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THE SPREAD OF *ELMINIUS MODESTUS* DARWIN IN NORTH-WEST EUROPE

By D. J. Crisp

Marine Biology Station, University College of North Wales

(Text-figs. 1–9)

The presence in northern waters of the Australasian barnacle *Elminius modestus* was first noted by Bishop (1947). In the course of examining some bakelite plates, which had been exposed to fouling in Chichester Harbour, he found a settlement of barnacles which differed from all indigenous species in having only four instead of six compartments. They agreed in every respect with Darwin's description of *E. modestus*. The settlement of many spat on this one plate indicated that the species was well established at least in Chichester Harbour. Crisp & Chipperfield (1948) stated that the species was present in 1947 along the whole of the south-east of England, that it had been present in the River Crouch since 1945, and had appeared also in South Wales. They also commented that the habitats favoured by the species in Britain were similar to those which it occupied in New Zealand (Moore, 1944). Knight-Jones (1948) reported that the prevalence of *Elminius* in the River Crouch constituted a further threat to the Essex oyster beds; he also recorded it from the Helford River in Cornwall. Fig. 1 shows the known distribution at the end of 1947, and at the time of writing (1956).

It is clear that the species must have occurred in Britain for several seasons prior to 1945 when it was present already at two widely separated places, viz. Chichester Harbour and the River Crouch. Stubbings (1950) has confirmed its prior occurrence in the Portsmouth area, based on examination of material collected before 1945, but it is not possible to give any precise information as to the year of its arrival there.

The earliest stages of colonization have therefore escaped notice, perhaps inevitably in view of the closing of the beaches of southern England during the war. It seems not improbable that the establishment of the species had some connexion with unusual conditions at the outbreak of war, in so far as they affected shipping from Australasia. It is, moreover, fairly certain that *E. modestus* was not prevalent at this time in many areas where it was very abundant in 1946.

Table 1 brings together several pieces of evidence to this effect, all based on the examination of material collected prior to 1940. This material consisted chiefly of shells and other substrata collected both from shallow dredge hauls

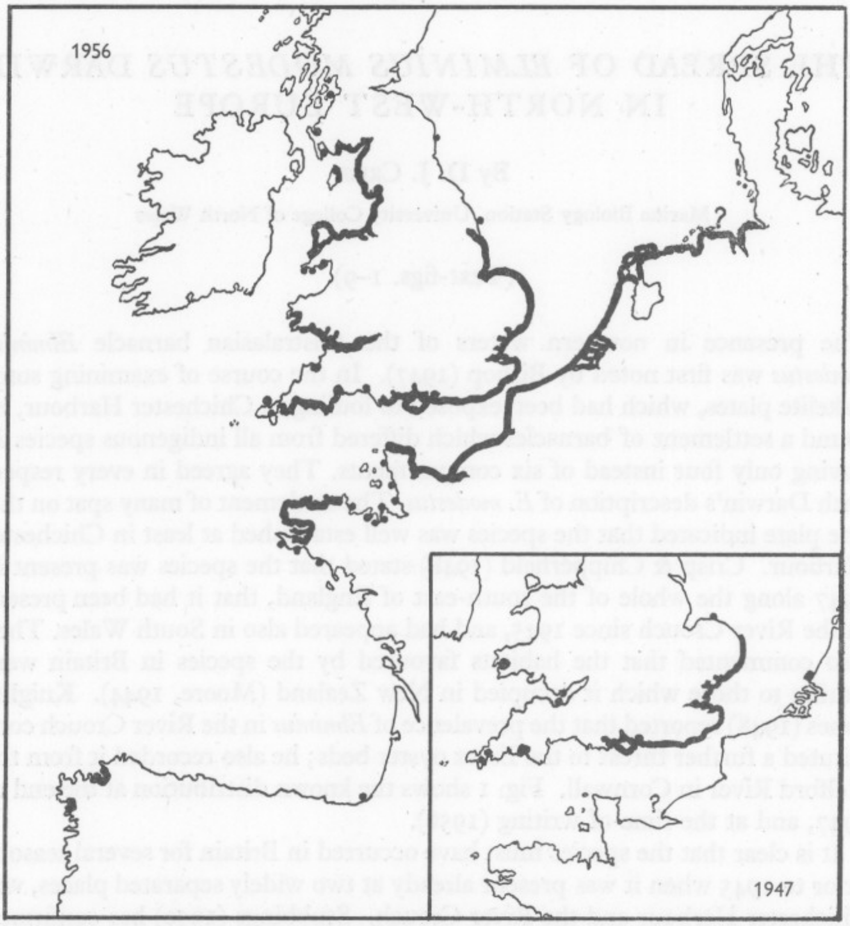

Fig. 1. Parts of the coast of Europe on which *Elminius modestus* was known to have been present in 1956, shown by a thickening of the coastline. Inset, same for 1947.

TABLE 1. OBSERVATIONS ON BARNACLE SETTLEMENT PRIOR TO 1940

Source of material	No. of barnacles found
River Alde, 1931. Shells and stones from low-water mark	*Balanus balanoides* 111 *B. crenatus* and *improvisus* 86 *B. porcatus* 1
Whitstable, 1937. Dredged shells	*B. improvisus* 1500
Tollesbury, 1939. Scrapings from piles	*B. balanoides* 33 *B. improvisus* 4
Steeple stone, River Blackwater, 1938. Scrapings from stones near low-water mark	*B. balanoides* 252 *B. improvisus* 2
Southend, 1938. Plankton hauls	*B. balanoides, B. crenatus* and *B. improvisus* larvae only

and from the shore, but also included a series of plankton samples taken from the Thames estuary at Southend throughout 1938 (Wells, 1938). In the plankton samples taken in the early part of the year, numerous larvae of *Balanus balanoides* and *B. crenatus* were identified, while in those taken during summer *B. improvisus* larvae were abundant (Jones & Crisp, 1954), but no *Elminius modestus* larvae were found in any of them.

Since 1946 a careful watch has been kept on the distribution of *E. modestus* in Britain. Quantitative records of its population density have been made repeatedly at numerous easily accessible stations along the coast of Great Britain, while visits have been made to those parts of the coast from which it has hitherto been absent as frequently as time and opportunity have permitted, in order to check its spread into new areas.

Changes are still going on. However, it seems unlikely that further changes will materially alter the general principles which follow from observations made up to the end of 1955. Nor is it likely that any new records will now be discovered to throw light on the early history of its arrival in British waters. It is therefore opportune to describe such changes as have been observed up to the present time.

The work reported in this paper was partly carried out during the period of my employment by I.C.I. Ltd. Paints Division, to whom I am indebted for access to my notes and records. I am also indebted to many colleagues who have from time to time given me information about the species, and whose records appear in the detailed appendix at the end of this paper. The work also constituted a part of a general investigation of British shores, for which generous grants were received from the Browne Fund of the Royal Society.

CHANGES IN DISTRIBUTION SINCE 1946

SOUTH-EAST ENGLAND

Records of the distribution of *Elminius* between the Isle of Wight and the Thames indicate no major change since 1946, as the species was already well established in the area at that time. Nevertheless, there is evidence that between 1946 and 1950 it was increasing steadily in abundance. This is demonstrated in Table 2A which gives the annual spatfall of *Elminius* during this period based on counts of numbers settling on regularly changed surfaces. The figure for 1946 is not entirely comparable with the others, since it was taken in the Blackwater, at West Mersea, a few miles to the north of the River Crouch where the rest of the observations were made. The Blackwater is probably not a more suitable river for *Elminius* than the Crouch, yet the records for 1946 in the Blackwater indicated a heavier spatfall than those for 1947 in the Crouch. This suggests that the severe winter of 1946–47 had an adverse effect. The lack of correspondence between the settlement on continuously submerged panels on a raft and on plates exposed between the tide-marks, especially between 1949 and 1950, is difficult to account for. The intertidal exposures probably give the best comparisons year by year, as they were made at the same place and in the vicinity of previously settled individuals, which are known to encourage settlement (Knight-Jones & Stevenson, 1950; Knight-Jones & Crisp, 1953; Knight-Jones, 1953). The settlement on plates exposed on the raft may have varied with its location in the tideway (it was shifted slightly from time to time) and with the amount of settlement already on it. Indeed, the spatfall in different parts of the river may show considerable

TABLE 2A. TOTAL ANNUAL SETTLEMENTS OF *ELMINIUS MODESTUS* IN ESSEX AREA AS TOTAL SPAT RECORDED PER SQUARE CENTIMETRE

Year	Settlement at low water	Settlement on raft	Location
1946	97	—	West Mersea
1947	28	1·9	Burnham-on-Crouch
1948	165	3·9	”
1949	531	59·4	”
1950	284	421	”

TABLE 2B. TOTAL ANNUAL SETTLEMENTS OF *ELMINIUS MODESTUS* BASED ON RECORDS GIVEN BY KNIGHT-JONES (1952)

Allowance has been made for the fact that his records do not cover the whole of the settling season. The figures below are therefore estimates only but probably correct in orders of magnitude. Units, number per square centimetre per season.

Locality	1947	1948	1949
Fambridge	0·2	42	160
Purleigh	—	55	53
Althone creek	—	4·7	—
Creeksea	—	27	410
Bush shore	72	270	470
Broadrakes	—	11	167
Shop laying	0·8	12	260
Pagglesham pool	—	3·1	—
Roach mud	—	0·75	9·8
Mean	24	47	219

variation, as demonstrated by Knight-Jones (1952). His observations from 1947–49 are given in Table 2B. They have been modified from the form given in his paper to make them directly comparable with those of Table 2A. Creeksea and Bush shore, about a mile, respectively, to the east and west of Burnham received the heaviest settlement indicating that this area, which is close to that on which Table 2A is based, represents the most heavily infested part of this river. It is interesting also to note from Knight-Jones's data that the proportionate increases in number settling, between 1947 and 1949, were greater in the upper parts of the river (e.g. Fambridge and Shop laying), where settlements were small, than in the more heavily infested part of the river nearer to its mouth. This suggests that the original colonies were probably located near the mouth, and that the species spread upstream, towards Fambridge and Battlesbridge, as the substrata available near the mouth became fully covered. Intertidal observations indicated that there was an increase in density of adults corresponding to the increase in numbers setting during the same period. For example in 1947 the barnacle population on wooden piles was composed of 10–15% *Elminius* and 85–90% *Balanus balanoides* at mean tide level. On small scoured stones from which barnacles were constantly removed by abrasion *Elminius* already constituted about 90% of the population. By 1949 *Elminius* everywhere outnumbered *Balanus balanoides* several times, and was practically the only barnacle found on small stones on the foreshore.

Similar increases were noted at Whitstable and Ramsgate between 1947 and 1951. On the other hand, no significant changes were seen elsewhere on the south coast, although observations were made at a number of places such as Hastings, Bexhill, Eastbourne, Brighton and Bognor during 1947–48 and between 1953–54. In sheltered areas, particularly those with wood and stone substrata, *Elminius* was everywhere abundant, but on more exposed parts of the coast, especially on wave-cut chalk reefs, such as those near Beachy Head and Seaford, *Elminius* was present only in scattered groups and was less common than *Balanus balanoides*.

Elminius has spread northward along the east coast during the past 10 years, as shown in Fig. 2. In 1947 it was fairly common as far north as Lowestoft, with isolated individuals recorded on the shores of the Wash at Brancaster, Hunstanton and Skegness. During 1948 and 1949 extensive settlements occurred in the Wash, so that by the end of 1949 *Elminius* had become the dominant intertidal species. The rivers entering the Wash were also heavily infested. In 1950 *Elminius* was abundant at such places as Kings Lynn, Holbeach and Fosdyke. It continued to spread northward. In 1948 isolated individuals were already present on piles at the extreme end of the pier at Cleethorpes, though none were to be found on the foreshore at Mablethorpe and Sutton-on-Sea. In 1950–51 *Elminius* became common along the whole of the Lincolnshire coast, as far as the entrance to the Humber at Cleethorpes. A single individual was found at Hornsea in 1953, but a further search in 1955 failed to reveal any *Elminius* on the Holderness coast, save within the Humber itself, a small number having been found at Paull and Kingston-upon-Hull. The only record of *Elminius* north of Hornsea is of one individual on a mussel shell from Blythe (Bull, 1950). This was evidently only a transient settlement, since it has not been followed by any general invasion of the area.

