in England.

E. arcuatus and *E. ensis* are fairly common on beaches in N. Finistère, but *E. siliqua* is not, being only found on one of the beaches investigated, S. Michel. Here *E. siliqua* was present in small numbers on the fairly exposed beach, together with many specimens of the pod-razor, *Pharus legumen major* Bucquoy, Dautzenberg & Dollfus, and *Mactra corallina cinerea*, in great abundance. *Ensis ensis* was not taken on this beach. Both *E. arcuatus* and *E. ensis* were found on the relatively sheltered beach at Térénès. At Goulven, a wide sandy beach some 5 km. across, the sand at the eastern, exposed, end is almost barren (one *Corystes cassivelaunus* was the only burrowing animal found). Towards the middle of the bay there are patches of *Zostera*, under conditions similar to those in which it was found in St Aubin's Bay, but no burrowing lamellibranchs were taken. In the middle of the bay there is slightly more shelter from the headland on the west side of the bay, but the sand is thrown up into ridges at right angles to the direction of wave incidence, evidence of considerable wave disturbance. On these ridges were found *Callista chione* (L.), *Donax variegatus* (Gmelin), *Spisula* sp., and *Ensis ensis* and *E. arcuatus* in small numbers. *Solen marginatus* is rare or absent on exposed beaches in Finistère, but is found in sheltered areas, as at Penpoull, in a habitat similar to that in which it occurs in S.W. England.

E. siliqua is also scarce farther south: in a survey of sandy beaches near Quiberon (S. Brittany), Prenant (1932) makes no mention of the occurrence of *E. siliqua*, although species living in a similar habitat, such as *E. ensis* and *Donax vittatus* (da Costa) are recorded. *Ensis siliqua* could hardly have been mistakenly identified as *E. ensis*.

Sea temperatures on either side of the Channel are given in Tables V and VI. The mean annual temperature at Plymouth and Jersey is almost the same, but the range of monthly means in Jersey is greater. At Roscoff the mean annual temperature is perhaps a little higher than at Plymouth, but the range of monthly means is much the same. Although the slightly higher summer temperatures on the southern side of the Channel may be important for the breeding of a species at the northern end of its range, such differences can hardly explain the differences in ecology of *Ensis* which ranges both north and south of the area. Another possible cause of the differences in ecology is discussed on p. 168.

TABLE V. MEAN MONTHLY AND ANNUAL SEA SURFACE TEMPERATURES FOR 1903–27 (° C.) AT THE NEAREST POSITIONS TO PLYMOUTH, JERSEY, AND ROSCOFF FOR WHICH SUCH DATA ARE AVAILABLE

(Data from Lumby, 1935.)

	50° 15′ N., 04° 15′ W. (Plymouth)	49° 08′ N., 02° 22′ W. (Jersey)	48° 52′ N., 04° 38′ W. (Roscoff)
Jan.	10·13	9·08	10·60
Feb.	8·70	8·06	9·83
Mar.	8·87	8·42	9·98
Apr.	9·43	9·29	9·74
May	10·96	11·45	11·10
June	12·88	13·75	12·43
July	15·16	15·59	14·72
Aug.	15·65	16·74	15·15
Sept.	15·02	16·27	14·22
Oct.	14·45	15·03	13·97
Nov.	12·76	12·86	12·90
Dec.	10·71	11·06	11·16
Mean annual	12·06	12·30	12·15

TABLE VI. MEAN MONTHLY AND ANNUAL SEA TEMPERATURES (° C.) AT PLYMOUTH AND JERSEY FOR THE YEARS 1947 TO 1951 INCLUSIVE

(Samples taken from the shore, daily. Data for Plymouth kindly supplied by G. H. Ivory and Partners, Plymouth; that for Jersey taken from the *Société Jersaise, Bulletin Annuel*, for 1948 to 1952.)

