MORPHOLOGICAL VARIATIONS IN *MYTILUS* FROM SOUTH-WEST ENGLAND IN RELATION TO THE OCCURRENCE OF *M. GALLOPROVINCIALIS* LAMARCK.

by

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Résumé

En rapport avec les différences de forme de la coquille de *Mytilus edulis,* les auteurs réexaminent la place systématique d'une Moule caractéristique, le type Padstow du sud-ouest de l'Angleterre.

Dans les ports et les endroits abrités, on peut trouver deux types faciles à identifier, mais le type Padstow est plus variable qu'on ne l'a cru jusqu'ici. Dans cet article, est décrite une gamme étendue de caractéristiques concernant les coquilles et est discutée leur valeur en ce qui concerne l'identification. Cependant, en d'autres localités, sur les côtes non abritées, par exemple, il est plus difficile de discerner les deux types de Moules.

Bien que l'espèce *Mytilus galloprovincialis* des côtes de l'Europe occidentale présente aussi beaucoup de variations, il semble que le type Padstow et la *M. galloprovincialis* soient des types de Moules identiques.

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INTRODUCTION

In 1957, Hepper reported that the south-west coasts of England were dominated by a form of mussel "the Padstow mussel" that accorded closely to *Mytilus galloprovincialis* (Lmk) the "Mediterranean mussel". Subsequent publications have accepted that this mussel occurs in warmer British waters (Barrett & Yonge, 1958; Kitching, Sloane & Ebling, 1959; Bassindale & Clark, 1960; Ebling, Sleigh, Sloane & Kitching, 1960). Lewis and Powell (1961) however, found that mussels apparently similar in shell form to the "Padstow mussel", occurred on many British coasts and concluded that these represented "a widely distributed but little known form of *M. edulis* resulting from slow growth and/or old age". After consideration of the literature relating to descriptions of the two forms, they further concluded that the most reliable distinguishing feature appeared to be the colour of the mantle edge, and that on present information, *M. galloprovincialis* could not be considered as anything but a race or sub-species of *M. edulis*, a view also held by several other workers (Dodge, 1952; Soot-Ryen, 1955; Bouxin, 1956). Subsequently, Lewis (unpublished) examined mussels from open coasts of Cornwall (but not from the Padstow area itself) and apart from à high incidence of the dark coloured mantle edges that characterised the "Padstow mussel", was unable to separate the two entities on the basis of the shell characters and proportions cited by Hepper. More recently, Hobden (1967) commented upon the variable extent to which the *galloprovincialis* characters occurred together in individual animals from Padstow.

During a recent study of *M. edulis* from habitats on the East coast of Yorkshire, a very wide range of shell form has been found, much of the variation depending on age and environmental conditions. Details are given elsewhere (Seed, 1968) and for present purposes it will suffice to record that the degree of variation in this one geographical area is even wider than that described by Lewis and Powell (1961) and included one habitat form (Plate III, A) that on shell characters alone appeared indistinguishable from the "Padstow mussel". When such shells were shown to B. Hepper, he agreed that, had he not known of their North Sea origin, he would have regarded them as "Padstow types".

In these circumstances and because of the previously mentioned failure to find the typical "Padstow type" on exposed Cornish shores, it appeared that this mussel might be but a phenotypic variant of *M. edulis* and that the entire matter warranted re-examination. Visits were therefore made to sites on the coasts of Devon and Cornwall between Instow and Penzance and we are most indebted to B. Hepper for directing us to the exact site in the Camel Estuary—near the village of Rock—at which his original Padstow type was first distinguished.

Over 2000 mussels were collected for later laboratory examination and many others were studied in the field. Those from the Camel Estuary and especially Rock, proved very interesting since here two fairly easily distinguishable forms were living together. They maintained their identity even in young individuals suggesting that the differences were under genetic control. Nevertheless, samples from some other habitats revealed that both forms respond in a similar way to environmental factors and to such extent that in some cases distinction between the "Padstow" and *edulis* types became difficult or even impossible in the field, especially in the open coast animals which constitue the bulk of the mussel population. In spite of these difficulties and anticipating the data given later in this paper, there now appears stronger evidence than existed before for believing that two "forms" of *Mytilus* do occur in S.W. Britain. This interim conclusion, based mainly on shell characters, clearly needs substantiation on other grounds, but in view of the wide interest in this problem, this interim report is presented pending the outcome of wider ranging and longer term investigations, especially of reproduction.

We shall first describe the differences between the "Padstow type" and *M. edulis* from Rock and then consider the variation found in other habitats, the difficulties of identification therein, and the relative diagnostic value of the various morphological features.

A COMPARISON OF THE PADSTOW MUSSEL AND *M. EDULIS* FROM ROCK IN THE CAMEL ESTUARY.

The features by which Hepper distinguished the "Padstow mussel" from local *edulis* were:

1) umbones more pronounced, more pointed and down-turned;
2) shells proportionately higher;
3) shells less angular, especially where the front and upper margins meet;
4) capable of attaining a larger size;
5) mantle edge blue, purple or violet compared with the light straw colour of *edulis*.

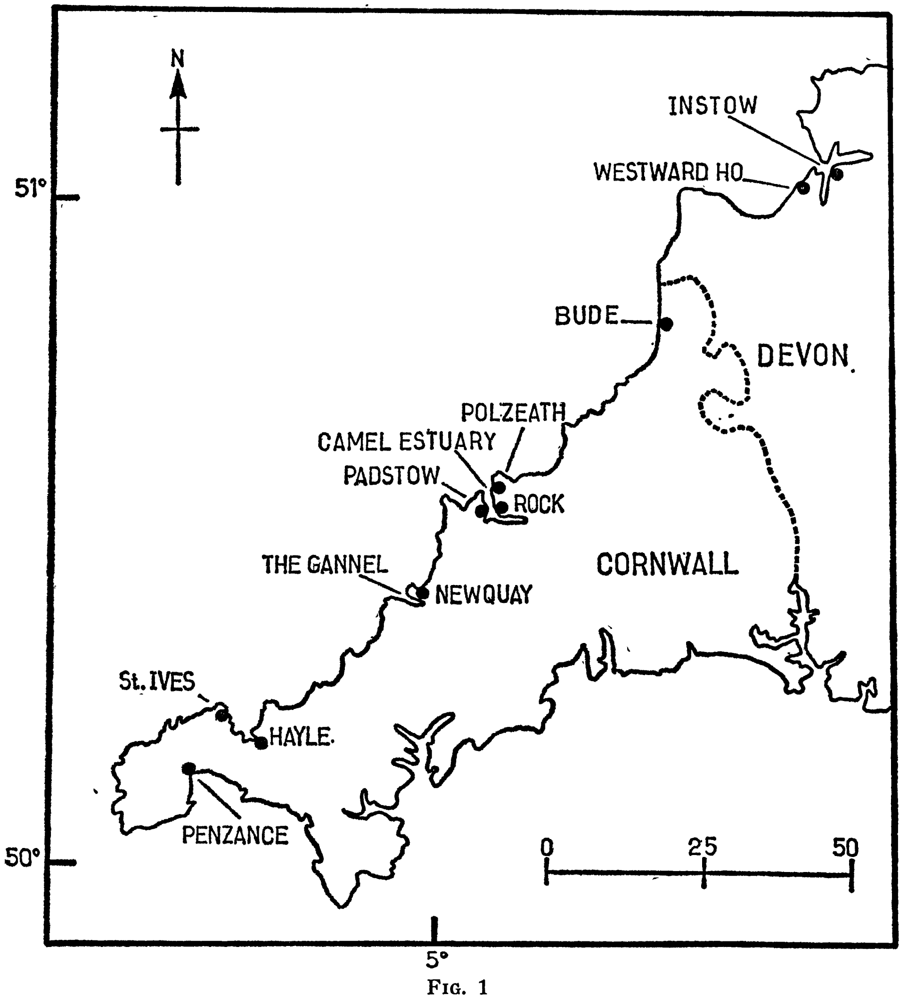


Fig. 1

Map of main area dealt with in the text. (Scale in km)

In general, we agree with this diagnosis but consider that amplification is needed in some cases, because of the range of variability and that other features are possibly more reliable. In the literature relating to differences between *M. edulis* and *M. galloprovincialis* (Bucquoy, Dautzenberg & Dolfus, 1887; Dautzenberg, 1897; Soot-Ryen, 1955; Bouxin, 1956; Lubet, 1959), additional characters used include the size and insertion of the anterior adductor muscle, the presence or absence of longitudinal bands or rays on the shell and differences in the sexual cycle.