The advance of *Elminius* has therefore been halted abruptly at the mouth of the Humber. Three possible factors may be put forward to account for the failure of the species to spread further. (i) The residual currents flow southward off the Holderness coast, thus opposing the dispersal of larvae northward (Tait, 1938; Edgell, 1943). (ii) There are no rock substrata, and little or no artificial substrata suitable for barnacles for some 30 miles of coast north of Spurn Head. The abrasion on this part of the coast is moreover very severe. At Withernsea abrasion appears to have prevented anything but *Enteromorpha* sp. from attaching to the groynes even towards low-water mark. (iii) The Humber, unlike the Wash, is not a suitable area for *Elminius*, probably on account of

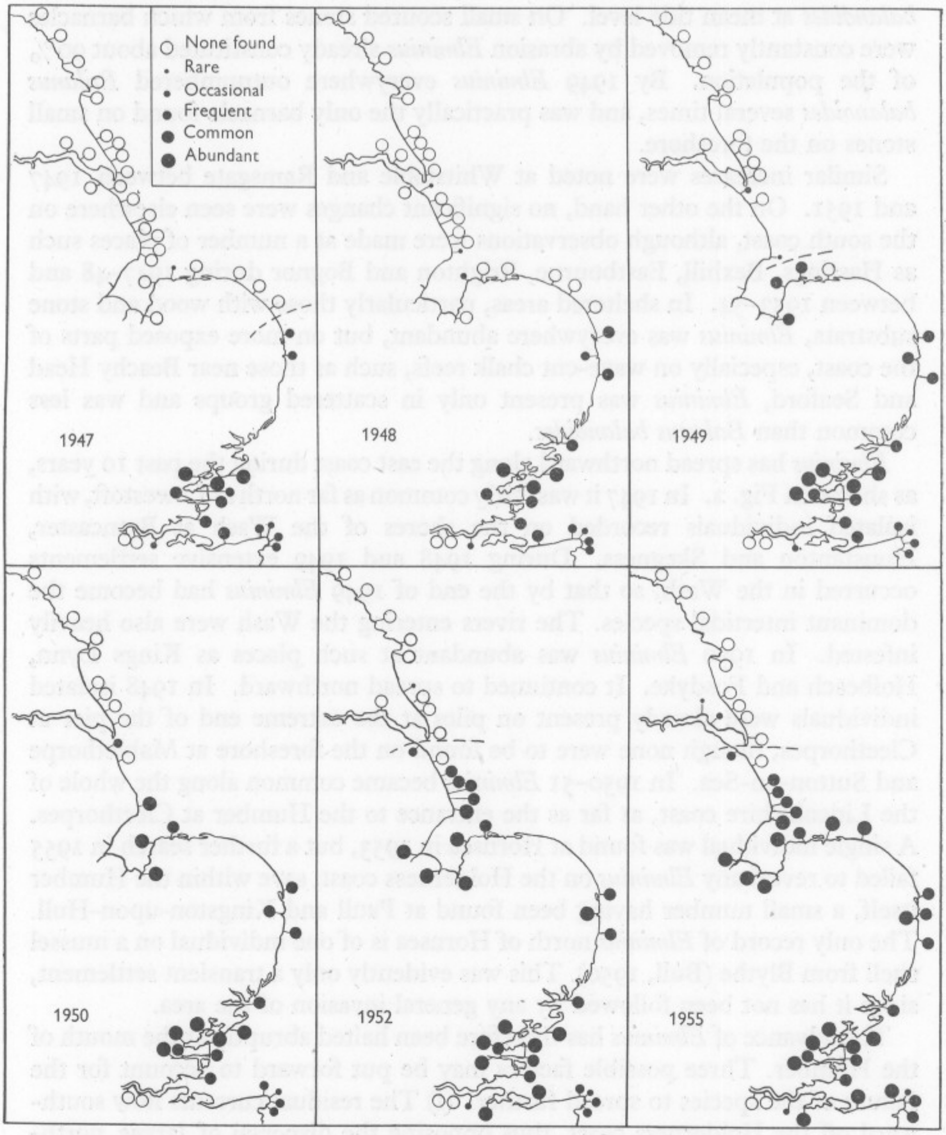

Fig. 2. Changes in the distribution of *Elminius* on the east coast from 1947 to 1955.

the pollution of the estuary. *Elminius* has not set up a dense population there, as it did in the Wash, and so may not be able to produce enough larvae to bridge the unfavourable Holderness coast.

It should be mentioned that many parts of the Yorkshire coast north of the Humber, particularly such places as Bridlington and Whitby, appear intrinsically suitable for *Elminius*, though sea-water temperatures north of the Humber are low, not usually exceeding 13–14° C in summer, and therefore unfavourable for rapid breeding.

SOUTH-WEST ENGLAND

In 1946 *Elminius* was common all along the south coast as far west as Poole Harbour. It was then rather rare at Swanage, and absent from the greater part of the Dorset coast, except for a possible centre discovered in 1947 at Weymouth (Fig. 3). By 1952 *Elminius* had become common at Swanage and Weymouth, and had appeared in smaller numbers in many of the intermediate anchorages, such as Kimmeridge Bay, Lulworth Cove, etc. Nevertheless, it has not spread westwards from Portland Bill. Apart from three specimens taken in West Bay in 1948, none has been found between Portland and Exmouth, despite repeated visits to the area. Whatever population once existed, none was found in West Bay in 1950 or in 1953.

Beyond the River Exe, *Elminius* is for the greater part confined to estuaries and drowned valleys, and absent from the open coast. Its first appearance in the area was at Plymouth in 1946. The following year an entirely separate colony was reported from the Helford River (Knight-Jones, 1948), and scattered individuals were found in Torbay late in 1947. It has since appeared in all the estuaries that have been examined between Helford and the Exe, but as it has not settled on the open coast, save as scattered individuals, it has spread somewhat erratically from one river estuary to another. For example, it became common to the west of Plymouth, in the rivers Fowey and the Looe in 1949, and to the east, in the Yealm (1948), Erme, Avon, Salcombe and Dart (1949). The Teign and Exe estuaries were colonized later, in 1949–50 and 1951, respectively. It therefore seems likely that Plymouth was the original centre of this dispersal, since the species appeared there as early as 1946 and achieved, by 1950, an average density of from 0·5–2·0 individuals per square centimetre on rocks and piles below mid-tide level in the rivers Plym and Tamar. Its colonization of these rivers may have been made easier by the widespread reduction in numbers of *Balanus balanoides* whose niche it has apparently filled (Southward & Crisp, 1952, 1954).

A significant feature of the spread into all the above rivers has been that the denser populations appeared first, and continued to increase, some distance upstream of the mouth. Gweek and Porth Navas in the Helford River and Greenway and Galmpton on the River Dart are good examples of sites where these early colonies developed, as shown in Fig. 4. The colonies in

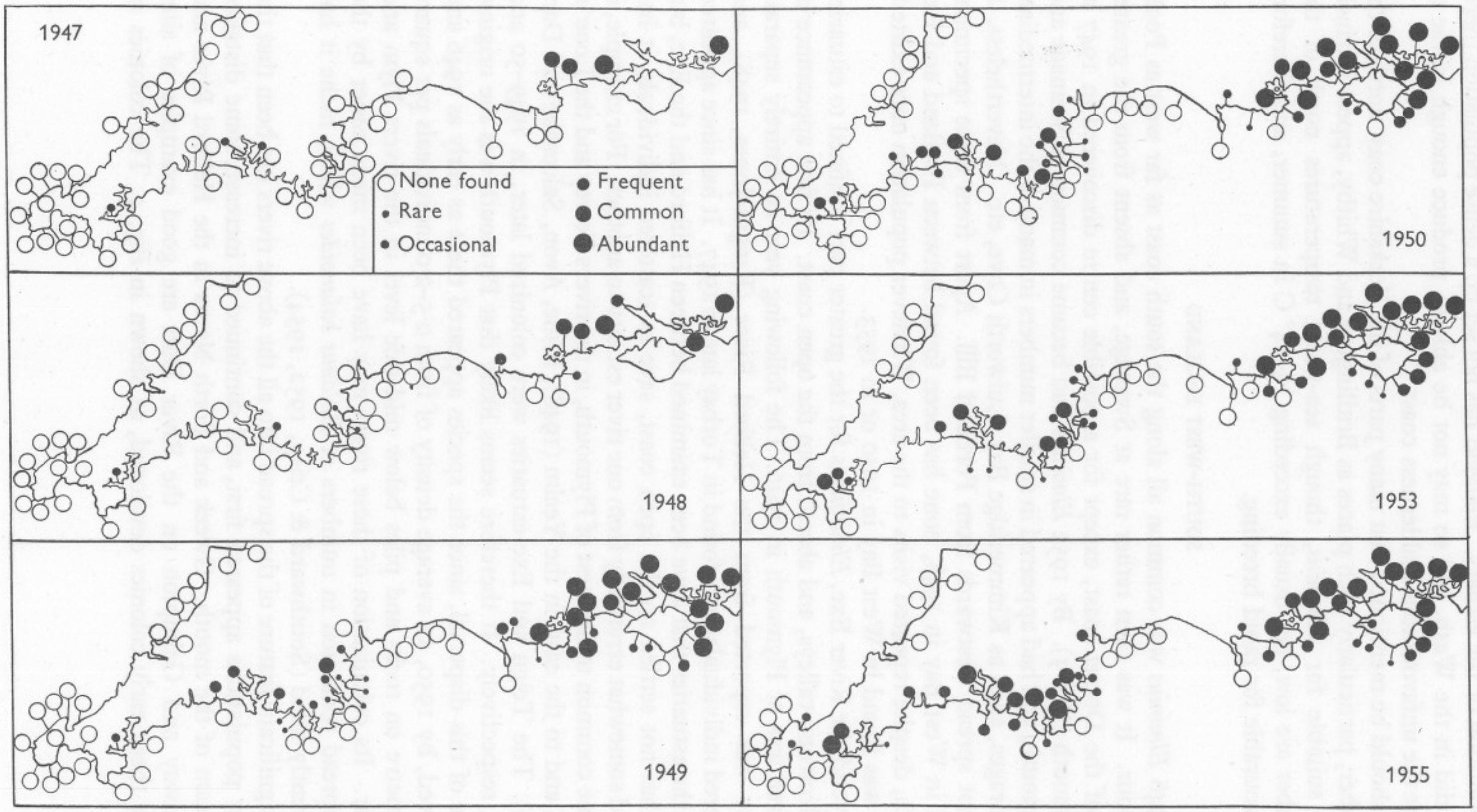

Fig. 3. Changes in the distribution of *Elminius* on the south-west coast from 1947 to 1955.

each estuary must therefore have become established and increased independently.

The spread of *Elminius* westwards from the Helford River into Penzance Harbour and on to St Ives occurred between 1951 and 1955, some years after it had first been found in the Helford River system.

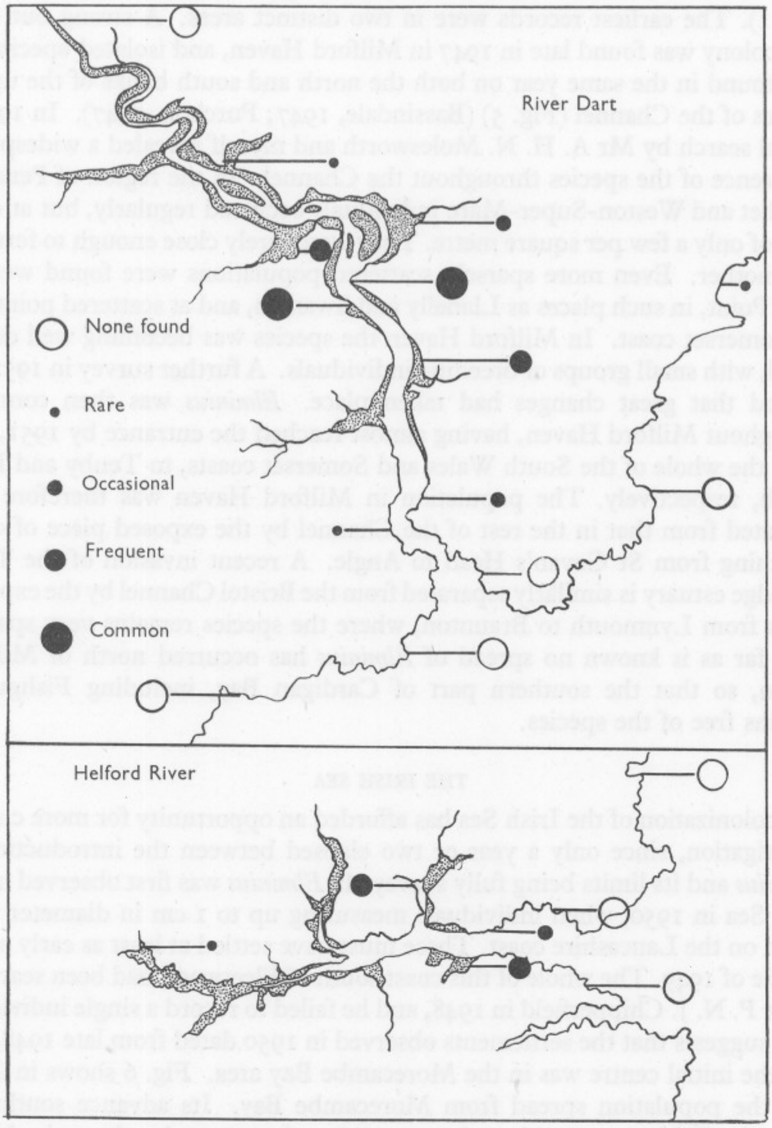

Fig. 4. The distribution of *Elminius* in the River Dart in 1949 (above) and in the Helford River in 1950 (below) to show where the first colonies develop in this type of estuary.

THE BRISTOL CHANNEL

The colonization of the Bristol Channel probably commenced at about the same time as that of Plymouth Sound. It arose as an independent population separated from those farther south by the unfavourably exposed coast of north Cornwall, which remains still for the greater part free of *Elminius* (Fig. 1). The earliest records were in two distinct areas. A strong but very local colony was found late in 1947 in Milford Haven, and isolated specimens were found in the same year on both the north and south banks of the upper reaches of the Channel (Fig. 5) (Bassindale, 1947; Purchon, 1947). In 1949 a careful search by Mr A. H. N. Molesworth and myself revealed a widespread occurrence of the species throughout the Channel. In the region of Penarth, Watchet and Weston-Super-Mare individuals occurred regularly, but at densities of only a few per square metre. They were rarely close enough to fertilize one another. Even more sparsely scattered populations were found west of Nash Point, in such places as Llanelly and Swansea, and at scattered points on the Somerset coast. In Milford Haven the species was becoming well established, with small groups of breeding individuals. A further survey in 1952–53 showed that great changes had taken place. *Elminius* was then common throughout Milford Haven, having almost reached the entrance by 1951, and along the whole of the South Wales and Somerset coasts, to Tenby and Lynmouth, respectively. The population in Milford Haven was therefore still separated from that in the rest of the Channel by the exposed piece of coast stretching from St Gavan's Head to Angle. A recent invasion of the Taw–Torridge estuary is similarly separated from the Bristol Channel by the exposed coasts from Lynmouth to Braunton, where the species remains very sparse.

So far as is known no spread of *Elminius* has occurred north of Milford Haven, so that the southern part of Cardigan Bay, including Fishguard, remains free of the species.