	Plymouth	Jersey
Jan.	9·0	6·9
Feb.	7·9	6·3
Mar.	8·3	7·3
Apr.	9·8	8·7
May	11·7	11·6
June	14·2	14·2
July	15·6	16·3
Aug.	16·6	17·6
Sept.	16·2	16·8
Oct.	14·7	14·6
Nov.	12·3	11·4
Dec.	10·2	8·9
Mean annual	12·2	11·7

NOTE ON THE LARVA OF *ENSIS*

All three species have a pelagic larva. Attempts at artificial fertilizations have not been entirely successful; adults collected during the spring of 1950 were never fully ripe, although Lebour (1938) states that *E. siliqua* breeds in early spring. A few larvae of each species were obtained, but only *E. ensis* was reared to metamorphosis. Shelled larvae, as described by Lebour, were obtained for all three species; these possess a large central cilium similar to that described by Lebour (1938, p. 139) for *Hiatella gallicana*, although Lebour states that no such cilium is present in *Ensis siliqua*.

Only a very few specimens of *E. ensis* were reared to metamorphosis, which took about 1 month at 13–15° C. The larvae were fed on Flagellate I, *Isochrysis galbana*. At metamorphosis these larvae had a shell length of *c.* 290 μ. A late larva was seen swimming by its velum and occasionally extending its foot: at this stage it will presumably settle under suitable conditions.

Discussion

The factors believed to be of importance in the distribution of species of *Ensis* may be summarized as follows. *E. siliqua* and *E. ensis* are restricted to sands of a fairly fine grade in which the percentages both of silt and of coarse particles are fairly low. *E. ensis* shows a rather greater tolerance of silt and of coarse particles than *E. siliqua*. *E. arcuatus* inhabits sands of a coarser grade, but has a wide tolerance of different grades, so that its distribution overlaps that of the preceding species to some extent.

Sands black below the surface are avoided by all species.

E. siliqua can withstand a moderate degree of wave-exposure, but is absent from fully exposed beaches. *E. arcuatus* and *E. ensis* are restricted to more sheltered beaches. The stability of the soil is an important factor in determining the occurrence of all species on fairly exposed beaches.

On the shore, *Ensis* occurs only below mean low-water mark of spring tides. Offshore, all three species are common in shallow water. *E. siliqua* occurs down to only *c.* 20 m., but the other species occur in small numbers in deeper water on the Continental Shelf. Where wave action is so severe as to exclude a species from a particular beach, it may occur below low-tide marks where disturbance is less extreme.

South of the English Channel *E. siliqua* is much less common, while the tolerance of *E. arcuatus* and *E. ensis* to wave action appears to increase, so that they are found on moderately exposed beaches.

There is no evidence that the mineralogical nature of the sand grains, their shape or surface texture, currents, food supply or other biotic factors influence the absolute distribution of the species, although certain biotic factors may influence population density.

Ecological factors may limit the distribution of a species, either through a direct lethal effect, or by their influence on the choice of a particular environment. In the latter instance the adult may be living well within the lethal limits imposed by the environment, due to the effect of some form of 'habitat-selection', and as a result of which not all habitats in which the individual could survive become populated (cf. Elton, 1935, pp. 40–1). In sedentary marine organisms there is some evidence that the distribution of the adult is partly related to a choice by the larva of a suitable substratum in which to metamorphose.

Postponement of metamorphosis until a suitable substratum is reached has been recorded for a number of species (summarized by Wilson, 1952), including at least one mollusc, *Teredo*. Although larvae of several species have been shown to respond to the nature or particle size of the substratum, it is possible that others are induced to settle in the vicinity of adults or newly settled spat of the same species (cf. Knight-Jones, 1951). If the larva reacts to some feature of the environment other than the presence of other individuals of the same species, suitably devised settling experiments should explain some features of distribution. No such experiments have so far been made owing to difficulties in rearing the larvae. If, however, the larva reacts to the presence of other individuals of the same species, or if there is no highly specific settling reaction, the distribution of adults must be explained in terms of conditions favourable or otherwise to the individual after settlement.

The preference of species of *Ensis* for soils of a particular grade may well be due to a larval settlement reaction. The three species are so similar in structure and habits that it seems likely that any one species could burrow into and live in any of the full range of soils inhabited by all species. Silt, alone, may be a limiting factor to survival of the adult. The high silt percentages tolerated by *Ensis ensis* may be lethal to the other species. Pratt (1953) has shown that the lamellibranch *Venus mercenaria* grows more rapidly in sand than in a muddy sand, and this may be explained by the observations of Loosanoff & Tommers (1948), who found that even small quantities of suspended silt decrease the filtration rate of oysters (*Ostrea virginica*), which would adversely affect their food intake.