I. General shell shape.

Although Hepper's length/height ratio of 1.77 for "Padstow types" and 1.95 for *edulis* appeared to be supported by our initial findings (1.75:1.90 for animals of mean length 5.5 cm) examination of all size groups in both forms indicates that this ratio varies considerably with age (=length) as it does in *edulis* on North Sea coasts (Seed, 1968). Table 1 shows shell height and weight values for unit length categories extracted from graphs based on samples of 150 specimens of each form ranging from 1-9 cm in length. Whilst the length/height values vary between ca. 1.5 and 2.2, those for the "Padstow type" are consistently slightly lower than those for *edulis* of the same length, indicating slightly greater relative height in the "Padstow type". The table also shows the *edulis* shells to be consistently heavier in animals of equal length.

TABLE 1.

Length (cm)	'Padstow mussel'			*M. edulis*		
	Height (cm)	Length/Height	Weight (g)	Height (cm)	Length/Height	Weight (g)
1.0	0.68	1.47	—	0.65	1.54	—
2.0	1.25	1.60	—	1.17	1.71	—
3.0	1.81	1.65	1.30	1.70	1.76	1.41
4.0	2.38	1.68	3.22	2.20	1.82	3.50
5.0	2.90	1.72	6.20	2.68	1.87	6.82
6.0	3.38	1.78	10.25	3.13	1.92	11.50
7.0	3.80	1.84	15.80	3.52	1.99	18.40
8.0	4.10	1.95	23.48	3.84	2.09	28.41
9.0	4.31	2.09	32.80	4.03	2.23	44.42

Plate I, A and B shows the range of overall shell shape in the two forms at Rock. In *edulis,* the majority of younger specimens are slightly convex on the whole or part of the ventral margin, while many of the older animals show the concave curvature (and divergent umbones) described by Lewis and Powell (1961) and Seed (1968).

While the "Padstow types" were often rounded dorsally rather than angular (as described by Hepper), this was by no means constant and the ventral margin varied from a few that were slightly convex, via many that were fairly straight, except for a down-turn at the anterior end, to some that were concave over the entire length and were exhibiting the same type of overall curvature found in some old *edulis*. These concave and the slightly convex forms together amounted to about 12 p. 100 of our sample so that the majority exhibited some form of anterior end curvature or beaking—as Hepper

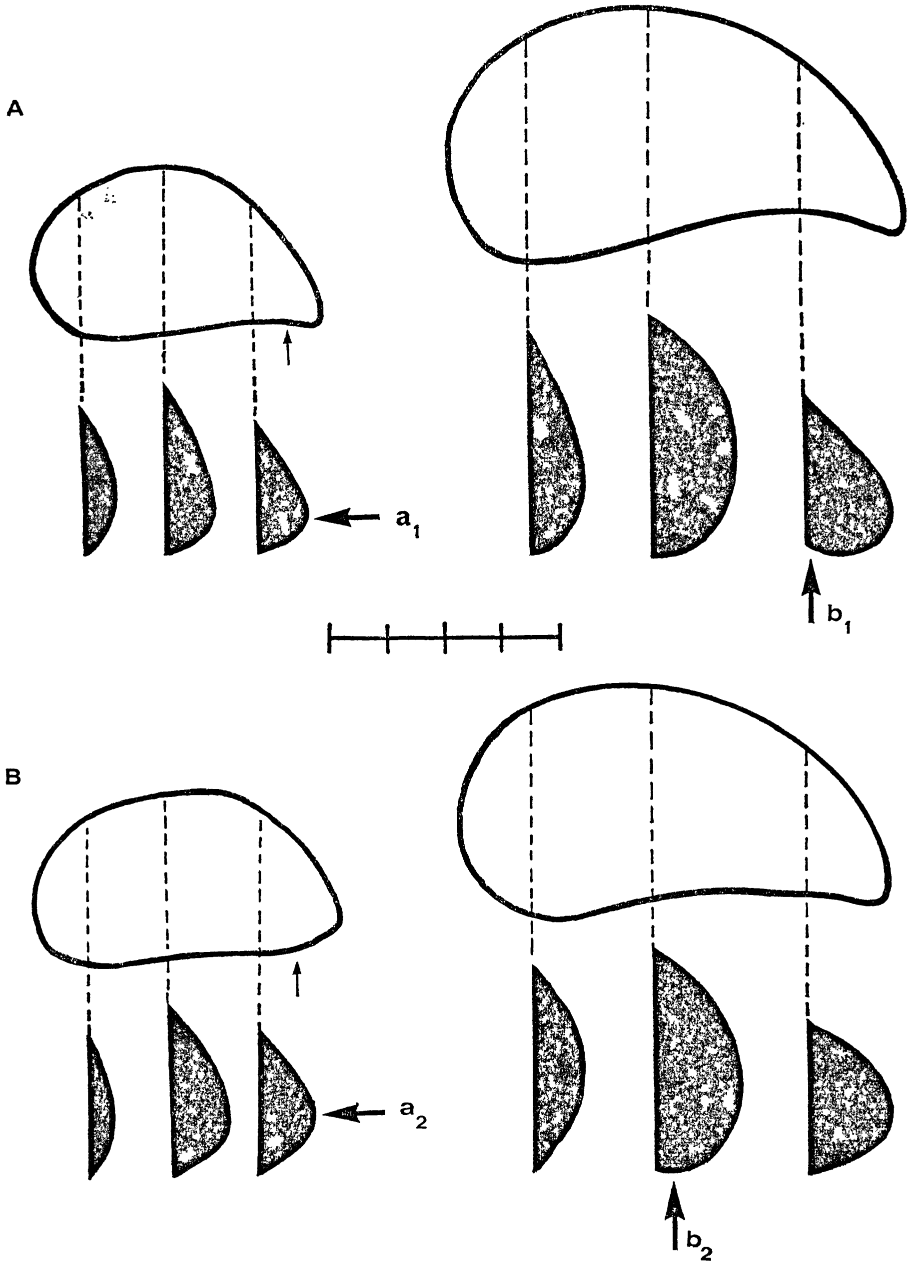


FIG. 2

Transverse sections of A) young and old "Padstow mussels", and B) young and old *M. edulis*, from Rock in the Camel Estuary.

Arrows, a_1, b_1, a_2, b_2 refer to points discussed in the text. (Scale in cm) first reported. (The extent to which this beaking involves the umbo, lunule and ventral margin, singly or jointly, varies greatly and the relationships of these parts are examined in detail below.) When this ventral variation is allied to that on the dorsal and ligamentary edges, it is clear that overall shell outline is not constant and by itself does not permit certain identification for all individual animals. Taken in conjunction with other characters described below, the differences between the two types at Rock were sufficiently great to be of help in identification. (Here it must be stressed that when the "Padstow type" from Rock is compared with *edulis* from other localities differences in overall shell shape are less discernable - cf. Plate I, B with the Whitby Harbour mussels in Plate III, A.)

2. Transverse profile of shell.

Fig. 2 shows sections cut at various points through young and old "Padstow mussels" and *edulis* and reveals a feature found to be very useful in field identification. The greatest width of the animal is nearer the ventral margin in the "Padstow type" than in *edulis* (Fig. 2, a_1 and a_2) and, consequently, the ventral part of the animal tends to be flatter. In older animals where shell growth is concentrated mainly on the ventral and posterior regions, the lower part of each valve comes to lie in an increasingly more horizontal plane, until in many "Padstow types" the ventral edge actually rises again in the mid line (Fig. 2, b_1). This inrolling is often most marked immediately behind the lunule and its effect on the shape of the anterior end is described below. Old *edulis* also exhibit this flattening of the ventral surface (Fig. 2, b_2) and even inrolling in a few very old specimens but here it occurs about midway along the ventral edge and is clearly a concommitant of the ventro/posterior shell deposition that causes the ventral curvature (Seed, 1968).