THE IRISH SEA

The colonization of the Irish Sea has afforded an opportunity for more critical investigation, since only a year or two elapsed between the introduction of *Elminius* and its limits being fully surveyed. *Elminius* was first observed in the Irish Sea in 1950, when individuals measuring up to 1 cm in diameter were found on the Lancashire coast. These must have settled at least as early as the middle of 1949. The whole of this coast south of Fleetwood had been searched by Dr P. N. J. Chipperfield in 1948, and he failed to record a single individual. This suggests that the settlements observed in 1950 dated from late 1948, and that the initial centre was in the Morecambe Bay area. Fig. 6 shows in detail how the population spread from Morecambe Bay. Its advance southward along the Fylde was rapid, and was continued westwards, along the North Wales coast, at a rate of some 30 km each year. Its advance northward along the Cumberland coast was less rapid until it reached the Solway, whence it appears to be spreading westwards more rapidly. No doubt the extensive sands of the Fylde were beneficial in producing summer temperatures higher

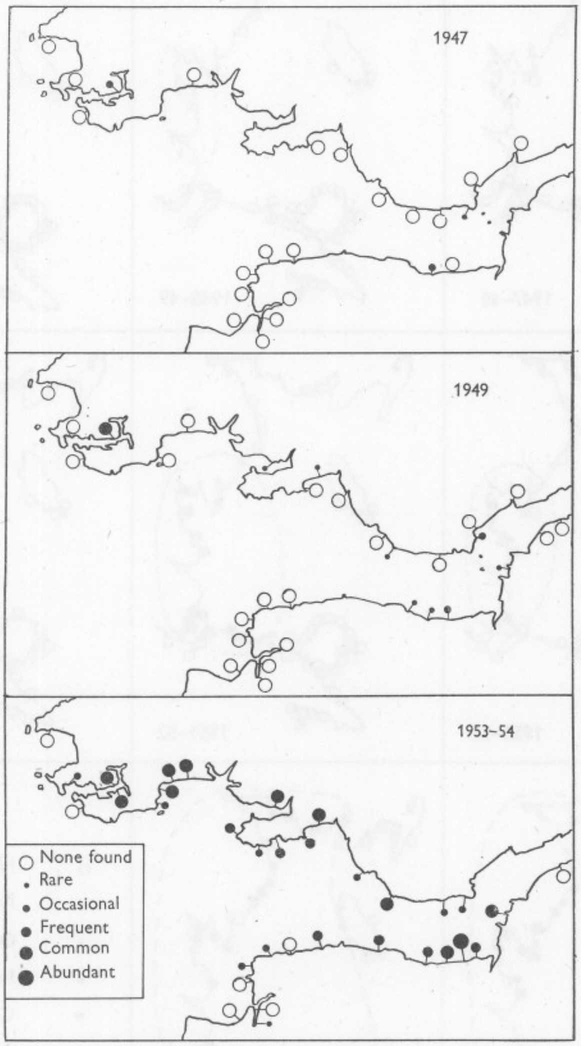

Fig. 5. Changes in the distribution of *Elminius* in the Bristol Channel from 1947 to 1954.

than those of the Cumberland coast, apart from the Solway. Perhaps more important, however, was the influence of residual drifts which are believed to flow southward along much of the Cumberland and Lancashire coasts and westwards along the Galloway and North Wales coast (Williamson, 1956).

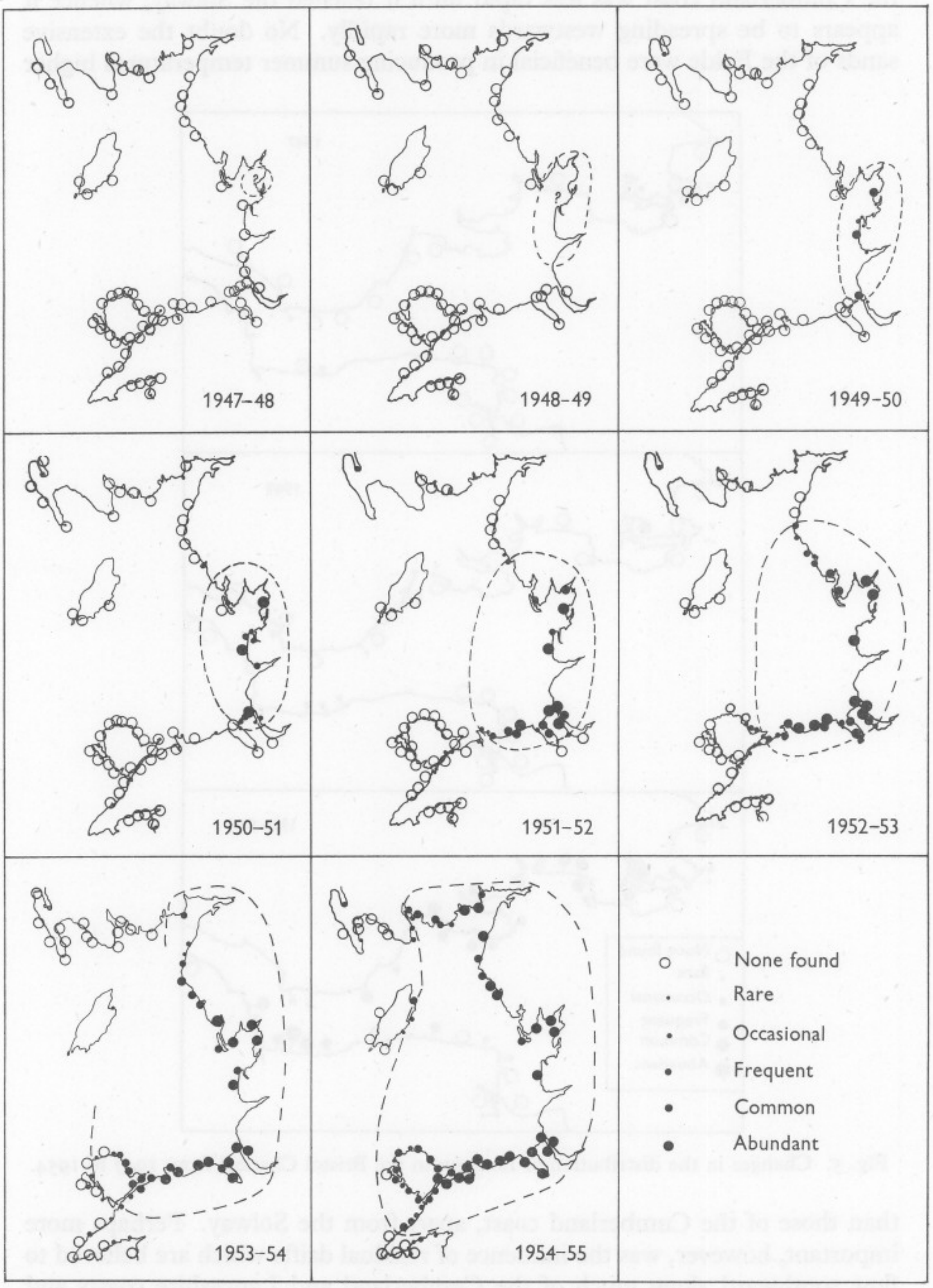

Fig. 6. Changes in the distribution of *Elminius* in the Irish Sea from 1948 to 1955.

Elminius has not advanced uniformly. Its advance has shown different patterns under differing hydrographical conditions. Along the north coast of Wales, from Rhyl to Bangor, the advancing population formed at any point of time a clearly marked front extending along a short stretch of the shore. Within a distance of about 20 km the density of the population fell from more than

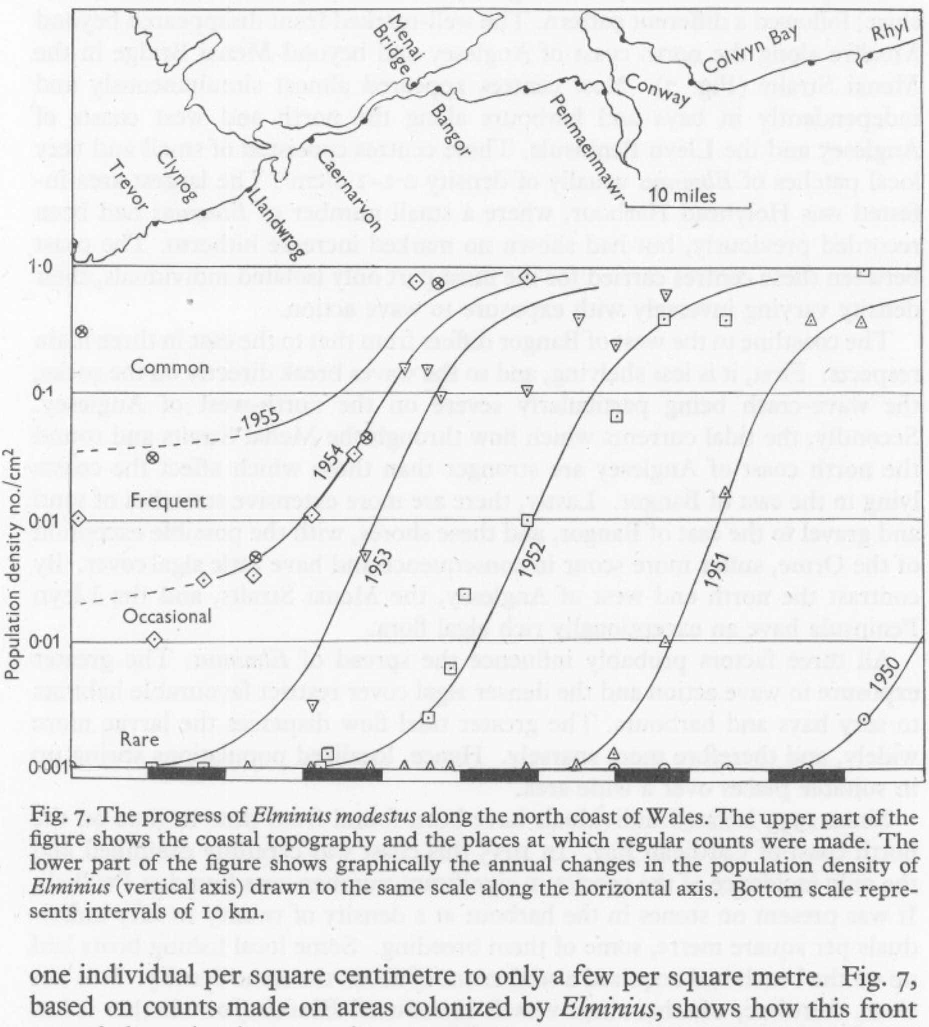

Fig. 7. The progress of *Elminius modestus* along the north coast of Wales. The upper part of the figure shows the coastal topography and the places at which regular counts were made. The lower part of the figure shows graphically the annual changes in the population density of *Elminius* (vertical axis) drawn to the same scale along the horizontal axis. Bottom scale represents intervals of 10 km.

one individual per square centimetre to only a few per square metre. Fig. 7, based on counts made on areas colonized by *Elminius*, shows how this front spread along the shore year by year. The proportion of young individuals was greater at the advancing edge of the front, particularly during August and September, when the spatfall often covered the greater part of areas left bare by other species during the summer. Thus, it was quite usual to find that where *Elminius* was present only as scattered adult individuals in one year, it formed a complete cover on all bare areas during the following season. For example, early in 1951 none could be found on the pier or elsewhere at Colwyn Bay, but by the end of the season the pier surfaces had acquired a density of $0{\cdot}04/cm^2$ of adult *Elminius* surrounded by spat which grew to maturity the following spring and reached a density of $0{\cdot}3/cm^2$ in July 1952.

The spread of *Elminius* round Anglesey to the Lleyn peninsula (Caernarvonshire) followed a different pattern. The well-marked front disappeared beyond Moelfre along the north coast of Anglesey and beyond Menai Bridge in the Menai Straits (Fig. 7). New centres appeared almost simultaneously and independently in bays and harbours along the north and west coasts of Anglesey and the Lleyn Peninsula. These centres consisted of small and very local patches of *Elminius* usually of density $0{\cdot}1$–$1{\cdot}0/cm^2$. The largest area infested was Holyhead Harbour, where a small number of *Elminius* had been recorded previously, but had shown no marked increase hitherto. The coast between these centres carried for the most part only isolated individuals, their density varying inversely with exposure to wave action.

The coastline to the west of Bangor differs from that to the east in three main respects. First, it is less shelving, and so the waves break directly on the rocks, the wave-crash being particularly severe on the north-west of Anglesey. Secondly, the tidal currents which flow through the Menai Straits and round the north coast of Anglesey are stronger than those which affect the coasts lying to the east of Bangor. Lastly, there are more extensive stretches of sand and gravel to the east of Bangor, and these shores, with the possible exception of the Orme, suffer more scour in consequence and have little algal cover. By contrast the north and west of Anglesey, the Menai Straits, and the Lleyn Peninsula have an exceptionally rich algal flora.

All three factors probably influence the spread of *Elminius*. The greater exposure to wave action and the denser algal cover restrict favourable habitats to silty bays and harbours. The greater tidal flow disperses the larvae more widely, and therefore more sparsely. Hence, localized populations spring up in suitable places over a wide area.

Since 1953 isolated individuals have been found from time to time on the north coast of Cardigan Bay. In 1955 this coast was carefully examined and the only incidence of the species in significant numbers was found at Pwllheli. It was present on stones in the harbour at a density of twenty to fifty individuals per square metre, some of them breeding. Some local fishing boats laid up on the beach had acquired a settlement of about the same density. It is not clear, therefore, whether these vessels introduced *Elminius*, or whether it has spread through Bardsey Sound by natural means.

By the end of 1955 the spread of *Elminius* westwards from the Solway along the south coast of Scotland had reached the Isle of Whithorn, and a single individual was found at Drummore near the Mull of Galloway. A small settlement which must almost certainly be regarded as a separate population has persisted at Stranraer since 1950 (Crisp & Molesworth, 1950). In 1953 and 1955 *Elminius* was confined to the same part of Stranraer harbour; its numbers had dwindled, and nearly all the specimens were old ones with corroded shells. Subsequently, it was discovered that a ship-breaking yard which previously existed on the east bank of Loch Ryan had been out of operation since 1949. Possibly ships awaiting breaking up had liberated larvae, giving an initial settlement in the Loch, but these were never in sufficient density to give rise to an expanding population. A more recent report of a single specimen of *Elminius* from the Clyde (Connell, 1955) has not been followed by further reports of its presence in that area. Occasional individuals are found not infrequently some 50 or 60 miles from the main stocks. Whether they are carried there by ships or by exceptionally favourable eddies is not certain.

An isolated record of two individuals was made by Dr Southward at Ramsey in the Isle of Man early in 1952, but no further specimens were found there in 1953. However, by 1955 a centre of dispersal had clearly been established at Ramsey and was spreading southward; moreover, some of the individuals were probably at least a year old.