Reducing conditions in the soil, which are probably lethal to the adult, might affect distribution either at the settling stage or through subsequent mortality of newly settled individuals.

It is hard to see that *Ensis* larvae could distinguish the normal conditions of wave-exposure on a beach. Abortive colonization of more exposed beaches probably occurs, perhaps during calm weather, and when normal conditions of wave-action return the spat are washed out of the sand.

Ensis is probably restricted to low spring-tide level on the shore because it is not adapted to withstand the fluctuations of temperature, salinity, etc., that occur higher up the beach, but no explanation can be offered of the restricted depth range of *E. siliqua* offshore. Certain other species, e.g. *Donax vittatus* and *Tellina fabula*, have a similar depth range to *Ensis siliqua*.

Previous work on the ecology of benthic animals provides little information on the precise effects of particular limiting factors. The importance of soil grade has long been recognized (e.g. Allen, 1899; Ford, 1923; Davis, 1925; Prenant, 1932; Powell, 1937), but most workers have directed their attention to a classification of species or 'communities' in relation to soil grade rather than to the study of the occurrence of individual species in different localities, as has been attempted here. The *range* of substrata inhabited by different species is very variable, but one may expect members of the infauna to be more restricted in their range than members of the epifauna. Powell (1937) considers that deposit feeders are more restricted in their choice of bottom than herbivores and suspension feeders, while carnivores appear to show no particular preference. Holme (1949*a*) has shown that the silt content of the soil has an important effect on the distribution of certain species on the shore.

Properties of sands other than particle size may also affect distribution. Wilson (1953) has shown the importance of 'attractive' or 'repellent' substances, possibly of organic origin, on the surface of sand grains for the settlement of the larvae of the polychaete *Ophelia bicornis*. Ekman (1947) has correlated the distribution of certain invertebrates with the firmness of the soil, as measured by a cone penetrometer. Preliminary experiments by the writer with a small cone penetrometer attached to the end of a slender rod have not been entirely satisfactory. It is essential that measurements be made in the undisturbed substratum, and not, as was done by Ekman, in a dish in which the sample has been allowed to settle for 24 hr. Under such conditions the original packing is not regained.

On the effects of wave action on burrowing organisms, there are little but general observations. It is generally accepted that wave action excludes many species from exposed beaches, and the importance of this factor is emphasized by Southward (1953).

Davis (1923) has shown that water movements in the North Sea may influence the distribution of settling larvae of *Spisula*. Settlement of spat in limited areas will occur only where the adults are more or less confined to isolated patches. In *Ensis*, where the adults of all species are widely distributed in coastal areas, there should usually be sufficient numbers of larvae in any one place for all suitable substrata to be occupied. A possible exception may be the Scilly Isles, where only *E. arcuatus* has been found, although there are undoubtedly patches of sand of a suitable grade for the other species. A few miles from the shore the bottom slopes away to some 80 m. depth, so it is unlikely that *E. ensis* and *E. siliqua* occur in any numbers in the vicinity of the islands. The Scilly Isles are 23 miles from the Cornish coast, so that the density of larvae of the latter two species in the Scilly Isles plankton is probably small. Consequently small patches of soil of a suitable grade may be only occasionally colonized by these species. Similarly, the relative scarcity of coarse-grade deposits in Great West Bay will result in a scarcity of breeding stock of *E. arcuatus*, so that suitable deposits in the area may not always be colonized.

Detailed observations have been confined to an area bordering the western half of the English Channel. The apparent differences in distribution on either side of the Channel makes one chary of applying conclusions to other areas, however. Temperature differences seem to be insufficient to account for the changes in distribution (pp. 163–4). There is probably little interchange between populations on either side of the Channel, so it is possible that races with different habitat-requirements occur. The western end of the English Channel is known to be an important boundary to the distribution of certain species (Ekman, 1953, pp. 81–2), and this boundary may be as much due to the geographical isolation of shallow-water species on each side as to temperature differences. Rees (1950) has shown that larvae of *Octopus vulgaris*, which have a pelagic life of at least a month, can spread to the south coast of England from breeding centres in the Channel Islands region, and one can presume that a similar interchange of *Ensis* populations does occur from time to time. Such interchange is probably on a restricted scale, and it is possible that different races could survive in spite of it.