3. Shape of the anterior end.

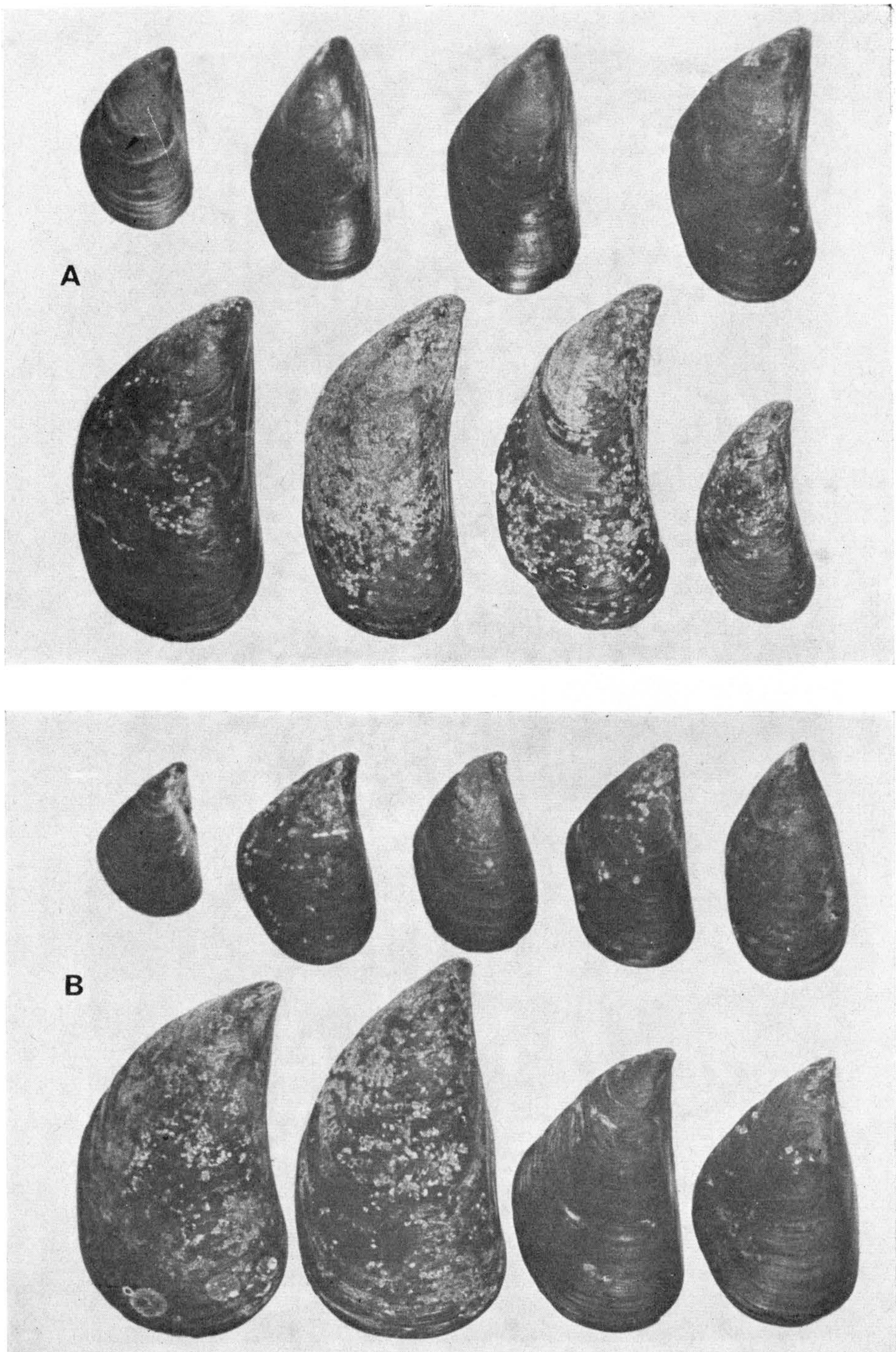
The more pointed and down-turned anterior end in "Padstow mussels" is not so much a function of the umbones themselves as

1) the way in which growth increments posterior to the umbo on the ventral side converge on the lunule;

2) the position and size of the hinge-plate and lunule relative to the umbo.

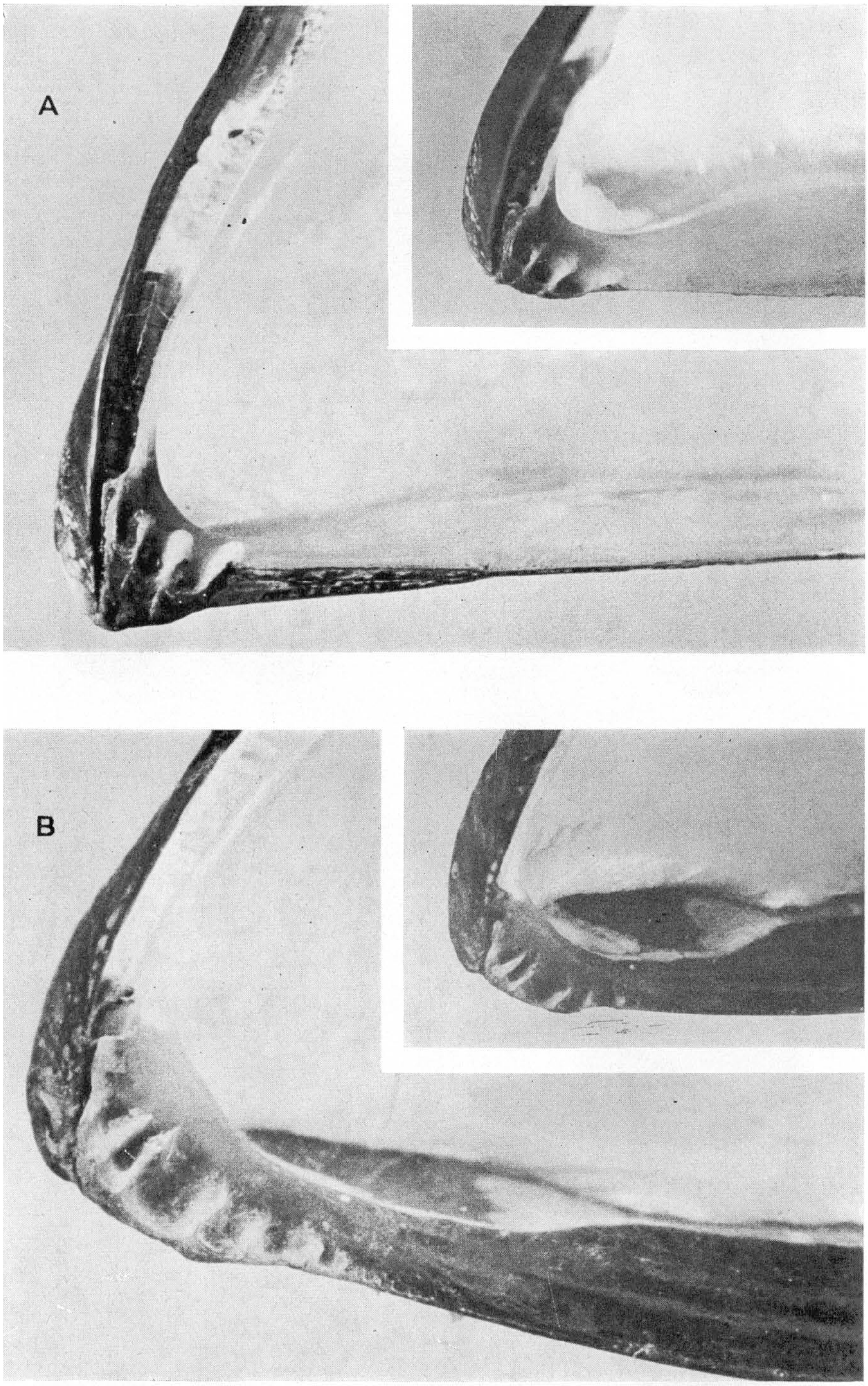
The angle at which the shell increments on the ventral edge lie in *edulis* causes the lunule (i.e. superimposed hinge-plates visible in ventral view) to grow in both a dorso-ventral and a lateral direction. Consequently, the hinge-plate and supporting lunule extend below the ventral tip of the umbo at most ages giving the blunt, snub-nosed appearance of the anterior end of the shell (Fig. 3; Plates II and IV). Although each increment must cause increasing separation of the umbones, this is barely detectable until the animals are old and shell increment is in an increasingly horizontal plane.