Ramsey is the most northerly point in the Isle of Man where suitable conditions exist for *Elminius*. Its arrival there, approximately 1 year after it had colonized the Solway, and simultaneously with its appearance at Whitehorn and Drummore, suggests that it had been carried by natural means across a sea barrier of some 25–30 miles. Crisp & Southward (1953) believed that this distance was near the critical limit for the spread of this species by normal water movements adjacent to a shoreline. At that time it was separated by a distance slightly exceeding 30 miles, and the numbers of larvae arriving at Ramsey were apparently not sufficient to start a colony.

INVASION OF THE MAINLAND OF EUROPE

Apart from records off the Dutch coast (den Hartog, 1953) the information regarding the colonization of the coasts of Europe remains scanty, and is insufficient for definite conclusions to be drawn.

The first record for the mainland of Europe was from the Kijkduin district in south Holland (Meulen, 1946). Its presence was subsequently reported by Boschma (1948). It has generally been assumed that the species was carried by ship from Britain and made its first appearance in the region of the Hook of Holland. It spread steadily northwards, reaching the southern end of the Zuider Zee by 1950, and the northernmost Friesian islands by 1951 (den Hartog, 1953). It was present in Cuxhaven in 1953 (Kühl, 1954). This migration, well documented by den Hartog, covered a distance of only 20–30 km in the first 2 years, but thereafter advanced probably at a steadily increasing rate of some 50–70 km a year, to reach Cuxhaven by 1953. The very rapid spread through north Holland and Germany is probably attributable to the residual current flowing through the Straits of Dover and turning eastwards past the Friesian archipelago and the north German coast (Carruthers, 1930).

According to den Hartog (1953) *Elminius* spread even more rapidly from the Hook of Holland southwards across Belgium and France. In a subsequent publication (1956) den Hartog realized that the occurrence of *Elminius* in France was too widespread to be considered as having originated from Holland, and suggested that ships had carried the species to Normandy from England during the invasion of Europe. Bishop (1954) and Bishop & Crisp (1958) have described in detail the distribution of *Elminius* in France in 1953–54. They show that there were at least two distinct population centres, one in Brittany, and another, extending eastwards from the north coast of Cotentin, continuous with the Dutch population. In a more detailed consideration of the factors involved in dissemination, notably the influence of the residual current, Bishop & Crisp (1958) have arrived at the conclusion that the two French populations were established independently, and that the eastern population centre probably merged with the Dutch population on the Belgian coast approximately in 1949–50 (see Leloup & Lefèvre, 1952). A further centre has now developed in South Brittany between Concarneau and Lorient (Crisp, 1958), and another was discovered in 1955, at a great distance from all existing stocks, in north-west Spain (Fischer-Piette & Prenant, 1956).

MEANS OF DISSEMINATION

A species invading new territory may follow either of two possible courses. It may spread only at the boundary of the existing population, by natural processes of dispersal, or it may be carried a long distance by means of a vector and so establish a new centre of dissemination. It will be useful to refer to the former as marginal dispersal, and the latter as remote dispersal.

Elminius has clearly spread by both means. We shall therefore consider the limitations governing the two processes.

MARGINAL DISPERSAL

The process of marginal dispersal demands ideally a suitable coastline with closely spaced objects such as piers, breakwaters, and boulders available for settlement. Most of the north coast of Wales, between the Dee and Anglesey, fulfils these conditions. Fig. 7 shows the population density at various times, based on sample counts on various substrata. The vertical axis is given for convenience on a logarithmic scale. It can be seen that at any given time, the population density falls with increasing distance from the main stocks, sharply at first, then less steeply, and finally asymptotically to the horizontal axis. This pattern of distribution at the population boundary would be anticipated if dispersal were a random process, whether the population were a stable or an expanding one. Because the population extends at ever-decreasing density beyond the obvious boundary, occasional records may be made at considerable distances, perhaps 40 or 50 miles in some instances, from the main population centre. Indeed over these wide areas where the animal is scarce records will depend as much on the diligence of the observer as on the density of the species. For this reason the practice of defining the boundary of a species as the point most remote from the main population at which an individual has been found is unsatisfactory. An objectively and accurately defined boundary can only be set by means of distribution contours (isopleths) such as those shown in Fig. 7. Any isopleth may be chosen, but the position of the boundary is determined most accurately where the isopleths are closest together and where the abundance of the species is sufficient to allow counts to be made. In Fig. 7 the choice is clearly between a density of 0·1 and 0·001/cm^2.

When measuring the rate of dispersal year by year the same isopleth must obviously be used for comparison. Due to irregularities in the distribution and in the environment, its position will not always be as clearly defined as in Fig. 7; nevertheless an estimate of the position of the isopleth should be made.

Table 3 summarizes existing information on the rate of progress of *Elminius* by marginal dispersal. The British records are based on the movement of the point of density 0·1/cm^2 on substrata favourable to the species. The table records only the results from areas where the limits were made certain from time to time by searches up to and beyond those parts of the coast known to have been invaded.

The rate of advance along different coasts, when taken over a number of years, is usually of the order of 20–30 km per year. The exceptions are confined to coasts influenced by strong residual currents. For example, the eastward drift along the Dutch and German coast accelerated the spread considerably; the southerly drift along the north-east coast of England appears to have arrested it altogether. With a strong and favourable drift, the relatively small numbers of larvae produced at first by an initial colony may be spread out so thinly and to such great distances that they escape unnoticed. As the population increases in density and in extent the larval output may become sufficient to supply the current with enough larvae to prevent their being unduly dispersed. An increasing rate of advance would then accompany the expansion of the initial population, as occurred off the Dutch coast.

REMOTE DISPERSAL

During marginal dispersal a fresh area is colonized from a large well-stocked area nearby, and becomes in turn a source of larvae for further dispersal. The supply of larvae is therefore practically unlimited; the chief factor limiting the spread of the species is the distance which, on average, a larva will be carried during its planktonic life. In remote dispersal, however, the number of larvae introduced is limited. Even under the best conditions, as, for example, when an old hull covered in barnacles is laid up, the actual numbers of larvae set free must be very small compared with those which would be produced on a neighbouring well-stocked shoreline. The small number of larvae available in a given area is therefore a feature which in practice distinguishes remote from marginal dispersal.

TABLE 3. RATE OF PROGRESS OF *ELMINIUS* BY MARGINAL DISPERSAL

Region	Year	Estimated position of boundary	Distance covered (km)	Average rate of advance
North coast of Europe*	1946	Scheveningen	—	—
	1947	North of Oude Rijn	16	
	1948	North of Ijmuiden	33	52 km/year (rate increasing sharply along Friesian archipelago)
	1949	North of Petten	32	
	1950	Isle of Tessel	36	
	1951	Isle of Schiermonnikoog	92	
	1953	Cuxhaven	155	
East coast of England	1947	North of Yarmouth		
	1949	Hunstanton	75	33 km/year up to 1955. Advance ceased abruptly at the Humber
	1950	North of Skegness	26	
	1951	Cleethorpes	31	
	1951–55	No further advance	—	
West coast of England, southern front	1947	Morecambe Bay		
	1949	Mersey estuary	73	
	1950	Point of Ayr	20	
	1951	Llandudno	36	
	1952	Red Wharf Bay, Aber.	25	30 km/year
	1953	Holyhead, Port Dinorwic	30	
	1954	South of Porth Dinlleyn	25	
West coast of England, northern front	1947	Morecambe Bay		
	1949	Barrow-in-Furness	17	
	1950	Millom	12	
	1951	Ravenglass	17	21 km/year (rate increasing as it spreads)
	1952	Whitehaven	28	
	1953	Rough Firth	38	
	1954	River Cree	35	
South coast, eastward spread from Plymouth. (No clearly marked front, populations confined to estuaries and bays)	1947	Plymouth Sound		
	1950	Rivers Dart and Torbay	60–75	19·5 km/year
	1952	River Exe	35–20	

* From den Hartog (1953).

These few introduced larvae become dispersed by water movement, which will vary in magnitude with the topography, currents, tides and winds prevailing. Enclosed waters, especially long narrow estuaries carrying little freshwater drainage, will disperse the larvae less than open coasts with unrestricted lateral movement of the water by tides and winds. Thus, the introduction of the same number of *Elminius* into an area where the water exchange and dispersal is small will result in a more local and therefore denser spatfall. The tidal range is also of importance in controlling the amount of mixing of enclosed water with the open sea (Bishop & Crisp, 1958) and so the ultimate density attained by an introduced population.

This density of the initial population is of critical importance as the following experiments indicate. *E. modestus* spat were artificially isolated at various distances from their neighbours, and allowed to mature in an area almost free of the species (Brixham Harbour, 1949). Individuals within only 3 cm of each other were fertilized at the normal rate, but those spaced out at a distance greater than 4 cm never became fertilized (Table 4). The distance of 3–5 cm is equal to that of the fully extended penis. There is a tendency for the larger size groups with correspondingly longer penes to fertilize over a greater distance. The experiments indicate that cross-fertilization is obligatory in this species (cf. Crisp, 1954; Barnes & Crisp, 1956) and that individuals separated

TABLE 4. EFFECT OF DISTANCE ON FERTILIZATION

The table gives, against the distance between individuals, the percentage which contained fertilized egg masses.

	Date and place of examination					
	Brixham transplants from Burnham-on-Crouch				Hunstanton natural population	Neyland natural population
Distance (cm)	Group A I. v. 49 (%)	Group B I. v. 49 (%)	Group C 23. v. 49 (%)	Group D 23. vii. 49 (%)	23. iii. 48 (%)	2. ix. 47 (%)
Controls, adjacent to each other	79	82	78	68	79	63
0 –1·0	70	80	83	—		55
1·0–2·0	72	22	67	—		50
2·0–3·0	50	0	75	27	69	20
3·0–3·5	30	0	30	73		0
3·5–4·0	0	0	25	20		
> 4·0	—	—	0	0	0	0
Mean size (cm)	0·89	0·77	0·97	1·11	0·92	0·7

by a distance exceeding 5 cm will not produce any offspring. Observations in the field confirm this view (Table 4, columns 6, 7). Unless, therefore, the introduced cyprids, or those produced in the lifetime of the introduced individuals, can settle at such a density that a sufficient number of them are within 5 cm of each other, the colony will never establish itself. One may call this the 'critical breeding density'. If settlement were at random, and the conditions for maintaining the colony required that, say, 10% of the population reproduced, then, for this proportion to settle within 5 cm of each other, the critical breeding density would have to be somewhat in excess of ten per square metre. Owing to the gregarious tendency shown during settlement, a greater proportion will be in close proximity than would otherwise be expected, and this will improve the chance of successful colonization (Knight-Jones & Stephenson, 1950). Nevertheless, it is clear that the odds against an introduction must usually be very great. Success can only be achieved when large numbers are introduced into enclosed waters having little exchange with the open sea.

Dock areas, small harbours, and narrow estuaries with piston-like tidal movement are likely places for an introduction. Old ships brought from infected areas and laid up for some time or quantities of shellfish bearing spat would be the most likely sources of a successful introduction, since the *Elminius* thereby carried to the area will remain long enough to release successive broods of larvae (Crisp & Davies, 1955). Ships spending only a few days in the area are less likely to cause an introduction, for the actual numbers of larvae shed in so limited a time will be relatively small. Seaplane hulls and floats, though they occasionally become fouled by weed and are often treated with anti-fouling paint, rarely carry mature barnacles, and do not generally stay in one area for a long time.

There is no evidence that barnacles usually suffer harm when carried on ships, unless they have visited fresh or polluted water. On the contrary, the steady water movement provided by the slower classes of shipping is probably beneficial. Large gravid individuals can often be found on such vessels, indicating that growth has been rapid and breeding normal. Large ships from Australian waters also arrive from time to time fouled with *E. modestus*. Even when the species is absent outside the vessel, it is common to find it in the condenser boxes and ducts, in company with *Balanus amphitrite* and *Bugula neritina*, two other immigrant species to British waters.

BARRIERS RESTRICTING DISSEMINATION

We shall next consider the situation where parts of a coastline suitable for maintaining a population are separated by an unfavourable area. This barrier may be a rocky exposed section of the coast, or part of the open sea too deep for *Elminius*. Let us suppose one favourable area is already populated by the species but not the other. Fig. 8 illustrates this system qualitatively. The barrier is assumed to commence sharply at the termination of the existing population. The curve A shows the most probable form of the relation between the density of cypris larvae and the distance from the existing population from which they have been dispersed by water movements for the duration of their planktonic life. The situation is one which can be represented in its essentials by the equations of diffusion (cf. Skellam, 1955) in which the eddy diffusivity is responsible for random dispersal. It will be seen that at increasing distances from the parent stocks the density of larvae falls asymptotically to zero, as in the case of marginal dispersal (cf. p. 498 and Fig. 7). Since these larvae are ready to settle the potential settlement is represented also by the curve A. The maximum distance from the existing stocks, over which colonization is likely to occur, will clearly be determined by the distance at which the curve of potential settlement intersects the critical breeding density. This point is shown in the figure at A'. Fig. 8 also shows how the critical distance for colonization is influenced by the fecundity of the species K, the existing population density θ, and the degree of water movement represented by the eddy diffusivity ϕ (Sverdrup, Johnson & Fleming, 1942). An increase in K (or θ) will not affect the shape of the curve A, but will increase the larval density proportionately throughout as shown by curve B. The effect of increasing the degree of water movement (ϕ) is shown by curve C. The number of larvae available (area under the curve) is equal to that in A, but curve C is flatter and the critical distance increased in consequence as shown by the position of the point C'. It should be noted that the idea of a critical colonizing distance does not imply a

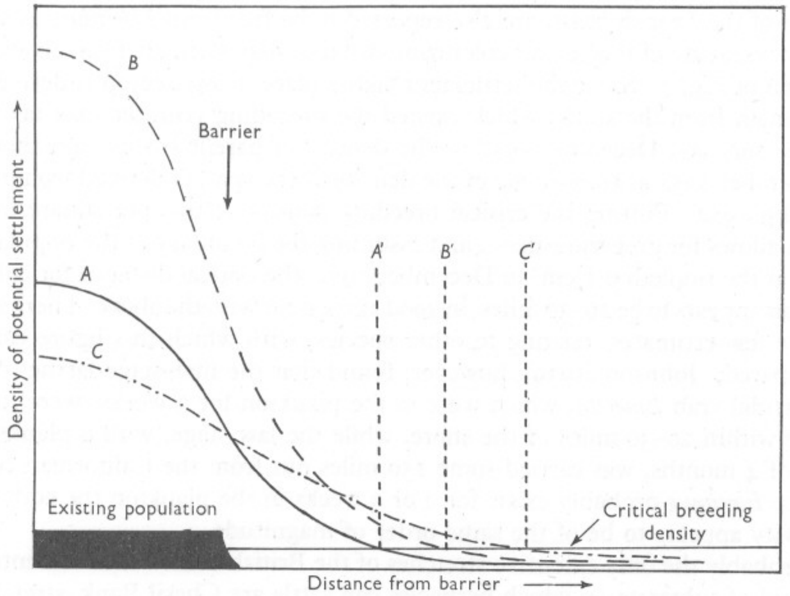

Fig. 8. Schematic representation of the influence of a faunistic barrier on dissemination of an animal with planktonic larvae. The existing population gives rise to larvae which, at the stage of potential settlement, are distributed according to diffusion theory as shown by curve A. Increasing the size or fecundity of the population will produce curve B, while increasing eddy diffusivity will modify curve A to curve C. The distance over which probable colonization may occur will be given by the intersection of curves A, B and C with the critical population level at which successful breeding can take place, that is at A', B' and C'.

clearly demarcated line beyond which colonization cannot occur under any circumstances. Owing to the assumptions involving probability in the above analysis, the effect of increasing the distance from the parent stocks is to diminish steadily the probability that a colony will be established. The critical colonizing distance is therefore definite only in relation to a given level of probability, and in the course of sufficient time increasing distances may eventually be bridged.