Summary

An attempt is made to analyse the ecological factors affecting the distribution of the three European species of *Ensis*: *E. siliqua* (L.), *E. ensis* (L.) and *E. arcuatus* (Jeffreys).

All three species appear to be confined to European waters, but the exact limits of their range have not been established.

None of these species appears to occur outside Europe, but the North American *E. minor* Dall may be the same as *E. ensis*.

Soil grade is shown to be an important factor limiting distribution, although no species is narrowly confined to soil of a particular grade composition. Population densities are in general higher in soils approaching the 'average' grade inhabited by each species.

There is no evidence that the shape or mineralogical composition of the sand grains affects distribution.

All species avoid black, reducing, sands.

All species require some shelter from wave action, but *E. siliqua* can withstand much greater wave exposure than the other two. Tolerance of wave-action seems to depend on the stability of the beach deposits.

The three species are found at LWST on the beach, and in shallow water offshore. *E. siliqua* has a restricted depth range of *c.* 20 m., but the other species may be found in small numbers in deeper water.

Distribution in Jersey and Finistère differs from that in south-west England in greater tolerance of wave exposure by *E. arcuatus* and *E. ensis*.

Each species has a pelagic larva. *E. ensis* larvae were reared to metamorphosis in about a month.

The mode of action of limiting factors is discussed, and the results are considered in the light of previous work on the ecology of benthic invertebrates.

REFERENCES

ALLEN, E. J., 1899. On the fauna and bottom-deposits near the thirty-fathom line from the Eddystone grounds to Start Point. *J. Mar. biol. Ass. U.K.*, Vol. 5, pp. 365–542.

BLOOMER, H. H., 1905. On the anatomy of certain species of *Siliqua* and *Ensis*. *Proc. malacol. Soc. Lond.*, Vol. 6, pp. 193–6.

BUCQUOY, E., DAUTZENBERG, P. & DOLLFUS, G., 1887–98. *Les Mollusques Marins du Roussillon*, T. 2, 884 pp. Paris.

DALL, W. H., 1900. Synopsis of the Solenidae of North America and the Antilles. *Proc. U.S. Nat. Mus.*, Vol. 22, pp. 107–12.

DAVIS, F. M., 1923. Quantitative studies on the fauna of the sea bottom. No. 1. Preliminary investigation of the Dogger Bank. *Fish. Invest., Lond.*, Ser. 2, Vol. 6, No. 2, 54 pp.

—— 1925. Quantitative studies on the fauna of the sea bottom. No. 2. Results of the investigations in the southern North Sea, 1921. *Fish. Invest., Lond.*, Ser. 2., Vol. 8, No. 4, 50 pp.

EKMAN, S., 1947. Über die Festigkeit der marinen Sedimente als Faktor der Tierverbreitung, ein Beitrag zur Associationsanalyse. *Zool. Bidr. Uppsala*, Bd. 25, pp. 1–20.

—— 1953. *Zoogeography of the Sea*. 417 pp. London.

ELTON, C., 1935. *Animal Ecology*. 209 pp. London.

FORD, E., 1923. Animal communities of the level sea bottom in the waters adjacent to Plymouth. *J. Mar. biol. Ass. U.K.*, Vol. 13, pp. 164–224.

FORSTER, G. R., 1953. A new dredge for collecting burrowing animals. *J. Mar. biol. Ass. U.K.*, Vol. 32, pp. 193–8.

HATCH, F. H. & RASTALL, R. H. (revised M. Black), 1952. *The Petrology of the Sedimentary Rocks*, 3rd ed., 383 pp. London.

HOLME, N. A., 1949*a*. The fauna of sand and mud banks near the mouth of the Exe estuary. *J. Mar. biol. Ass. U.K.*, Vol. 28, pp. 189–237.

—— 1949*b*. A new bottom-sampler. *J. Mar. biol. Ass. U.K.*, Vol. 28, pp. 323–32.

—— 1950. The bottom fauna of Great West Bay. *J. Mar. biol. Ass. U.K.*, Vol. 29, pp. 163–83.