In the "Padstow mussel", on the other hand, where shell incre-



J.R. Lewis and R. Seed PLATE I

Examples of the range of shell shapes in A, *M. edulis* and B, the "Padstow mussel" from Rock in the Camel Estuary. (Scale in cm)



J.R. Lewis and R. Seed PLATE II

The anterior end of type specimens of A, the "Padstow mussel" and B, *M. edulis* from Rock.

Note the differences in hinge-plate form and size, the inrolled ventral edge behind the hinge-plate in A and the differing extent to which the anterior adductor muscle scar is visible before the shell is held at an inclined attitude, as it is in the insets. Both animals are 5.8 cm in length and the magnification is approximately the same.

ments behind the umbones are almost always in a more horizontal plane, the lunule grows laterally rather than dorso-ventrally and, therefore, is less likely to project below the umbo which retains its identity as a sharp, pointed structure as the anterior end. In ventral view, the lunule appears as a broad lateral structure the growth of which must cause the tips of the umbones to diverge.

Variations in the positions of the lunule, hinge-plate and ventral edge of the valve relative to the umbo, modify the degree of pointedness and down-turn at the anterior end (Plate IV). In many *edulis,* the blunt umbo/lunule curve leads into the curve of the valve edge without any change of profile (Plate IV, A) but in some young, thin-shelled forms, the combined umbo/lunule area protrudes as a slight bulbous

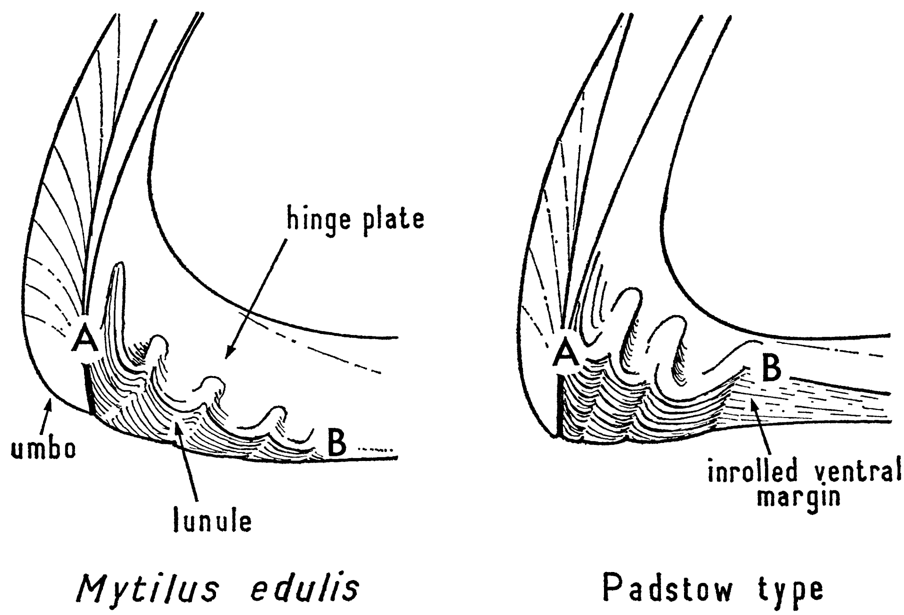


FIG. 3

Diagrams showing the form of the hinge-plate in *M. edulis* and the "Padstow mussel". The distance between points A and B indicates the measurement taken as length of the hinge-plate in Figs. 4, 5 and 8. The rearmost point was placed either behind the last major crenulation or depression, or midway along the series of accessory crenulations when present.

swelling, even in animals that are convex ventrally. This swelling is rare in old, thicker shelled animals partly because these are often badly eroded anteriorly but also because the changed angle of shell deposition tends to raise the hinge-plate towards a higher position in the mid line (Plate IV, D).

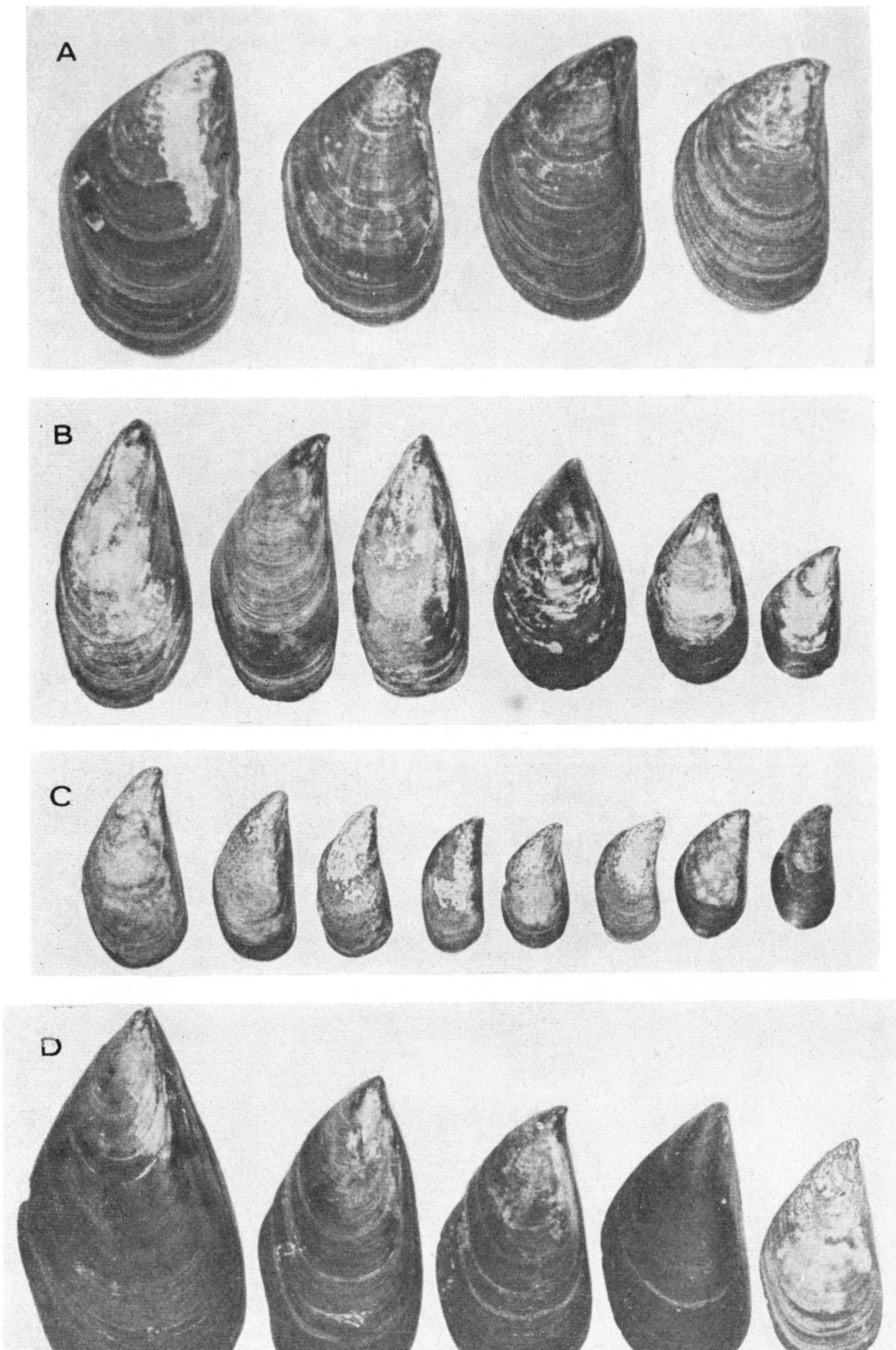
In the "Padstow type", the hinge-plate may be slightly dorsal to the umbo leaving the anterior end very pointed or slightly beaked, or it may lie parallel to it so that the lunule projects slightly to give an umbo/lunule swelling as in *edulis.* In this case, however, it is usually rendered more prominent because of the slight inrolling of the valve edge immediately behind the hinge-plate (Plate IV, F and G). Moving backwards from this point, the valve edge rapidly twists through the horizontal to the normal outward slope. This region with the rapid change of angle therefore acts as a pivot anterior to which growth increments widen the animal and leave the anterior end pointed in side view, but behind which growth increases the dorso-ventral measurement. This downward growth over most of the ventral edge therefore has the effect of making the anterior end appear to turn downwards. Not all specimens illustrate this feature as here described but its presence accentuates the prominence of the sharp umbo or umbo/lunule swelling. In very old specimens, the pivotal point appears to move backwards and produces curvature over more of the ventral edge. There are some "Padstow types", however, in which slight initial beaking has not been followed by further curvature. Without being able to follow growth parameters in marked individuals at different stages of their lives it is not possible to explain how such exception to this general hypothesis arises.