It is rare to find a stretch of coast of any great distance wholly unsuitable or devoid of any substrata on which the species can settle. Probably the open sea is the most effective barrier, though even in the sea, fixed buoys may sometimes be present and provide regular oases. From the observations made in the northern Irish Sea area, it appears that the Isle of Man was colonized from a distance of some 20–25 miles away, but remained outside the critical range when the nearest *Elminius* were about 30 miles distant. This puts the critical distance for colonization in the order of 30 miles. Ireland, which is more than this distance from the coasts of England and Wales, had not been colonized by 1953, though a recent record shows that it has appeared in the south-west (Beard, 1957). The Channel Islands, separated by some 30 miles from infected parts of the French coast, are also reported to be free from *Elminius*. A more direct estimate of the critical colonizing distance may be made from an examination of Fig. 7. Since the settlement taking place in any season is derived in the main from the stocks which existed the preceding year, we may take the curve for, say, December 1951 as the density of parent stocks, and that for December 1952 as an estimate of the density of the spatfall derived from them during 1952. Putting the critical breeding density at two per square metre (this allows for gregariousness), and assuming the boundary of the population was at the isopleth $0{\cdot}1/cm^2$ in December 1951, the critical distance for colonization appears to be 29–30 miles, in good agreement with the above. There seem to be few estimates, relating to other species, with which this figure can be compared. Johnson (1939), however, found that the first-stage larvae of the intertidal crab *Emerita*, which were in the plankton for 3 weeks, were found only within 20–30 miles of the shore, while the last stage, with a planktonic life of 4 months, was carried some 150 miles out from the Californian coast. Since *Elminius* probably exists for 2 or 3 weeks in the plankton the eddy diffusivity appears to be of the same order of magnitude.

Probably the only extensive stretches of the British coast which are entirely devoid of substrata on which barnacles can settle are Chesil Bank, stretching from Portland to West Bay, and the Holderness coast of Yorkshire. There are, however, other places where *Elminius* has been temporarily or permanently halted; these are tabulated in Table 5. To what should the halt be attributed in these places?

Obviously the greater the proportion of unfavourable coastline, the smaller will be the numbers of larvae released and scattered along it, and the more likely will these larvae settle in unsuitable places or fail to reach the critical breeding density. Much of the Devon and Cornish coast is rugged and exposed, with few sheltered inlets. These conditions will diminish the rate of spreading of the species, for the majority of larvae produced will be wasted in unsuitable places. Another type of wastage may be important in such an environment, namely, the wastage of larvae offshore. Thorson (1950) draws attention to the calamitous wastage of larvae of littoral species from coasts where the prevailing winds and drifts are away from the land. Similar losses may occur at headlands which cause an offshore set of the current over a large part of the tidal cycle (Crisp & Knight-Jones, 1955), or where the tidal streams are particularly strong, as at Portland and Cap de la Hague. Larvae in such areas may have little chance of returning to the shore to settle. This wastage, taken together with the high proportion of unsuitable shoreline, would account for the halts in the spread of *Elminius* at Portland Bill, Cap de la Hague, the Lizard, and the Pembroke peninsula.

TABLE 5. BARRIERS TO THE PROGRESS OF *ELMINIUS*

Barrier	Possible causes	Distance separating suitable habitats	Period over which advance was retarded
Holderness coast	Lack of substrata. Opposing residual drift, low temperature	Hornsea–Humber	1953–
Portland Bill and Chesil Bank	Lack of substrata. Rocky headland. Strong tidal races. Opposing residual drift	Portland Harbour–West Bay Harbour	1947 or earlier–
Lizard and Land's End peninsula	Rocky and exposed headlands	Helford River–St Ives Bay (except for a few small harbours, e.g. Porthleven, Penzance)	1947 or earlier–1953 approx.
Pembroke Peninsula	Rocky and exposed headland. Strong tidal races	Milford Haven–Fishguard (except for small harbours such as Solva, Porthgain)	1947–
Irish Sea	Sea barrier	Cumberland coast–Isle of Man	1949–53
	Sea barrier	Holyhead–Dun Laoghaire	1953–
St George's Channel	Sea barrier	Milford Haven–Rosslare	1947–
English Channel	Sea barrier	Cap de la Hague–Channel Isles	1950?–
Straits of Dover	Sea barrier	Dover Harbour–Calais	1945 or earlier–1949?
Cap de la Hague	Rocky headland. Strong tidal races. Opposing residual drift	Cap de la Hague–Carteret	1950?–

The conditions on rocky coasts will in general be such that marginal dispersal can scarcely operate, or will do so only slowly. Larvae from sparse and scattered populations will be dispersed over a wide area, many being lost out to sea. Thus there will be a few larvae everywhere, but probably in most places not in sufficient density to breed. A few larvae liberated from craft lying up in a small creek or from the few individuals settled close enough together to breed, may add sufficiently to those being dispersed from outside to pass the critical breeding density. The area would then eventually become populated. Thus, where *Elminius* has spread from one harbour to the next, without appearing on the neighbouring exposed parts of the coast, as in south Devon, the Bristol Channel and west Caernarvonshire, it is possible that both marginal and remote means of dispersal have played a part. Where the distance traversed in one leap greatly exceeds 30 miles, however, it is reasonable to assume that the species has not spread naturally but has been carried by a vector.

PROBABLE HISTORY OF DISPERSAL

When first discovered in 1946 the species was already widespread in southern England. The two most likely areas for its original introduction from Australasian shipping would therefore be Southampton Water and the Thames estuary. Both are areas very favourable to *Elminius*, having high summer temperatures, and now support abundant populations. Of these two, Southampton is more likely to have been the original centre on the following grounds. First, Southampton Water is very enclosed, and because of the small tidal range it exchanges water only slowly with the sea outside. Secondly, there is little freshwater flow and less pollution there than in the Thames estuary. Thirdly, in the Thames all the docks are in areas too fresh or too polluted for survival of *Elminius* larvae, except possibly at Tilbury. In Southampton Water vessels are docked in sea water suitable for larval development. Lastly, though there are no continuous records for the Southampton area, we know that *Elminius* was still increasing in density in the Essex rivers from 1946–50.

No more than a guess can be made as to the time of arrival. The rate of spreading along comparable coasts of shingle and sand, such as north Holland, eastern England, and Liverpool Bay, lies between 52 km/year (with a favourable drift) and 30 km/year. There exists a general eastwards drift through the whole of the English Channel and Straits of Dover (Carruthers, 1930) and this probably extends to the shoreline as evidenced by the direction and movement of shingle bars by predominant wind and waves (Steers, 1946). A small contrary coastal eddy is shown by Edgell (1943) in Pevensey Bay. A rapid advance eastwards could therefore be assumed after the necessary time for establishment in Southampton Water. The many coastal defences in the area would also have assisted in providing substrata. Taking 50 km/year as a probable rate, then an introduction in 1939–40 would have reached the Thames estuary in 1945, and if the rate continued up the east coast it could have just reached Lowestoft by 1947. This timetable, however, appears only just adequate, and taking other factors into account an introduction by remote dispersal into the Thames estuary area probably in 1943 or 1944 seems more probable. In 1947 the species was more abundant in the area between the Thames and Harwich than on the Thanet coast, suggesting that the latter area was colonized after a population had been established in the Thames estuary. Furthermore, the Dutch coast was probably invaded as a result of remote dispersal between East Anglia and the Hook of Holland in 1946 (Bishop & Crisp, 1958). It is necessary, therefore, to assume that *Elminius* had been established in the Harwich area prior to 1946. Since the rate of advance northward from the Thames would not be accelerated by residual drifts, but on the contrary retarded since the strongest winds are from the north-east, it is not easy to account for the spread of *Elminius* to Harwich by 1945, unless it was already established in the Thames by 1943 or 1944. Making this assumption, the probable history may be summarized as follows.

Shipping conditions were exceptional at the outbreak of war in 1939. As convoys assembled, large numbers of vessels were anchored just offshore. This may have allowed the barnacles on Australasian shipping time to liberate sufficient numbers of larvae to colonize Southampton Water. The large concentration of shipping which then occurred might have given *Elminius* a unique opportunity. The following summer (1940) was a warm one, and would have assisted in building up stocks above the critical level for maintaining a population; from Southampton *Elminius* spread rapidly eastwards aided by the residual drift, and more slowly westwards. In about 1943 or 1944 a new centre was established in the Thames estuary, probably by remote dispersal, and the East Anglian and Thanet coasts were colonized from this centre.

The westward extension along the coast from Southampton was halted at Portland, and no further westward spread has taken root in Lyme Bay. Several distant centres, however, were set up to the west of Southampton, between 1944 and 1946, presumably by remote dispersal. These were in the Helford River (1946 or earlier), Plymouth Sound (1946), Milford Haven (1947), and possibly in another place further up the Bristol Channel. These two centres in South Wales may have arisen simultaneously, though independently. The centre in Milford Haven has remained isolated up to the present time by exposed headlands, while *Elminius* has steadily colonized the remainder of the coasts north and south of the Bristol Channel. Perhaps, however, the original breeding stocks were present in Milford Haven, and larvae were carried by the prevailing surface drift to coasts higher up the Channel.

A major centre was next set up in Morecambe Bay in 1948, from which the coasts of North Wales, Lancashire, Cumberland and Galloway have now been populated. Small centres, probably arising by remote dispersal, have been set up in St Ives Bay (1951–54) and Tremadoc Bay (1953–54).

On the continental coast there appear to have been four, possibly five, main centres. The invasion of the coast of Holland began near the Hook of Holland about 1946. For reasons given elsewhere, another centre was probably established in the estuary of the Seine soon after the invasion of Normandy in 1944 (Bishop & Crisp, 1958). A third centre in the Brest area has been described by Bishop from which other areas in south Brittany have been colonized in a manner similar to that of the invasion of the coasts of south Devon (Crisp, 1958). Judging from the rather slow establishment on rocky coasts of this type, the centre in the Rade de Brest was probably established at least 3 or 4 years earlier than the date (1953) when Bishop first surveyed the area. The river estuaries in the Morlaix–Roscoff area may represent other separate centres established at about the same time as that in the Rade de Brest. Much farther south yet another centre has been established in north-west Spain. Its discovery in 1955 (Fischer-Piette & Prenant, 1956) and its present rather limited area give it the appearance of recent origin, probably between 1950 and 1953. It may be distinct from recently reported settlements in Portugal (Fischer-Piette & Prenant, 1957).

The dates in which these centres have probably been established are shown in Fig. 9 .There can be seen to be some regularity in the order of their appearance, for the new centres have not sprung up at random. They seem to have arisen more readily in the vicinity of old ones than at great distances from them. Such is perhaps to be expected, since harbours are usually visited more frequently by craft from neighbouring localities than by craft from any other particular area. Local craft are also more likely to be allowed to accumulate fouling than are those which travel greater distances, and their shallower draught is more suitable for the settlement of an intertidal species. Larvae will thus be liberated continually into harbours once a neighbouring area is infected, to add to the numbers borne by water currents. It is therefore not easy to differentiate between remote and marginal dispersal in areas where suitable harbours are scattered and many local fishing vessels are operating.

ECOLOGICAL EFFECTS OF THE INTRODUCTION OF *ELMINIUS*

The introduction of a new species is bound to influence the balance existing between endemic species. A species occupying as dominant a place in its environment as *Elminius* may bring about profound changes. The main differences between *Elminius* and native barnacles are summarized in Table 6.

Elminius competes for space mainly with *Balanus balanoides*, which is the only indigenous intertidal barnacle on those parts of the British coast where *Elminius* thrives best, notably in south-eastern England. To a lesser extent it competes with *Balanus improvisus* and *B. crenatus* at low-water mark. *Elminius* ranges over a greater part of the intertidal zone than does *Balanus balanoides*, for small numbers grow at levels slightly above the highest *B. balanoides*, and it penetrates into the sublittoral, some 5 m below L.W.S. It is usually less common in the sublittoral, however, than *B. improvisus* and *B. crenatus*.

When *Elminius* first appears, the zone in which it settles is usually occupied by adults and spat of *Balanus balanoides*. Except in very muddy or brackish places, *B. balanoides*, which settles 2 months earlier than *Elminius*, initially covers the greater part of the available settling space, so that *Elminius* is often found attached to the upper parts of the shells of *Balanus balanoides* or even to the valves. As the spat of *Elminius* become more numerous they often form circlets of small grey barnacles round the apertures of large specimens of *Balanus*. Some *Elminius* settle regularly above the *Balanus balanoides* zone, almost as high as *Chthamalus* would be found if it were present.