—— 1951. The identification of British species of the genus *Ensis* Schumacher (Lamellibranchiata). *J. Mar. biol. Ass. U.K.*, Vol. 29, pp. 639–47.

—— 1953. The biomass of the bottom fauna in the English Channel off Plymouth. *J. Mar. biol. Ass. U.K.*, Vol. 32, pp. 1–49.

KING, C. A. M., 1951. Depth of disturbance of sand on sea beaches by waves. *J. sediment. Petrol.*, Vol. 21, pp. 131–40.

KNIGHT-JONES, E. W., 1951. Gregariousness and some other aspects of the setting behaviour of *Spirorbis*. *J. Mar. biol. Ass. U.K.*, Vol. 30, pp. 201–22.

KRUMBEIN, W. C. & PETTIJOHN, F. J., 1938. *Manual of Sedimentary Petrography*. 549 pp. New York.

LEBOUR, M. V., 1938. Notes on the breeding of some lamellibranchs from Plymouth and their larvae. *J. Mar. biol. Ass. U.K.*, Vol. 23, pp. 119–44.

LOOSANOFF, V. L. & TOMMERS, F. D., 1948. Effect of suspended silt and other substances on rate of feeding of oysters. *Science*, Vol. 107, pp. 69–70.

LUMBY, J. R., 1935. Salinity and temperature of the English Channel. Estimation of mean values for the upper water layer over the 25-year period 1903 to 1927. *Fish. Invest., Lond.*, Ser. 2, Vol. 14, No. 3, 67 pp.

MADSEN, F. J., 1949. Marine bivalvia. *The Zoology of Iceland*, Vol. 4, Part 63, 116 pp.

MOORE, H. B., 1936. The biology of *Echinocardium cordatum*. *J. Mar. biol. Ass. U.K.*, Vol. 20, pp. 655–71.

PILSBRY, H. A. & McGINTY, T. L., 1943. *Ensis minor megistus* n. subsp., a West Florida razor clam. *Nautilus*, Vol. 57, pp. 33–4.

POWELL, A. W. B., 1937. Animal communities of the sea-bottom in Auckland and Manukau harbours. *Trans. roy. Soc. N.Z.*, Vol. 66, pp. 354–401.

PRATT, D. M., 1953. Abundance and growth of *Venus mercenaria* and *Callocardia morrhuana* in relation to the character of bottom sediments. *J. Mar. Res.*, Vol. 12, pp. 60–74.

PRENANT, M., 1932. Études de bionomie intercotidale. La baie et la pointe de Quiberon. *Trav. Sta. biol. Roscoff*, Fasc. 10, pp. 35–103.

PRUVOT, G., 1897. Essai sur les fonds et la faune de la Manche occidentale (Côtes de Bretagne) comparés à ceux du Golfe du Lion. *Arch. Zool. exp. gén.*, Ser. 3, T. 5, pp. 511–660.

REES, W. J., 1950. The distribution of *Octopus vulgaris* Lamarck in British waters. *J. Mar. biol. Ass. U.K.*, Vol. 29, pp. 361–78.

SOUTHWARD, A. J., 1953. The fauna of some sandy and muddy shores in the south of the Isle of Man. *Proc. Lpool biol. Soc.*, Vol. 59, pp. 51–71.

STILLMAN BERRY, S., 1953. West American razor-clams of the genus *Ensis*. *Trans. San Diego Soc. nat. Hist.*, Vol. 11, pp. 393–404.

WILSON, D. P., 1948. The relation of the substratum to the metamorphosis of *Ophelia* larvae. *J. Mar. biol. Ass. U.K.*, Vol. 27, pp. 723–60.

—— 1952. The influence of the nature of the substratum on the metamorphosis of the larvae of marine animals, especially of the larvae of *Ophelia bicornis* Savigny. *Ann. Inst. océanogr. Monaco*, T. 27, pp. 49–156.

—— 1953. The settlement of *Ophelia bicornis* Savigny larvae. The 1951 experiments. *J. Mar. biol. Ass. U.K.*, Vol. 31, pp. 413–38.

APPENDIX

TABLE VII. LIST OF LOCALITIES

The name of the locality is followed by the serial number of the soil sample, enabling cross-reference to Tables I–III to be made. The occurrence and density of the species is shown next, in brackets: A, *Ensis siliqua*; B, *E. arcuatus*; C, *E. ensis*. This is followed by a National Grid Reference to the station, or its latitude and longitude. The depth of water at offshore stations is also given.