4. Size of the hinge-plate.

The hinge-plate in *edulis* is usually a gently curving structure whereas in the "Padstow type" it describes a much tighter arc with its rear often more clearly delimited from the adjacent ventral edge of the valve (Plate II; Fig. 3). This difference in appearance accentuates the smaller relative size of the hinge-plate in the "Padstow type". Measurement of the hinge-plate presents some difficulties especially in *edulis* where the rear may be poorly defined and in old specimens of both types where small accessory crenulations (teeth) extend onto the valve edge—up to 40 have been found in extreme cases in very old *edulis*. (In a few specimens of both types, teeth were completely absent.)

Fig. 4 shows actual hinge-plate measurements for approximately 100 individuals of each type, and Fig. 5 illustrates the frequency distribution of values for the ratio hinge-plate length/shell length (×1000). The points measured are shown in Fig. 3. Both sets of data indicate that differences exist in the size of the hinge-plate as well as in its form, the mean value of the ratio in *edulis* being 72 ± 9 compared with 56 ± 8 for the "Padstow type". However, the degree of overlap is such that a random sample might well give a unimodal distribution and separation of individual mussels by size alone, without reference to the shape of the hinge-plate, would be uncertain except where values were very high (*edulis*) or very low ("Padstow type").

The above data relates to a low-level population that appeared to be fast-growing. A sample from higher levels at Rock containing smaller, more eroded and probably older animals gave values of 83 ± 13 and 67 ± 10 respectively for *edulis* and "Padstow types", while very high level, very eroded and gnarled specimens (just separable by other means) from another site had even higher values: 94 ± 12 and 74 ± 10 respectively. Thus, the difference between the two entities persisted at higher values, the latter possibly resulting from the cessation of length increment but continued ventral shell deposition that characterises old age.



J.R. Lewis and R. Seed **Plate III**

A, *M. edulis* from low levels in Whitby Harbour, N.E. England. B, C and D, "Padstow types" respectively from Polzeath (low level, exposed), Newquay (high-level, exposed) and Newquay Harbour (low-level, sheltered).

Note the sharply pointed and beaked anterior end in some *edulis* and the absence of these features in some Polzeath and Newquay specimens identifiable as "Padstow types" on other grounds. The small specimens from exposed sites at Newquay (C) are indistinguishable externally from *edulis* from similar habitats on North Sea Coasts. (Scale in cm)

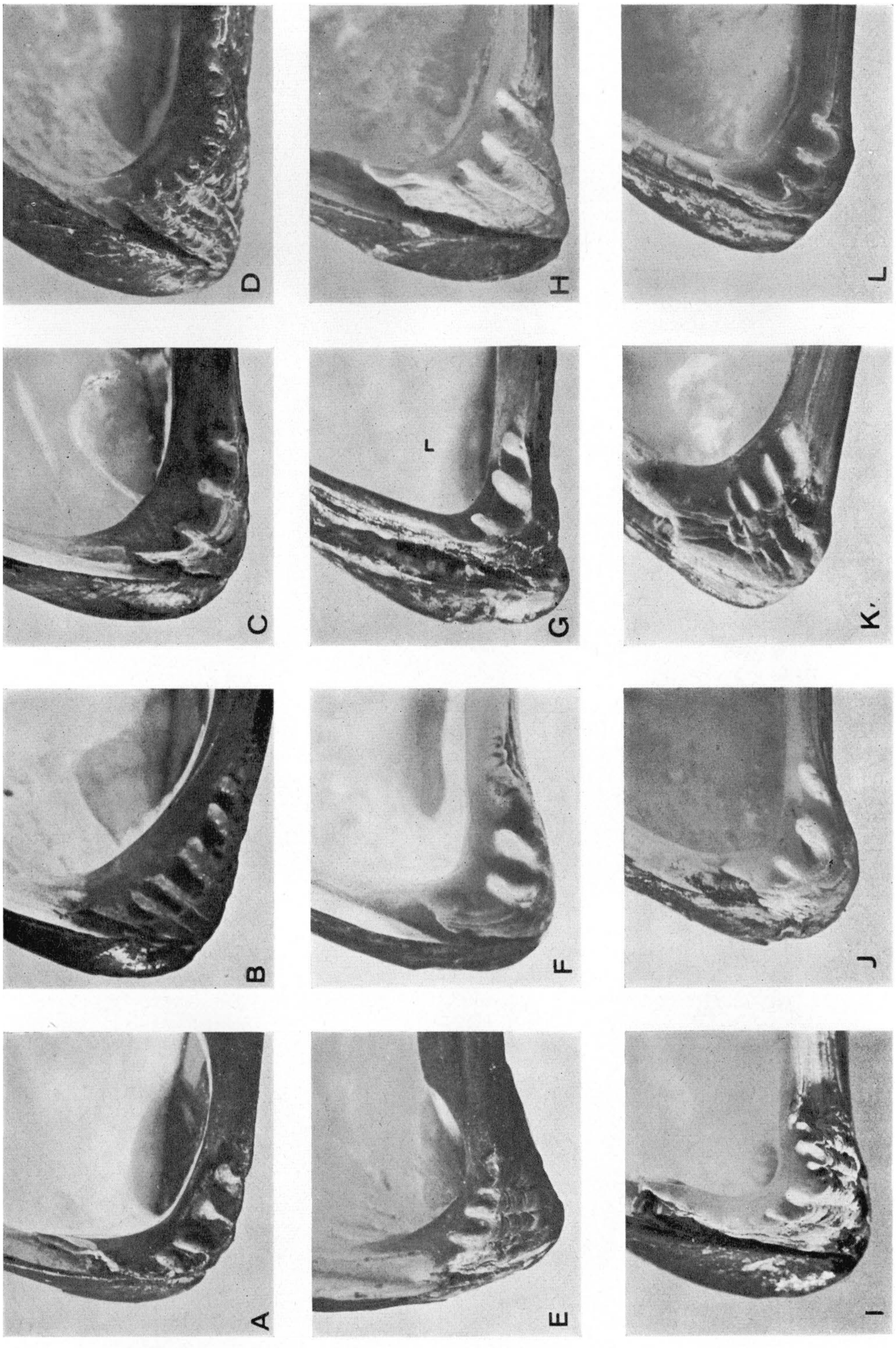


PLATE IV

Examples of hinge-plate variation.

M. edulis: A-D from Rock, E from Whitby Harbour.

"Padstow types": F-I from Rock, J from Newquay Harbour, K-L from Polzeath.

In *edulis*, note the large, gently-curving hinge-plate with more of the lunule visible as the hinge-plate becomes more dorsal in position in the older specimens. (e.g. D and E, and compare with old "Padstow types" H and I). Whilst the hinge-plate is small and cupshaped in most "Padstow types" its position relative to the umbo greatly modifies the profile of the anterior end.