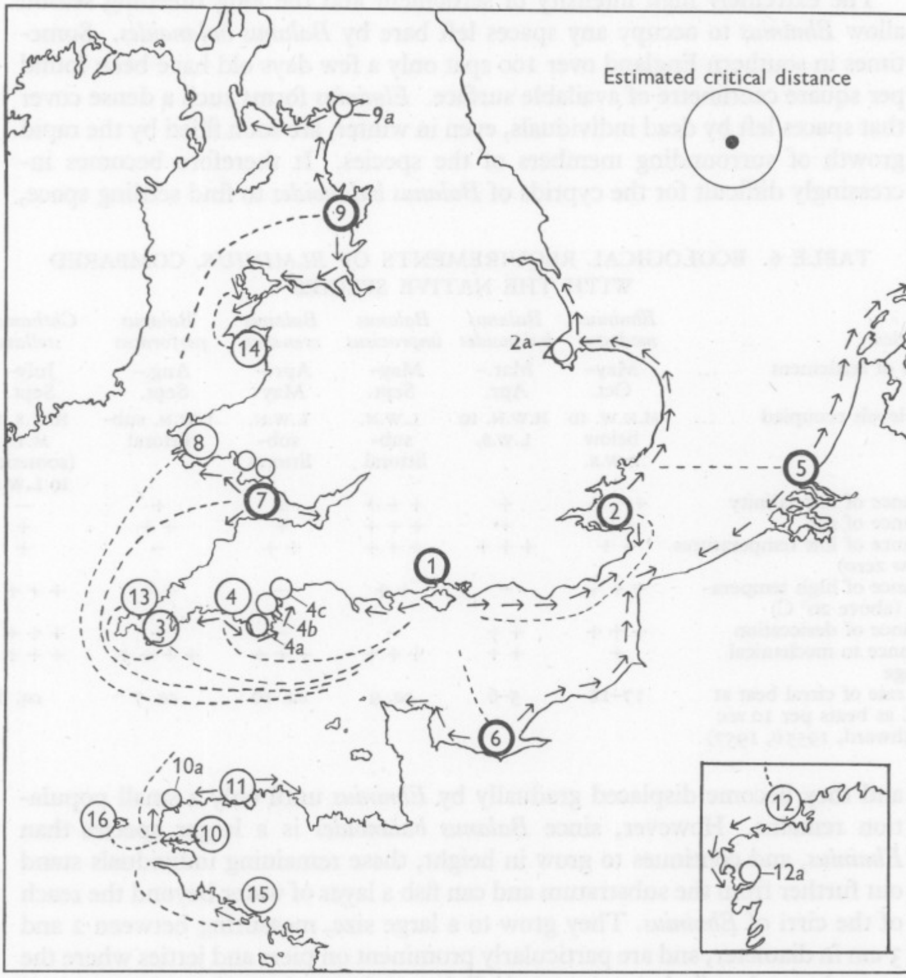

Fig. 9. Illustration of the probable order in which centres of dissemination of *Elminius* were established. Major centres responsible for the colonization of large areas of coast are shown by large dense circles. More localized centres also set up by remote dispersal are shown by large open circles. Subsidiary centres probably reached by marginal dispersal by small circles. Arrows show direction of marginal dispersal, dotted lines the probable routes of remote dispersal. Inset: north-west Spain

1, Southampton Water, ? 1940–43; 2, Thames estuary, ? 1943–44 [2*a*, the Wash, 1948]; 3, Helford River, ? 1944–46; 4, Plymouth Sound, 1946 [4*a*, River Dart, 1948; 4*b*, Salcombe, 1948; 4*c*, River Exe, 1951]; 5, South Holland, 1946; 6, Seine estuary, ? 1944–49; 7, Bristol Channel, 1946–47; [7*a*, Llanelly Bay, 1949; 7*b*, Swansea Bay, 1949]; 8, Milford Haven, 1947; 9, Morecambe Bay, 1948 [9*a*, Solway firth, 1953]; 10, Rade de Brest, ? 1944–52 [10*a*, l'Aber Wrach, l'Aber Beniot, ? year]; 11, Roscoff area, ? 1944–52; 12, north-west Spain, ? 1950–53 [12*a*, Noya, ? year]; 13, St Ives Bay, 1951–54; 14, Tremadoc Bay, 1953–54; 15, south Brittany, 1954–57; 16, Ile d'Ouessant 1956.

The extremely high intensity of settlement and the long breeding season allow *Elminius* to occupy any spaces left bare by *Balanus balanoides*. Sometimes in southern England over 100 spat only a few days old have been found per square centimetre of available surface. *Elminius* forms such a dense cover that spaces left by dead individuals, even in winter, are soon filled by the rapid growth of surrounding members of the species. It therefore becomes increasingly difficult for the cyprids of *Balanus balanoides* to find settling space,

TABLE 6. ECOLOGICAL REQUIREMENTS OF *ELMINIUS*, COMPARED WITH THE NATIVE SPECIES

Species ...	*Elminius modestus*	*Balanus balanoides*	*Balanus improvisus*	*Balanus crenatus*	*Balanus perforatus*	*Chthamalus stellatus*
Season of settlement ...	May–Oct.	Mar.–Apr.	May–Sept.	Apr.–May	Aug.–Sept.	July–Sept.
Tidal levels occupied ...	M.H.W. to below L.W.S.	H.W.N. to L.W.S.	L.W.N. sub-littoral	L.W.N. sub-littoral	L.W.N. sub-littoral	H.W.S. to M.T.L. (sometimes to L.W.N.)
Tolerance of low salinity	+++	+	+++	+	+	−
Tolerance of silt	++	+	+++	+	++	+
Tolerance of low temperatures (below zero)	++	+++	+++	++	−	+
Tolerance of high temperatures (above 20° C)	+++	−	++	−	++	++++
Tolerance of desiccation	+++	++	−	−	+	++++
Resistance to mechanical damage	+	++	+++	+++	++++	++++
Mean rate of cirral beat at 20° C as beats per 10 sec (Southward, 1955*b*, 1957)	17–18	5–6	*ca.* 9	*ca.* 10	*ca.* 7	*ca.* 6

and they become displaced gradually by *Elminius* until only a small population remains. However, since *Balanus balanoides* is a larger species than *Elminius*, and continues to grow in height, these remaining individuals stand out further from the substratum and can fish a layer of water beyond the reach of the cirri of *Elminius*. They grow to a large size, measuring between 2 and 3 cm in diameter, and are particularly prominent on piers and jetties where the water is continually being renewed. Being no longer in such severe competition with their own species they are individually large, healthy and successful.

The process of replacement of the *Balanus* population by *Elminius* is relatively slow; for example, at Hunstanton, *Elminius* was introduced late in 1947, and present in small numbers chiefly on the parieties of *Balanus* on the pier piles in 1948. By 1949 it was abundant, and smothered all existing individuals of *Balanus*, though the latter were still present to a density of 2–3/cm². In 1952 some reduction in *B. balanoides* was noticeable, and those remaining were no longer close packed and columnar, but were in the main isolated, their density being about 0·7/cm². They were rather larger than hitherto. By 1955 the density of *B. balanoides* had fallen further to about 0·15/cm², most of these being between 2 and 3 cm across the base, and about 1·5–2 cm in height.

In the less saline parts of an estuary and below low-water mark, *Elminius* may replace *Balanus improvisus*. There was a reduction in the numbers of *B. improvisus* settling on experimental panels between 1946 and 1950 in the River Crouch, and, judging from plankton samples taken in 1938 in the Thames, a reduction has taken place in the numbers of *B. improvisus* larvae in the plankton. It will be especially interesting to observe this interaction if *Elminius* spreads to the Baltic, where *Balanus improvisus* is the dominant species. The competition between *Elminius* and *Balanus crenatus* is probably less important as there is less overlap in their habitats. They are found together only at low-water mark where the salinity is fairly high.

The effect of the introduction of *Elminius* is negligible on rocky exposed shores of the west and south-west, where the dominant intertidal barnacle is *Chthamalus stellatus*. Nevertheless, in sheltered inlets and estuaries of these coasts *Elminius* is of importance. In the Plymouth estuaries *Elminius* had in 1950 largely occupied the situations from which *Balanus balanoides* had disappeared during its decline (Southward & Crisp, 1954). Though *B. balanoides* has begun to return to the outer parts of this coast it has not re-established itself in the estuarine regions where *Elminius* remains dominant (Southward & Crisp, 1956). Its effect on the indigenous fauna within these estuaries has therefore been mainly at the expense of *Balanus balanoides* as on the coasts of south-east England. In many of the estuaries in the south-west where *B. balanoides* is not very common, *Chthamalus* and *Elminius* are found together, *Chthamalus* being able to penetrate up the estuary beyond the seaward limit of *Elminius*.

Elminius is microphagous and behaves like other barnacles (Southward, 1955*a*) utilizing a wide range of particle sizes and taking in both animal and plant material. It grows rapidly, sometimes reaching maturity (diam. 6–7 mm) in 8 weeks. The cirral beat at temperatures from 15–25° C is faster than that of indigenous species (Table 6). It continues to feed vigorously after maturity, and produces broods of nauplii at regular intervals (Crisp & Davies, 1955). Under optimum conditions broods may be liberated every 10 days, each brood containing about the same amount of living matter as is present in the soft parts of the parent. A dense population of *Elminius* therefore removes during summer a great bulk of suspended food and transforms it into larvae. These larvae are extremely abundant, often forming the dominant component of the plankton in May, June and July, in estuaries of south-east England. The nauplii probably feed mainly on particles less than 10 μ in size, as the diameter of the oesophagus is of this magnitude.

The replacement of a large proportion of the previously existing population of *Balanus balanoides* by *Elminius* may therefore have a considerable influence on other members of the marine fauna, for *Balanus balanoides*, unlike *B. improvisus*, is by no means the ecological equivalent of *Elminius*.

While both species as adults feed and so remove suspended food particles during summer, *Elminius*, judging from its rate of cirral beat (Southward, 1955*b*), is probably more efficient than *Balanus balanoides* at the highest temperatures. Hence, more food may be diverted to barnacle growth and so made unavailable to other microphagous forms. But by far the more important difference is that whereas *B. balanoides* accumulates reserves for winter breeding, *Elminius* rapidly converts the food into nauplii which enter the plankton during summer. Moreover, the large number of *Elminius* cyprids which develop and settle (see above) is a clear indication of the success of *Elminius* nauplii in obtaining the necessary food in the face of competition by other larvae having a similar diet. Consequently, there has been a great increase in the total number of summer nauplii, following the introduction of *Elminius* which must adversely affect the growth of the planktonic larvae of other animals which breed in summer, such as *Balanus improvisus*, *Polydora ciliata*, *Littorina littorea*, *Crepidula fornicata* and *Ostrea edulis*. *Ostrea* is harmed also in the early stages of growth as spat by competing for space with *Elminius* (Knight-Jones, 1948). Little is known of the relative ease with which different barnacles may be browsed by predators such as *Nucella lapillus* or *Asterias rubens*. The more delicate and fragile shell of *Elminius* might make it more readily devoured than indigenous species, and so allow these predators to be more successful.

Elminius tolerates the presence of silt and pollution probably better than any other species of British barnacle, with the possible exception of *Balanus improvisus* and in warmer situations *B. amphitrite*. In dirty harbours and muddy rivers within the intertidal zone it may have few or no competitors. On the other hand, on clean and especially on wave-beaten shores, *Elminius* has not displaced either *Balanus balanoides* or *Chthamalus stellatus*, and is indeed often very sparse on these habitats. Mechanical explanations at first suggest themselves, for the species is more fragile and might suffer more from wave crash or pebble pounding. Perhaps, it might be supposed, limpets, which are rare or absent from the usual haunts of *Elminius*, destroy any settlement on exposed shores. But these explanations are not entirely satisfactory. Exposed rocks very close to stocks of *Elminius*—Point Lynas, Anglesey, for example—may have numbers of *Elminius* settled on them which from their eroded appearance seem to have survived for some time. There is no marked preponderance of young individuals and spat in these places. *Chthamalus*, the larvae of which are as small as those of *Elminius*, settles successfully in spite of limpet browsing. It seems more probable, therefore, that the species is uncommon on exposed coasts because its larvae do not settle there, rather than because of high mortality. There are no definite facts to indicate whether *Elminius* larvae could develop in the clearer waters that surround more exposed coasts, but it seems probable that the more turbid water of tidal estuaries contains particles of the appropriate kind to nourish them, while offshore water in general does not.

When considering the influence of other organisms competing with

Elminius for rock space, algae probably rank equally in importance with animals (cf. Barnes & Powell, 1953; Southward, 1953). Where the water is sufficiently clear and where, as in shelter, limpets are few, the growth of algae prevents barnacles from colonizing much of the illuminated surface of rocks. Hence, barnacles may appear to avoid insolation (cf. Moore, 1944) and to collect in dark crevices under piers, or beneath boulders and overhangs. Thus, there exist in temperate waters two extreme situations in which rock surfaces are available for barnacle settlement; one where the rocks are so covered in silt, scoured, or affected by low salinities that algae do not greatly flourish, and the other where algae are kept down by the grazing activities of limpets and by heavy surf. *E. modestus* and *Balanus improvisus* are adapted to the former habitat, *Chthamalus* to the latter. In adapting itself to these turbid estuarine conditions it is possible that it has become nutritionally dependent on the type of food particles found in silty estuaries and is ill adapted to survive in clear water.

SUMMARY

Material collected prior to 1940 indicates that *Elminius modestus* was not present on British coasts at that time.

Elminius increased in abundance in south-east England from 1946 to 1950 and extended its range as far as the Humber, where it halted.

Its advance westwards along the south coast was similarly halted at Portland, but by 1948 independent colonies had been established in several of the river systems of Devon and Cornwall, in Milford Haven, and in the Bristol Channel.

The first populations in the Irish Sea were in Morecambe Bay. From there *Elminius* spread rapidly south and west along the north coast of Wales, and more slowly north and west towards Galloway, eventually bridging the sea to the Isle of Man.

Detailed observations showed that *Elminius* advanced along the uniformly favourable north coast of Wales as a definite front moving at a rate of approximately 20–30 km per year. Around Anglesey where tidal currents were stronger it appeared simultaneously in many scattered centres.

A distinction is drawn between marginal dispersal taking place under the influence of normal agencies at the boundary of an existing population, and remote dispersal due to an artificial or freak transport over a long distance. In the case of *Elminius* the maximum distance that is likely to be bridged by marginal dispersal in the absence of strong residual drifts is about 30 miles.