Shore Collections

DEVON

Polesands, Exmouth. S.W. corner. 47 (A, scarce). 20/998792.

Dawlish. Mid-way between Dawlish and Langstone Pt. 74 (A, occasional). 20/971773.

Torr Abbey Sands. 139 (A, common), 140 (C, scarce), 141 (A, common). 20/912635.

Paignton beach, S. end. 10 (A, common). 20/896605.

Goodrington Sands. N. end of beach. 60 (A, common). 20/895598.

Middle of S. half of beach. 59 (A, common). 20/895593.

Saltern Cove. 53 (A, scarce). 20/896585.

Broadsands. N. end of beach. 11 (A, common; C, occasional). 20/897578.

Middle of beach. 2 (A, common; C, occasional). 20/897576.

Elbury Cove. 105 (C, scarce), 106 (A, common; C, scarce). 20/903570.

Salcombe, E. S. side of Millbay. 6 (A, occasional; B, occasional). 20/740382.

N. side of Millbay. 3 (B, common), 12 (B, common; C, occasional), 63 (A, scarce). 20/740383.

Salcombe, W. 200 yd. S. of Marine Hotel. 64 (B, scarce). 20/738385.
Woodville Rocks. 65 (B, scarce), 163 (C, scarce). 20/736384.
Yealm River. Cellars beach. 70 (B, occasional), 71 (B, occasional), 72 (C, scarce). 20/531476.
Below Passage Wood. 69 (B, scarce). 20/537476.
Yealm sand bank. 1 (B, common). 20/539481.
Thorn Pt. 171 (B, scarce). 20/542490.
Drake's Island. E. end of N. side. 172 (A, scarce; C, scarce). 20/470529.
E. side. 173 (B, occasional). 20/471528.
E. of pier. 174 (C, scarce), 176 (A, scarce). 20/469529.
W. of pier. 175 (A, scarce; B, occasional; C, occasional). 20/468529.

CORNWALL

Whitsand Bay, Sharrow Pt. 117 (A, scarce). 20/393521.
Par Sands. E. end of beach. 68 (A, common). 20/087524.
Nr. Callyvador rocks. 66 (A, occasional). 20/083524.
Duporth. 62 (A, common). 20/036511.
Porthpean. 61 (A, scarce). 20/033507.
Pentewan. 136 (A, occasional). 20/019464.
Helford River, Gate Beach. 24 (C, occasional). 10/760268; 36 (C, occasional), 38 (A, occasional), 40 (C, occasional), 41 (A, scarce; C, occasional), 164 (B, scarce), 165 (A, occasional; B, scarce; C, occasional). 10/762268.
Flushing Cove (Gillan harbour). 56 (B, scarce). 10/787252. 54 (C, scarce), 55 (A, common; C, occasional), 57 (B, scarce), 58 (A, scarce), 162 (C, occasional). 10/784252.
Marazion. 52 (A, common). 10/509309.

SCILLY ISLES

Tresco, E. of Rushy Pt. 50 (B, common). 00/903151.
Tresco-Bryher channel. 120 (B, common), 121 (B, common). 00/886145. 122 (B, common), 00/886144. 130 (B, common). 00/884149. 131 (B, common). 00/884152.
Foreman's Island. 126 (B, common). 00/901158. 127 (B, common). 00/901160. 128 (B, occasional). 00/900161. 129 (B, common). 00/898162.

AYR

Fairlie Sands. 18 (A, common). 26/196541.

NORTHUMBERLAND

Newton Haven. 19 (B, common). 46/247241.

PEMBROKE

Dale Flats. 25 (A, occasional), 12/813058. 73 (A, common). 12/814060.

CHANNEL ISLANDS

Grouville Bay. 7 (C, scarce), 9 (B, common), 16 (B, occasional; C, scarce). 49° 10′ 25″ N., 02° 00′ 45″ W.
St Aubin's Bay. 15 (B, scarce), 21 (C, common). 49° 11′ 00″ N., 02° 09′ 35″ W.