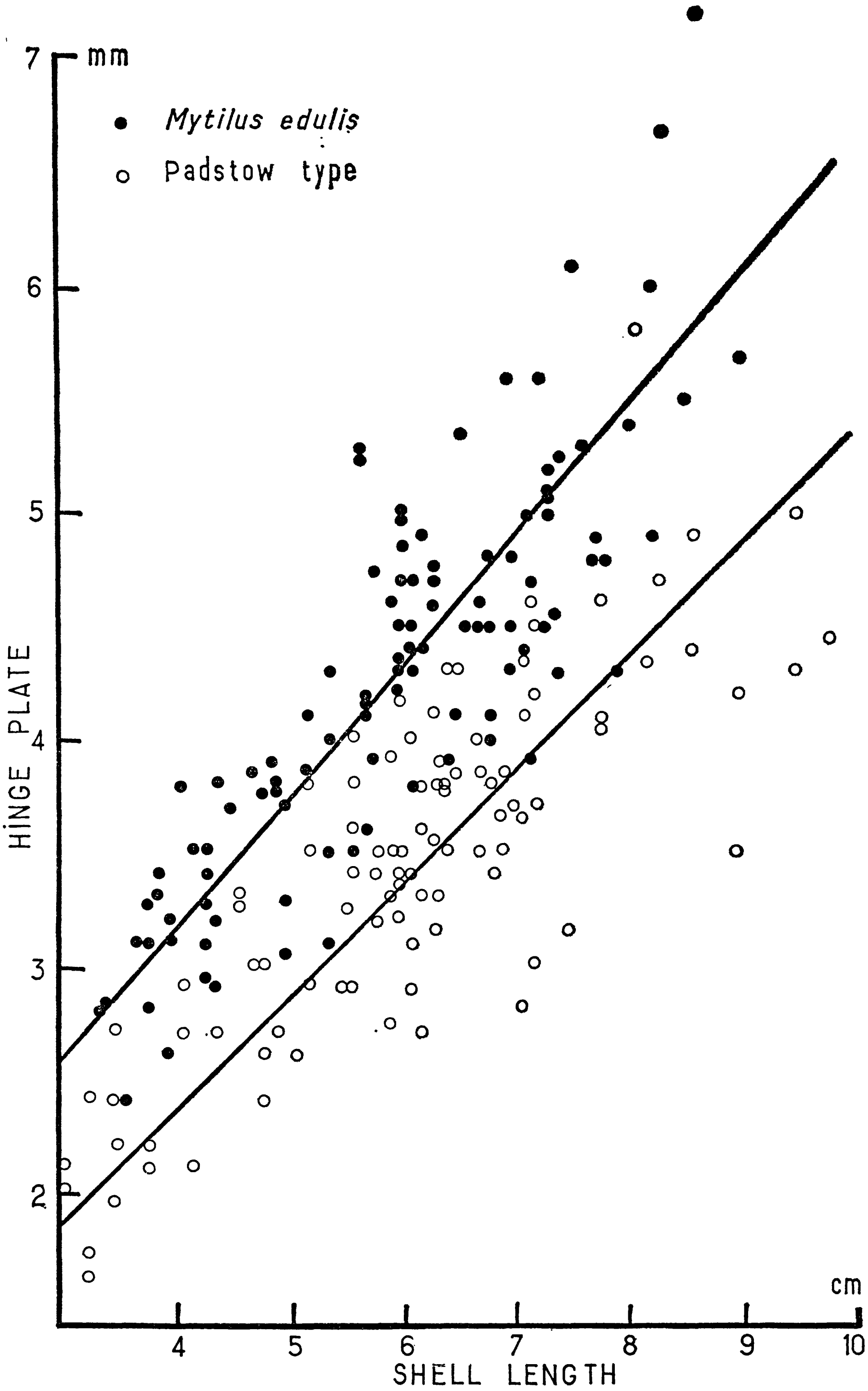


FIG. 4

The relationship of hinge-plate length to shell length for low-level samples of *M. edulis* and the "Padstow mussel" from Rock.

5. Anterior adductor muscle scar.

This character was not referred to by Hepper but differences in size and insertion have been used by other authors in comparisons of *M. edulis* and *M. galloprovincialis* although with conflicting results. Lubet (1959), for example, referring to *M. galloprovincialis* states "muscle adducteur antérieur plus gros et à insertion moins latérale", whereas Soot-Ryen (1955) comments upon "the higher flatter forms

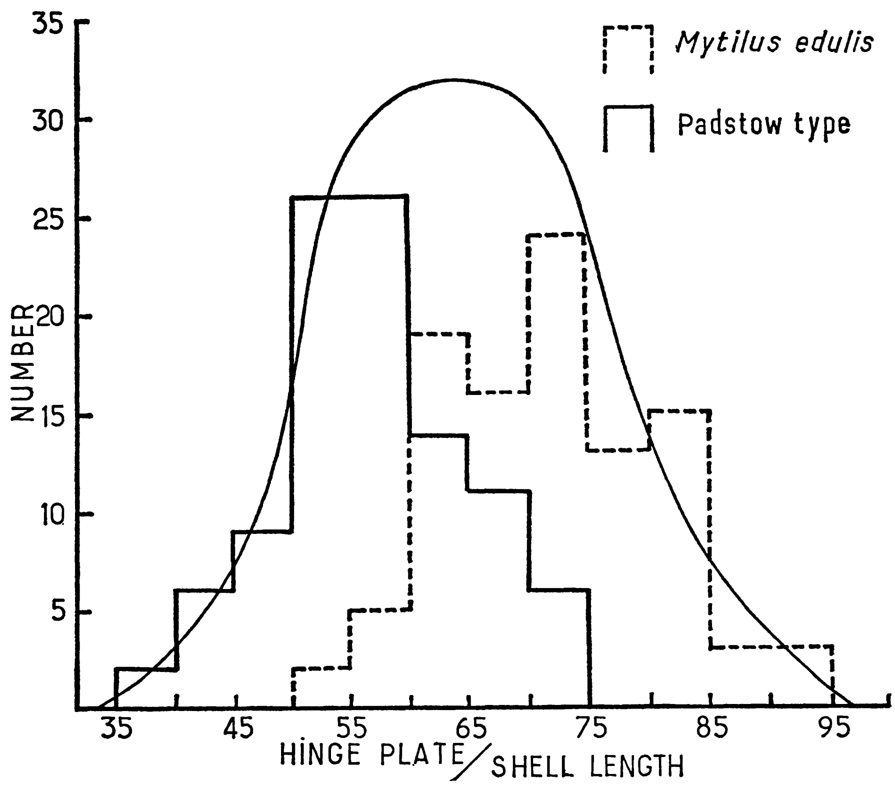


FIG. 5

Histogram showing the frequency distribution of values for the ratio hinge-plate length/shell length (×1000) for *M. edulis* and the "Padstow mussel" at Rock. (Data derived from Fig. 4.) The smooth curve indicates the unimodal distribution that would have resulted if the two samples had not been separated by other means beforehand.

with small anterior adductor muscles which are named *M. galloprovincialis* in the Mediterranean and *M. edulis diegensis* Coe in California".

Fig. 6 shows, for our Rock sample, the actual lengths of the scar at different shell lengths while Fig. 7 indicates the frequency distribution of values for the ratio scar length/shell length (×1000) giving mean values of 105±13 for *edulis* and 64±10 for "Padstow types". The distinctly bimodal frequency distribution for this