Elminius probably first appeared near Southampton, and was introduced into the Thames estuary area probably by remote dispersal. Thence it spread along the east coast and was transported to Holland. Its extension into south Devon, the Bristol Channel, the Irish Sea, and to the French coast must also be attributed to remote dispersal.

The main ecological effects of *Elminius* result from competition for space with *Balanus balanoides*. Since *Elminius* breeds in summer, its dominance has a profound effect on the composition of the summer plankton, greatly increasing the number of barnacle nauplii, presumably at the expense of other larvae.

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APPENDIX

TABLE 7

Key: A Abundant. All available surfaces well covered to 30 % of area or more. Adults at 1·0/cm² or more. C Common. Covering less than 30 % of available area, the majority within 1–2 cm of each other. Density 0·1–1·0/cm². F Frequent. Readily found, but about half the population within 3 cm of each other and so just able to breed. Spat not usually in evidence. Adults 0·01–0·1/cm². O Occasional. Very local and must be searched for, very rarely close enough to breed. Density 1–100/m². R Rare. Only a few isolated individuals found in an hours' search. Density below 1/m². N. None found after 1 hr search in suitable area.

Records of Elminius modestus

Place	Date	Density	Notes*
Dunbar	vi. 55	N	—
Berwick-on-Tweed	vi. 55	N	—
Blyth	x. 47	N	P.N.J.C.
	1949	R	Specimen on mussel, but no subsequent records here. H.O.B.
Whitley Bay	ix. 49	N	—
Cullercoats	ix. 53	N	—
Runswick	vi. 55	N	—
Robin Hood's Bay	ix. 50	N	P.N.J.C.
	1954	N	E.A.S.
Scarborough	vi. 55	N	—
Flamborough Head	vi. 55	N	—
Bridlington	vi. 55	N	—
Hornsea	vi. 52	R	1 specimen only
	vi. 55	N	—
Aldburgh	vi. 52	N	—
	vi. 55	N	—
Withernsea	vi. 55	N	—
Kilnsea	vi. 55	N	—
Paull	vi. 55	O	—
Hull	vii. 48	N	—
	vi. 52	N	Area unsuitable from pollution?
	vi. 55	R	—
Grimsby	vii. 48	N	Few suitable substrata
Cleethorpes	vii. 48	R	Single specimen at far end of pier
	ix. 50	O–F	Just self-maintaining population
	vi. 52	F	Less increase than expected
Saltfleet	vi. 52	(N)	No suitable substrata
Mablethorpe and Sutton-on-Sea	vii. 48	N	—
	vi. 52	C	—
Ingoldmells and Chapel Point	vii. 48	N	—
	vi. 52	C	—
Skegness	vii. 48	O–R	5 specimens on pier
	ix. 50	C–A	—
	vi. 52	A	Much commoner than *B. balanoides*
Fosdyke	vi. 52	A	—
Sutton Bridge	vi. 52	A	—
	vii. 55	A	—
King's Lynn	vii. 48	N	P.N.J.C.
	xii. 49	C	On mussels. G.D.W.
	vii. 50	A	Adults 3·5/cm². Spat fall up to 60/cm²
	vi. 52	A	—
Hunstanton	viii. 47	N	—
	iv. 48	R–O	On pier piles only
	vii. 50	A	Heavy spatfall of 40–50/cm². Adults much commoner than *B. balanoides* and growing on them
	i. 53	C–A	A few damaged on pier after heavy storm, which caused widespread damage on east coast; much scouring of rocks and low substrata
	vii. 55	A	Only a few *B. balanoides* of large size (3–4 cm) on pier, 0·07/cm². Rest of area completely covered by *Elminius*
Brancaster	viii. 47	R	One small specimen only
	iii. 48	N	—
	vi. 49	F	Many small specimens on old wreck, off Scolt Head. A.H.N.M.
	ix. 49	C	Many small spat (up to 10/cm²) on stones near main creek. P.N.J.C.
	vii. 50	C–A	Settlement local, two or three times as abundant as *B. balanoides*. Spat 30/cm²
Wells	ix. 49	N	P.N.J.C.
	vii. 55	A	On mussels in creek
Sheringham	i. 48	N	Little suitable substrata. P.N.J.C.
	vii. 55	A	Confined to low water owing to scour
Cromer	i. 48	N	P.N.J.C.
Sea Palling	i. 48	N	P.N.J.C.
Great Yarmouth	i. 48	C	P.N.J.C.
Lowestoft	x. 47	F	On sheltered side of north jetty
	i. 48	F	P.N.J.C.
	v. 49	C	—
	xi. 51	A	—
	vii. 55	A	More restricted on open coast owing to scour. *Elminius* 98 % of population

* Initials refer to observers.

Place	Date	Density	Notes
Southwold	ii. 48	C	P.N.J.C.
	i. 53	C	—
Harwich	ii. 48	C	P.N.J.C.
Clacton	ix. 47	A	—
West Mersea	v. 46	C–A	Regular settlement throughout 1946
Maldon	ix. 49	A	—
Mayland	viii. 47	F	—
Steeplestone and Bradwell	viii. 47	A	—
Burnham-on-Crouch	i. 47	C	—
North Fambridge	viii. 46	C	On hull laid up above H.W. mark since July 1945
Hullbridge and Battlesbridge	ix. 49	C–A	—
Shoeburyness	ix. 47	C	—
Woolwich	ix. 47	N	Too much pollution
Erith	ix. 47	N	Too much pollution
Gravesend	x. 47	O	Limit of penetration of Thames estuary
Rochester	iv. 51	A?	Had been abundant, but nearly all dead
Whitstable	ix. 47	C	—
	iv. 51	A	—
Birchington and Margate	ix. 47	F	—
	iv. 51	C–A	Abundant on piers ($5/cm^2$) fairly common on chalk ($0{\cdot}5$–$1{\cdot}0/cm^2$)
North Foreland	ix. 47	O	—
	iv. 51	O	—
Broadstairs and Ramsgate	ix. 47	F	—
	iv. 51	C	—
Dover	ix. 54	C	—
Folkestone	viii. 56	F	Less common than *B. balanoides*
Hythe	viii. 56	O	On groynes, few barnacles present, much abrasion
Rye Harbour	ix. 48	A	—
Fairlight	viii. 56	F	—
Hastings	viii. 48	C–A	—
	vii. 53	C–A	—
Bexhill	ix. 48	A	—
	vii. 53	C	—
Eastbourne	viii. 48	C	—
	vii. 53	A	—
Seaford	vii. 53	O	Much abrasion by shingle
Brighton	ix. 47	F	—
	iii. 49	F	—
Portslade and Shoreham	ix. 47	A	—
	iii. 49	A	—
Worthing	xi. 48	A	—
Littlehampton	xi. 48	A	Abundant on training wall of River Arun
	vi. 53	A	—
Bognor	xi. 48	C	—
	vi. 53	A	—
Chichester Harbour	vii. 44	F?	Several spat on panel exposed for 3 weeks. H.G.S.
	vii. 45	A	About 30 spat/cm^2 of test surface. M.W.H.B.
	vii. 48	A	—
Portsmouth and Gosport	v. 44	?	2 specimens from boom defence vessel settled in 1943. H.G.S.
	1944	C?	Numerous specimens on ship's hull. H.G.S.
	iii. 49	A	A.H.N.M.
Southampton	vii. 49	A	Intense settlement covering all substrata
River Test, Redbridge	xi. 48	F	—
Cowes	vii. 49	A	—
Ryde	viii. 48	A	—
	vi. 53	A	—
Bembridge	vii. 49	A	—
Culver	vii. 49	F	Less common on chalk than elsewhere
Sandown	vii. 49	A	—
	vi. 53	C	Less common than *B. balanoides*
Shanklin	vii. 49	F	—
	vi. 53	C	—
Ventnor	vii. 49	F	—
	vi. 53	F	—
St Catherine's Point	vii. 49	N	—
	vi. 53	R	—
Brook and Freshwater	vii. 49	O	—
	vi. 53	O	—
Alum Bay	vi. 53	O	—
Totland and Colwell Bay	vii. 49	C	Up to $2{\cdot}5/cm^2$ in sheltered areas
	vi. 53	C	—
Yarmouth, Isle of Wight	vii. 49	A	—
Fishbourne	vi. 53	C–A	—
Lymington	vii. 49	A	Present on piles withdrawn from the sea in July 1947
Milford to Highcliffe	vii. 49	(N)	No suitable substrata
Mudeford	vi. 49	A	—
Hengistbury Head	vii. 49	O	—
Bournemouth	viii. 47	C	—
	vi. 49	A	—
Sandbanks, Poole Harbour	vi. 47	C	Settlement of spat at rate of 3–$5/cm^2$
	iv. 48	C	10–15 % of population
	vi. 49	C	—
Studland	vi. 49	A	—
	vi. 53	A	—
Swanage Bay	iv. 48	O	Absent beyond Peveril Point
	vi. 49	F	Absent beyond Peveril Point
	vi. 53	F	Rare beyond Peveril Point
Kimmeridge Bay	xi. 48	N	—
	vi. 53	F	—
Lulworth Cove	v. 49	R	—
	vi. 53	N	—
Osmington Mills	vii. 49	O–F	—
	vi. 53	O	—
Weymouth	iv. 48	F	5 % of *B. balanoides* population
	vi. 49	F	No perceptible increase
Portland Bill	vi. 49	N	—
	vi. 53	N	—
West Bay	xi. 48	R	5 small specimens in inner harbour
	vii. 49	N	—
	vii. 54	N	—
Seatown	vii. 49	N	—
Lyme Regis	xi. 48	N	—
	vii. 50	N	—
	vii. 54	N	—
Seaton	vi. 47	N	—
	xi. 48	N	—
	vii. 54	N	—
Sidmouth	vii. 54	N	—
Budleigh Salterton	viii. 47	N	—
	vii. 54	N	—
Starcross	ix. 47	N	—
	iii. 49	N	A.H.N.M.
	xi. 51	R	—
	iv. 54	F	—
Dawlish	v. 53	O	—
Teignmouth	viii. 49	O	Confined to River Teign estuary
	vii. 50	F	One specimen from Teignmouth pier
Torquay	ii. 48	N	P.N.J.C.
	vi. 49	R	—
	vi. 51	O–R	—
Paignton and Broadsands	xii. 47	R	—
	vi. 48	R	—
	vii. 50	R–O	—
	iv. 54	O	—

APPENDIX (*cont.*)

Place	Date	Density	Notes
Brixham Harbour	vii. 48	N	—
	viii. 49	R	—
	vii. 50	R–O	A self-maintaining colony at foot of breakwater
	xii. 51	O	—
	iv. 54	O	—
St Mary's Bay and Mansands	iv. 48	R	P.N.J.C.
	viii. 50	R	—
Dartmouth	iii. 48	N	—
	x. 49	R	P.N.J.C.
	iii. 50	O	G.W.R. Ferry
	iv. 54	C–A	Higher Ferry
Greenway, River Dart	ix. 49	C	P.N.J.C.
Galmpton	v. 48	N	P.N.J.C.
	iii. 49	O	M.W.H.D.
Stoke Gabriel	v. 48	N	P.N.J.C.
	iii. 50	O	—
Blackpool, Devon	iv. 50	N	—
Torcross	iv. 50	N	—
Charleton Bridge	iii. 50	C	—
	iv. 54	A	—
Kingsbridge	viii. 49	O	—
Head of Frogmore Creek, Salcombe	iv. 56	A	*Elminius* only barnacle. A.J.S.
Salcombe Harbour	iv. 49	R	—
	iii. 50	F	—
Salcombe, south beach	x. 48	N	—
	iii. 50	N	—
	iv. 54	O	—
Bolt Head	vi. 49	N	P.N.J.C.
	iv. 57	N	—
Thurlestone	vi. 49	N	P.N.J.C.
	iv. 57	N	—
Bantham, River Avon	iv. 49	N	P.N.J.C.
	vi. 49	R	—
Ermemouth	viii. 49	R	—
	v. 55	F–C	A.J.S.
Steer Point, River Yealm	vi. 49	N	P.N.J.C.
Newton Ferrers	x. 48	R–O	—
	viii. 49	F	—
	iv. 57	C	—
Breakwater, Plymouth	ix. 51	F–C	A.J.S.
	xii. 54	F–C	A.J.S.
	ii. 56	C	Abundance confined to sheltered side of breakwater. A.J.S.
Rum Bay, Plymouth	viii. 48	N	P.N.J.C.
Tinside, Plymouth	v. 46	O	On mussels on old pier. P.N.J.C.
	xii. 46	O	G.W.R. dock
	xii. 54	C–A	A.J.S.
River Plym, Laira Bridge	iii. 50	C	—
River Tamar, near Saltash	viii. 49	F	—
	xii. 54	A	A.J.S.
Torpoint	viii. 49	C	—
Hole's Hole, Tamar	ii. 56	C	A.J.S.
Rame Head	i. 50	R	P.N.J.C.
	v. 52	R	J.H.O.
	x. 56	F–C	A.J.S.
Looe Beach	ix. 49	N	A.H.N.M.
	i. 50	O	None to east of Looe on exposed rock. P.N.J.C.
Looe River	viii. 48	N	P.N.J.C.
	ix. 49	F	A.H.N.M.
	i. 50	F	P.N.J.C.
Polperro	viii. 48	N	P.N.J.C.
Fowey	i 50.	F	—
Par	i. 50	O	—
	v. 55	F	—
Charlestown	i. 50	N	—
Falmouth	i. 50	N	—
	iv. 56	R	A.J.S.