FINISTÈRE

Penpoull. 145 (C, occasional). 48° 41′ 42″ N., 03° 57′ 00″ W.
Térénès. 147 (C, scarce), 149 (B, scarce; C, scarce). 48° 40′ 45″ N., 03° 51′ 12″ W.
Grève de S. Michel. 155 (A, occasional). 48° 41′ 15″ N., 03° 36′ 00″ W.
Grève de Goulven. 156 (C, scarce), 157 (B, occasional), 158 (B, common). 48° 39′ 40″ N., 04° 15′ 00″ W.
Perharidy. 159 (B, occasional). 48° 43′ 55″ N., 04° 00′ 06″ W.

TABLE VII (*cont.*)

Grab and Dredge Samples

Great West Bay. Station 12. 27 (C, occasional). 50° 35′ 12″ N., 03° 26′ 25″ W. 5·5 m.
Station 16. 29 (C, occasional). 50° 34′ 40″ N., 03° 26′ 48″ W. 10·5 m.
Station 17. 28 (C, occasional). 50° 34′ 25″ N., 03° 27′ 05″ W. 10·5 m.
Station 19. 30 (C, common). 50° 33′ 10″ N., 03° 27′ 00″ W. 16·5 m.
Torbay. Station 9. 167 (A, common; C, occasional). 50° 24′ 30″ N., 03° 32′ 54″ W. 3·2 m.
Station 18. 169 (A, occasional). 50° 25′ 24″ N., 03° 33′ 12″ W. 6·1 m.
Station X. 170 (C, occasional). 50° 24′ 12″ N., 03° 32′ 36″ W. *c.* 5·0 m.
Plymouth. 22 (A, common). 50° 15′ 45″ N., 03° 53′ 00″ W. 20 m.
116 (C, scarce). 50° 10′ 00″ N., 04° 10′ 00″ W. 60 m.
113 (C, scarce). 50° 15′ 00″ N., 04° 12′ 30″ W. 49 m.
32 (C, scarce). 50° 11′ 00″ N., 04° 05′ 00″ W. 58·5 m.
31 (B, scarce; C, occasional). 50° 19′ 42″ N., 04° 14′ 45″ W. 14·5 m.
St Austell Bay. 33 (C, occasional). 50° 17′ 15″ N., 04° 46′ 18″ W. 9 m.
34 (C, occasional). 50° 17′ 24″ N., 04° 45′ 42″ W. 13 m.
35 (C, occasional). 50° 19′ 30″ N., 04° 45′ 06″ W. 6 m.
Aberporth Bay. 160 (C, common). 52° 08′ 48″ N., 04° 31′ 48″ W. 13 m.
Irish Sea. 14 (C, occasional). *Approx.* 54° 23′ N., 03° 35′ W.

'*Negative*' *Records*

Records of sandy beaches on which no *Ensis* was found. Where the beach was examined on a very low spring tide, the name is in italics. The probable reasons for absence of *Ensis* are given thus: R, black, reducing sands; S, shifting, unstable sands; E, wave action extreme; L, lowered salinity owing to fresh water running over the beach at low tide. *, beaches where *Ensis* may have been washed up from deeper water, most of the beach being barren.

DEVON
Exmouth, nr. Maer Rocks. R. (30/010798.)
Polesands.* S. (30/002794.)
Salcombe, S. of Millbay. S. (20/737379.)
North Sands. L? (20/731381.)
South Sands. L? (20/729377.)
Borough Island and Challaborough Bay. E. (20/655439, 648443, 648448.)
Mothecombe. R., L? (20/612471.)
Bovisand. R. (20/492506.)
Saunton Sands (N. Devon). E. (21/435345–438378.)

CORNWALL
Whitsand Bay.* E. (*ca.* 20/407510.)
Charlestown. L? (20/040514.)
St Michael's Mount. R. (10/515303.)

SCILLY ISLES
Bryher, two beaches at S.W. end of island. E. (00/873141, 876140.)

JERSEY
St Aubin's Bay (middle). E. (49° 11′ 18″ N., 02° 08′ 42″ W.)

FINISTÈRE
Grève de Goulven (E. end). E. (48° 39′ 48″ N., 04° 14′ 00″ W.)
South of Isle de Sieck. E? (48° 42′ 00″ N., 04° 04′ 30″ W.)