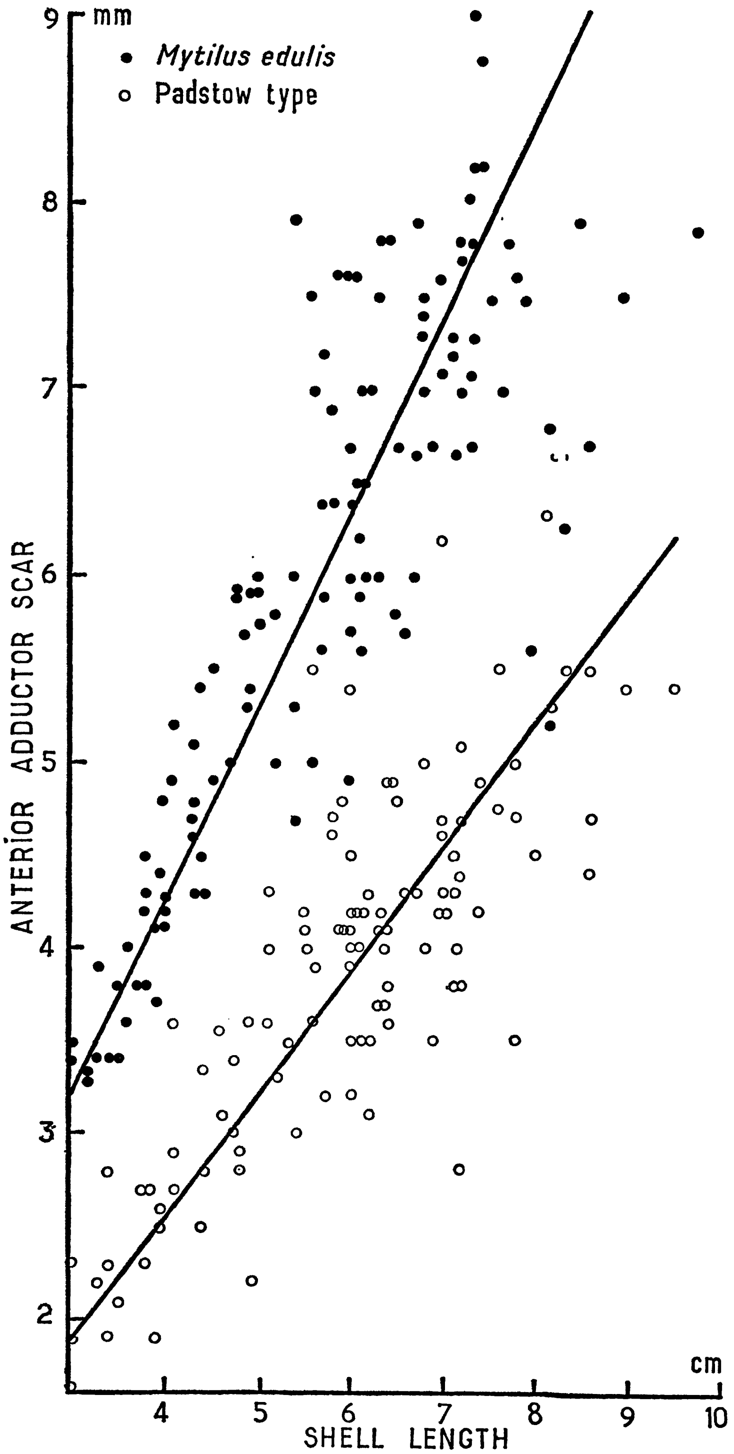


FIG. 6

The relationship between the length of the anterior adductor muscle scar and shell length in *M. edulis* and the "Padstow mussel" from Rock.

character would permit identification of individuals with a much higher degree of accuracy than was provided by the hinge-plate ratio. The greater size in *edulis* is accentuated by the conspicuousness of the blue prismatic layer standing out against the surrounding white nacrous layer, whereas in "Padstow types" the prismatic layer is often very pale at this point and examination under binoculars is often needed to determine the limits of the smaller scar. Because of the different plane of the valve at this point, the scar in "Padstow types" tends to lie further from the mid line of the animals, is on a more horizontal surface and, in old animals, is often enclosed by the inrolled ventral edge and hinge-plate to an extent that is rare in *edulis*.

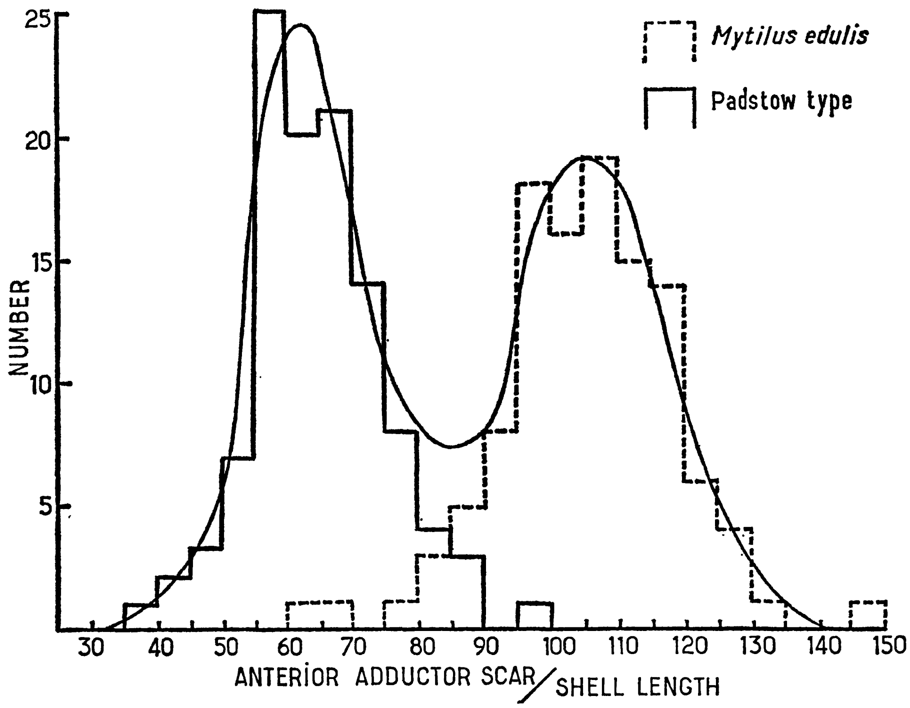


FIG. 7

Histogram showing the frequency distribution of values for the ratio anterior adductor scar length/shell length ×1000 for *M. edulis* and the "Padstow mussel" at Rock. (Data derived from Fig. 6.) The smooth curve shows the bimodal distribution that would have resulted if the two samples had not been separated by other means beforehand, and is in marked contrast with the unimodal curve in Fig. 5.

The scar of the posterior adductor muscle is less discrete and therefore less easy to measure, but some analyses of the diameter of the muscle itself suggest that it is larger in *edulis*. Values for mussels 3-9 cm in length ranged in Rock *edulis* from 0.5-1.66 cm and in "Padstow types" from 0.48-1.32 cm. However, in view of the very wide range of muscle sizes recorded in *edulis* from different habitats (Hancock, 1965 and personal observations), no further attempt was made to use this feature for identification purposes.

6. Shell colour.

The presence of longitudinal rays of deep colour on the shells of *M. edulis* and their absence in *M. galloprovincialis* has been postulated by Dautzenberg (1897) and Lubet (1959) although the colour plates in List's monograph (1902) show rays in his *M. galloprovincialis.* In Rock mussels, 24 p. 100 of *edulis* (166 in sample) were without rays while 12 p. 100 of the "Padstow types" (178 in sample) possessed them. Field observations elsewhere in the Camel Estuary confirmed that although rays are much more common in *edulis,* this character is not a reliable criterion for separating the two forms in this area. (It may be pointed out here that rays are seen in North Sea *edulis* in only 20-25 p. 100 of the population, in sites where shells are eroded.)

When the periostracum had been removed by boiling in soda, the prismatic layer of "Padstow types" was generally lighter (sometimes pale lilac or almost white) than the consistently deep blue of *edulis.* Occasional specimens of both forms lacked colour in the prismatic layer but appeared brown/straw in colour in the field due to the presence of the periostracum. A few such types had longitudinal rays of bluish purple.

7. Colour of mantle edge.

Hepper's finding that the "Padstow mussel" had a dark mantle edge was fully supported. The colour was a deep purplish blue or violet which although sometimes penetrating into the gills, left the rest of the mantle a contrasting creamy white. Although the majority of mantle edges in *edulis* were a light straw colour, darker shades existed and, in some cases, the darkest browns presented some difficulty, especially as the colour of the "Padstow types" appeared to lose some of its intensity when the animal had been opened for a short time.

Of the above characters, we found that the following criteria were the most useful for initial separation of the two entities *in the field* at Rock.

1) The shape of the anterior end.

2) The transverse section of the whole animal and the degree of flattening of the ventral surface, especially just behind the lunule.

3) The colour of the mantle edge.

The anterior beaking of the "Padstow type" was fairly useful once one had learnt to distinguish it from the curvature associated with old age that occurs in both forms. Overall, shell outline was less reliable by itself and, in some cases, very misleading but it is the most obvious and most quickly appreciated feature of bivalves. We found that with increasing experience it gave an initial identification that proved to be correct in about 80 p. 100 of cases, on the basis of the other characters above.

Our identifications were based, therefore, on the weighting of a number of characters but especially the three listed above. Thereafter the laboratory measurements of the anterior adductor scar (and to a lesser extent the hinge-plate form and size) supported the field diagnoses.

Confirmation of these morphological distinctions is now being sought by biochemical and cytological means and the times and duration of the breeding periods of the two types living under identical conditions are under investigation. The single samples of november 1966 showed the "Padstow type" to be rather less advanced in gametogenesis, the mantle being consistently thinner than those of *edulis* (25 *edulis* of mean length 6.52 cm had a mean mantle width of 2.82 mm whereas "Padstow types" of mean length 6.41 cm gave a value of 1.81 mm). 81 p. 100 of individuals, under 2 cm in a mixed sample, were of the "Padstow type" and, although this could be due to slower growth, it is more likely to reflect different spawning periods in 1966.