Place	Date	Density	Notes
Malpas	vi. 49	C	E.W.K.J.
Meanporth and Durgan	v. 50	N	—
Helford Passage	1947	O	Well established but not common. H.A.C.
	v. 50	O	—
Porth Navas	v. 50	F	—
	v. 55	C	A.J.S.
Gweek	v. 50	R	—
	v. 55	A	A.J.S.
Coverack	vi. 51	N	—
Lizard	vi. 51	N	—
	v. 55	N	A.J.S.
Porthleven	v. 50	N	—
	v. 55	N	A.J.S.
Prah Sands	v. 50	N	—
Penzance	v. 50	N	—
	v. 55	O	A.J.S.
Scilly	v. 55	N	A.J.S.
Mousehole, Lamorna, Treen, Sennen, Morvah, Zennor	v. 55	N	A.J.S.
St Ives	v. 50	N	—
	v. 55	O	A.J.S.
Hayle	v. 50	N	—
Porthcothan	viii. 48	N	D.P.W.
Padstowe	viii. 48	N	D.P.W.
Port Isaac	viii. 48	N	D.P.W.
	v. 53	N	—
Porth Gaverne	v. 53	N	—
	v. 55	N	A.J.S.
Tintagel	v. 53	N	—
Boscastle	v. 53	N	—
	v. 55	N	A.J.S.
Bude	v. 53	N	—
	v. 55	N	A.J.S.
Clovelly	viii. 49	N	P.N.J.C.
	v. 51	N	—
Westward Ho!	vii. 49	N	E.N.
	v. 51	N	—
	viii. 54	N	—
Barnstaple	vii. 49	N	E.N.
Appledore and Bideford	viii. 48	N	—
	vii. 49	N	E.N.
	vii. 52	R	E.N.
Saunton sands	vii. 49	N	E.N.
	viii. 54	N	—
Woolacombe	vii. 49	N	E.N.
	viii. 54	O	—
Ilfracombe	vii. 49	N	E.N.
	viii. 54	O	—
Combe Martin	v. 54	N	A.J.S.
Lynmouth	viii. 54	F	—
Porlock	viii. 54	F–C	—
Minehead	ix. 49	R	—
Blue Anchor	xii. 47	O	C.M.H.
	i. 48	R	P.N.J.C.
	ix. 49	R	—
	viii. 54	F	—
Watchet	xii. 47	N	C.M.H.
	ix. 49	O	—
	viii. 54	C	—
Kilve	viii. 54	A	—
Lylstock	v. 54	F	A.J.S.
Weston-super-mare	iii. 50	R	—
	v. 54	C	A.J.S.
Clevedon	iii. 50	N	—
Portishead	iii. 50	N	—
	v. 54	N	A.J.S.
Newport (Mon)	viii. 49	N	A.H.N.M.
Cardiff	viii. 49	N	A.H.N.M.
Penarth	viii. 49	O	A.H.N.M.
Sully Point	viii. 49	N	A.H.N.M.
Barry	x. 47	R	G.D.W.
	vii. 54	O	—
Rhoose and Aberthaw	viii. 49	N	A.H.N.M.
	vii. 54	O–R	—
Stout Point	viii. 49	N	A.H.N.M.

Place	Date	Density	Notes
Nash Point	viii. 49	R	A.H.N.M.
	vii. 54	C	—
Dunraven Castle	viii. 49	N	A.H.N.M.
Porthcawl	vii. 54	O	—
Port Talbot	viii. 49	N	A.H.N.M.
Swansea	viii. 49	R	A.H.N.M.
	vii. 54	C	—
Mumbles	viii. 49	N	A.H.N.M.
	vii. 54	F	—
Oxwich	viii. 53	F	—
Port Eynon	vii. 54	O	—
Worms Head, Gower	vii. 54	F	Mostly towards L.W.M.
Llanelly	viii. 49	R	A.H.N.M.
	viii 53	C	—
Pendine	viii. 49	N	A.H.N.M.
	viii. 53	C	—
Amroth	viii. 53	C	—
Saundersfoot	viii. 53	C	—
Tenby	viii. 49	N	A.H.N.M.
	viii. 53	O	—
Freshwater, west	viii. 53	N	—
Dale Fort	xi. 51	O	Just appeared at H.W.N. tide level. J.H.B.
Neyland	x. 46	N	—
	ix. 47	R–O	—
	iii. 49	C	A.H.N.M.
	viii. 53	C–A	—
St David's	viii. 53	N	—
Porthgain	viii. 53	N	—
Goodwick and Fishguard	iii. 49	N	A.H.N.M.
Newport	iii. 49	N	A.H.N.M.
Gwbert	viii. 53	N	—
Aberporth	viii. 53	N	—
Aberayron	viii. 53	N	—
Aberystwyth	viii. 53	N	—
	vii. 57	N	—
Borth	iv. 52	N	—
Barmouth	viii. 53	N	—
	v. 57	O	—
Mochras	viii. 53	N	—
Harlech	iv. 50	N	—
	iv. 56	N	—
Criccieth	vi. 52	N	—
	iii. 53	N	—
	iii. 54	R	E.W.K.J.
	v. 56	R	—
Afon Wen	v. 53	N	—
Pwllheli	v. 53	N	—
	viii. 55	O	E.W.K.J.
Llanbedrog	v. 53	N	—
	viii. 55	O–R	—
Abersoch	v. 53	N	—
	viii. 55	R	—
Trwyn Cilan	viii. 55	N	—
Hell's Mouth	viii. 55	N	—
Porth Oer	viii. 55	N	—
Nevin and Porth Dinlleyn	iv. 50	N	—
	viii. 55	C	None on exposed reefs, confined to bays
Trevor	v. 53	N	—
	viii. 55	F	—
Clynnog	iv. 50	N	—
	xii. 54	O	—
Llandwrog	xi. 51	N	—
	v. 55	O	—
Caernarvon	iv. 50	N	—
	x. 51	R	—
	xii. 52	N	—
	v. 53	N	—
	ix. 53	R	—
	viii. 55	F	—
Port Dinorwic	ii. 52	N	—
	v. 53	N	—
	v. 54	F	—
	vii. 55	F	—
Bangor	xi. 51	N	—
	ii. 52	N	—
	iii. 53	O–R	—
	xi. 53	C	Common, tubular bridge
	iii. 54	C	—
	iii. 55	A	—

Place	Date	Density	Notes
Llanddwyn	iv. 52	N	—
	v. 55	F	On mussel bed
Aberffraw	x. 51	N	—
	iii. 53	N	—
	xi. 53	N	—
	vi. 54	O	—
	viii. 55	F–C	—
Rhosneigr	iii. 52	N	—
	iii. 55	O	—
	viii. 55	F	—
Rhoscolyn	viii. 53	N	—
Porth Dafarch	v. 53	N	—
	viii. 55	N	—
Holyhead	iv. 50	R	—
	xi. 51	N	—
	v. 53	N	—
	viii. 55	F–C	Rather more common in inner harbour where there are fewer *B. balanoides*. Very common in inland sea
Church Bay	v. 53	N	—
	viii. 55	R	Little suitable substratum
Cemaes Bay	iv. 50	N	—
	vii. 53	N	—
	viii. 55	C	On walls, inner harbour
Bull Bay	iv. 50	N	—
	ii. 53	N	—
	vi. 53	N	—
	vi. 54	N	—
	viii. 55	F	—
Amlwch	iv. 50	N	—
	i. 53	N	—
	iii. 54	O	In submarine tunnel
Point Lynas Bay	xii. 52	N	—
	vi. 54	F	Occasional specimens on headland
Llys Dulas	ix. 52	N	—
Moelfre	xii. 52	O	—
Benllech	xi. 51	N	—
	vi. 52	N	—
	xii. 52	F	All of small size
	vi. 55	C	—
Penmon	iv. 52	N	—
Black Rock	viii. 52	O	—
	iv. 53	F	—
	iii. 54	C	—
Menai Bridge	vii. 51	N	—
	iv. 52	R	—
	iv. 53	O	Young spat frequent on pier, few elsewhere
	xii. 54	A	—
	vii. 55	A	—
Llanfairfechan	x. 51	N	—
	vi. 52	R	—
	xi. 53	F–C	—
	xii. 54	A	—
Conway	vii. 51	R	One specimen on a boat. E.W.K.J.
	x. 51	R	
	ix. 52	O	On mussels in River Conway
	vi. 53	C	Settling in fair numbers, 2–3/cm²
	vii. 55	A	—
Llandudno	x. 47	N	P.N.J.C.
	iii. 50	R	—
	xi. 51	R–O	—
	vii. 52	F–O	—
	x. 54	C–A	Less common towards Orme's Head
Colwyn Bay	ix. 47	N	—
	iii. 50	N	—
	iii. 51	N	—
	xi. 51	F	0·04/cm² on pier piles, where it is most abundant
	vii. 52	C	Adults 0·3/cm², spat settling heavily
	ix. 52	A	—
Abergele	xi. 51	A	—
Rhyl	ix. 47	N	—
	v. 50	N	—
	xi. 51	A	Common in river, abundant on piles of pier

APPENDIX (*cont.*)

Place	Date	Density	Notes
Rhyl	vi. 53	A	—
Mostyn	xi. 51	O	—
	vi. 53	F	—
Greenfields	vi. 53	A	—
Connahs Quay	vi. 53	A	Survived high cyanide concentration during fish mortality of 1953, except in immediate vicinity of effluent
Heswall	xi. 51	C	—
West Kirby	v. 50	N	—
	xi. 51	C	—
	vi. 53	C–A	—
New Brighton	x. 47	N	P.N.J.C.
	v. 50	A	—
	xi. 51	A	—
	vi. 53	A	—
Liverpool	x. 47	N	P.N.J.C.
	v. 50	O	—
	xi. 51	C	—
Point of Air	ix. 55	N	Very unsuitable area, shingle scour
Ramsey	i. 52	R	A.J.S.
	ii. 53	N	A.J.S.
	ix. 55	F	A few 1–1½ years old
Laxey	ix. 55	O	Rare except at H.W near stream
Douglas	ix. 55	R	Two large individuals only
Castletown	ix. 55	N	—
Port Erin	ix. 55	N	—
Peel	ix. 55	N	—
Lytham St Anne's	x. 47	N	P.N.J.C.
	v. 50	O	—
Blackpool	v. 50	C	—
	ix. 53	A	—
Rossal	x. 47	N	P.N.J.C.
	v. 50	F	—
	x. 53	C	Heavy scour reduces numbers
River Wyre, Fleetwood	v. 50	O	—
Morecambe	vi. 50	A	Growing on parieties and valves of existing *B. balanoides* population
Grange-over-Sands	viii. 52	A	—
Bardsea	vii. 53	A	—
Barrow, Walney Channel	vi. 50	O	—
Barrow, Walney Island	vi. 50	N	—
	vii. 53	F–C	—
Millom	viii. 52	F	—
Ravenglass	vi. 50	O	On railway bridge, only 1 or 2 specimens
	viii. 52	C	On mussel beds, less common than *B. balanoides*
	vii. 53	C–A	Nearly as common as *B. balanoides*
	viii. 55	A	*Elminius* three times as common as *B. balanoides*. Spatfall 1·5/cm²
Seascale	vi. 50	N	—
	viii. 52	F–C	About 0·1/cm², patchy, much less common than *B. balanoides*
	vii. 53	C	About 0·25/cm² in groups
	viii. 55	A	About 1·5/cm², equal to *B. balanoides*
St Bees	vi. 50	N	—
	viii. 52	O–R	—

Place	Date	Density	Notes
St Bees	vii. 53	C	As high as 0·2/cm² in patches
	viii. 55	C	Adults 0·06/cm², spat 1/cm²
Whitehaven	vi. 50	N	—
	vii. 53	F–O	Up to 0·04/cm²
	viii. 55	C–A	Abundant on loose stones in harbour
Harrington	vi. 50	N	—
	vii. 53	R	—
Workington	viii. 52	N	Much scour, not very suitable
Maryport	vi. 50	N	—
	viii. 52	N	—
	viii. 55	C–A	—
River Nith, Overton Merse	iii. 51	R	Found at H.W. where only suitable stones exist. P.N.J.C.
	viii. 55	F	—
Sutherness Point	x. 50	R	—
	viii. 55	A	Spatfall 25/cm²
Rockliffe, Rough Firth	viii. 55	A	—
Port Mary	viii. 55	O	Mainly at L.W. under stones
Manxman's Lake	viii. 55	F	—
Kircudbright Bridge	viii. 55	C	—
Fleet Bay	ix. 53	N	—
	viii. 55	C–A	All rather small, spatfall 10/cm²
Ravenshall Rocks	viii. 52	N	—
	ix. 53	N	—
	viii. 55	O	—
Creetown	viii. 52	N	—
	viii. 55	C	Much less common than *B. balanoides*
Garliestown	viii. 55	O	No spatfall seen
Isle of Whithorn	viii. 55	O	—
Monreith Bay	viii. 55	N	—
Luce Bay, Port William	ix. 53	N	—
	viii. 55	N	—
Auchenmalg Bay	ix. 53	N	—
	viii. 55	N	—
Sandhead	ix. 53	N	—
	viii. 55	N	—
Ardwell	ix. 53	N	—
	viii. 55	N	—
Drummore	ix. 53	N	—
	viii. 55	R	—
Port Patrick	i. 50	N	—
Corsewall Pt	ix. 53	N	—
Stranraer, Loch Ryan	i. 50	O	—
	ix. 53	O–R	All old specimens
	ix. 55	O–R	No change
Kirkcolm	ix. 53	R	—
Ballantrae	i. 50	N	—
	ix. 53	N	—
Lendalfoot	ix. 53	N	—
Girvan	ix. 53	N	—
Ayr	i. 50	N	—
Troon	i. 50	N	—
	x. 53	N	—
Ardrossan Saltcoats	i. 50	N	—
	x. 53	N	—
West Kilbride	x. 50	N	—
Fairlie	x. 50	N	—
Largs	x. 50	N	—
	x. 53	N	—
Dumbarton	x. 50	N	—
Millport, Isle of Cumbrae	x. 50	N	—
	1955	R	J.H.C.

Observers: J.H.B., Mr J. H. Barrett; M.W.H.B., Mr M. W. H. Bishop; H.O.B., Dr H. O. Bull; P.N.J.C., Dr P. N. J. Chipperfield; H.A.C., Dr H. A. Cole; J.H.C., Dr J. H. Connell; M.W.H.D., Mr M. W. H. Dowell; C.M.H., Miss C. M. Harrison; E.W.K.J., Prof. E. W. Knight-Jones; A.H.N.M., Mr A. H. N. Molesworth; E.N. Mr E. Norris; J.H.O., the late Prof. J. H. Orton; A.J.S., Dr A. J. Southward; E.A.S., Prof. E. A. Spaul; H.G.S., Dr H. G. Stubbings; G.D.W., Dr G. D. Waugh; D.P.W., Dr D.P. Wilson.

Careful searches have also been carried out on west, north and east coasts of Scotland, and on the coasts of Ireland, especially the ports Belfast, Dublin, Larne and Rosslare. Up to 1953 no *Elminius* was found north of Loch Ryan in Scotland, nor anywhere in Ireland.