THE RANGE OF VARIATION IN OTHER HABITATS IN S.W. ENGLAND.

Experience of *M. edulis* in other districts has shown that the shell form and proportions are greatly influenced by age (irrespective of size) tidal level, density of mussels, and type of habitat (e.g. horizontal wave-swept rocks; sheltered harbour walls and pier piles). A continuous gradation of types exists (Seed, 1968) but, in summary, it can be said that low density, low-level pile and harbour mussels tend to be high and rounded in marked contrast with the elongate form more typical of the high density mussel beds of exposed coasts. High-level animals are much smaller and can live very much longer, because of lack of predators, and consequently may show the features of old age, i.e. they are wide rather than high, have overall curvature and divergent umbones, and are badly eroded at the anterior end.

Knowing that such variation could exist, we accordingly attempted to examinate mussels from habitats that differed from the Rock site which is a sheltered, flat or gently sloping area of rock and shingle. On the walls of Padstow Harbour, there was little difficulty of separation on the basis of our three principle criteria, but it was apparent that the *edulis* here were higher than the ground-living *edulis* of Rock (as occurs in Whitby Harbour) and that the "Padstow types" exhibited further variation in the overall shell outline. About half a mile west of Padstow Harbour, the large, low-level forms were similar to those at Rock, but the small, curved and eroded forms of the highest levels had lost their distinctive shell differences and were identifiable in the field only on the basis of mantle colour. In animals of less than 1-1.5 cm even, this became difficult to apply in many cases.

On exposed shores at Polzeath (at the entrance to the Camel Estuary), all specimens examined had dark mantles and were provisionally assigned to the "Padstow type" but the range of shell form differed considerably from that at Rock. The majority of animals were elongate, the largest low-level specimens having a mean L/H ratio of 2.16 (compared with 1.75 at Rock and 1.90 for Rock *edulis* in animals of similar length i.e. 5.5 cm) and a straight or convex ventral surface (Plate III, B). Although the anterior end was sometimes sharp, it only occasionally showed slight beaking. In the upper shore at Polzeath, animals greater than 3 cm in length were rare, many old forms showing some degree of overall curvature culminating in extreme reniform shapes and width/height ratios greater than unity, the condition described by Lewis and Powell (1961) for high-level *edulis* from Yorkshire.

Further south in the area of Newquay and the Gannel Estuary, only two animals with light mantle edges were found and so, assuming the constancy of this character, we provisionally classed the mussel populations as being almost entirely of the "Padstow type". At Hayle and St. Ives Harbour, the numbers of light types increased to 7 p. 100 and 6 p. 100 respectively. The variations in shell characters visible in the field then followed the same general pattern as in the Rock, Padstow and Polzeath area. Thus harbour and pile mussels of low density at low levels (e.g. Newquay and St Ives Harbours) or on very sheltered low-level rock (e.g. Gannel Estuary) were similar to those at Rock but smaller and with a tendency towards being more rectangular and less rounded dorsally (Plate III, D). Similarly, the closely packed, smaller animals of exposed sites were of the elongate or slightly curved form (Plate III, C) and had it not been for their purple mantles, would have been regarded by us as typical of *edulis* from similar habitats elsewhere in Britain. It was clearly animals of this type that one of us (J.R.L.) had previously examined in the St. Ives - Lands End region.

North of Padstow, at Instow and Westward Ho!, regions where Hepper respectively found 35 p. 100 and 88 p. 100 of the population to be of the "Padstow type", prolonged searching revealed only one animal with a purple mantle, but a wide range of *edulis* types, including some with the curvature and divergent umbones of old age.

It is most unfortunate that so few light mantle types (i.e. *edulis*) were available in the Polzeath, Newquay and St. Ives areas for comparison with the "Padstow type" growing under exposed conditions. Without this strict comparison we can only report that the responses of the "Padstow type" to environmental conditions appears to be so similar to that of *edulis* that the shell characters permitting field identification in the Rock/Padstow area can be partly or completely masked. Since so many of the open coast elongate forms of 2-3 cm or more are probably quite old, if not very old (Seed, 1968), their greater width destroys the transverse profile character, the shape of the anterior end is obscured by erosion, shell thickening and divergence of umbones, and the anterior beaking can be masked by general curvature, all these features being most evident in upper shore animals.

Because identification in the field in these localities was necessarily based mainly, and in some cases entirely, on mantle colour our failure to recognise any *edulis* types could have resulted from faulty application of this criterion or from lack of constancy in this character. Our later analyses of the relative sizes of the anterior adductor scar and of the hinge-plate suggest, however, that all the open coast samples were indeed of the "Padstow type" and that such characters may prove to be reliable diagnostic features.

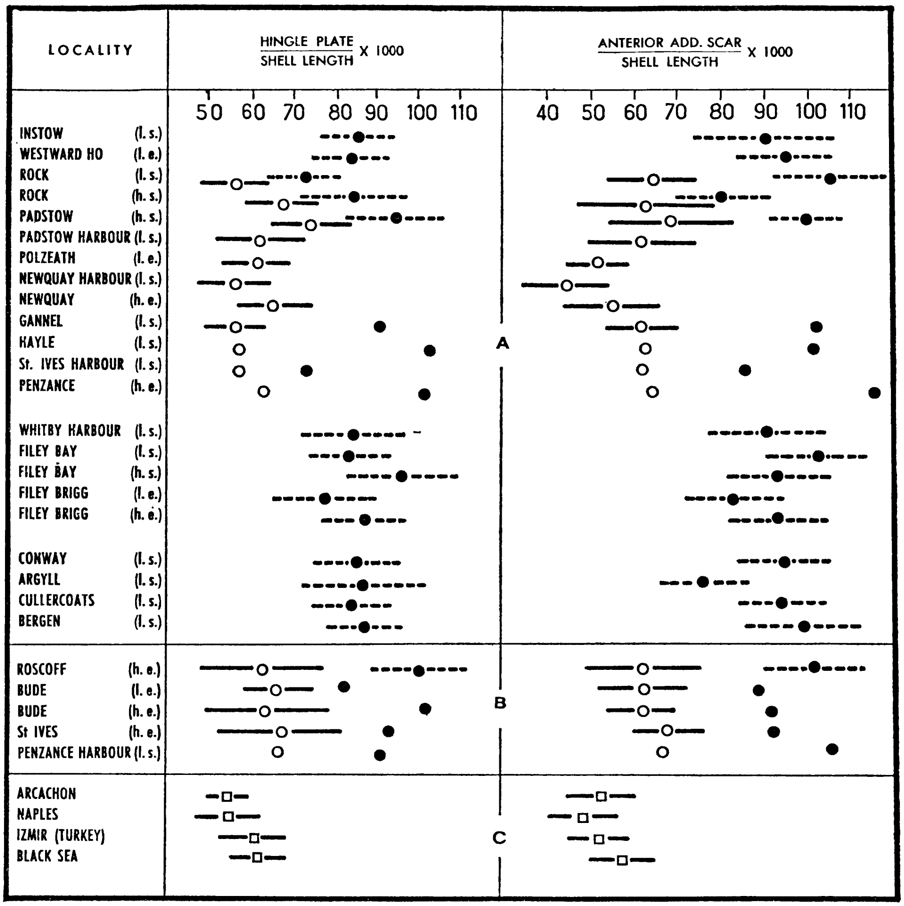


FIG. 8

The mean and standard deviation in the ratios hinge-plate length/shell length, and adductor scar length/shell length for mussels from a range of European localities. White circles: "Padstow types"; black circles: *M. edulis*; white squares: *M. galloprovincialis*.

(h) high-tidal level, (l) low tidal level, (e) exposed sites, (s) sheltered sites.

Where no standard deviation is shown, the sample is less than 20 specimens, elsewhere it is a minimum of 50, except at the Rock sites where the minimum sample was 125.

The division of the figure into sections A, B and C is explained in the text.

Fig. 8 shows the mean value and standard deviation in both ratios for samples from a range of S.W. England sites, together with data for mussels from a wide range of localities in Britain and Western Europe. The identification of the samples for sites in S.W. England in the upper section of the figure (A) rests on the three characters given on p. 238, or on the mantle colour alone for exposed shore populations. All mussels for localities further north were regarded as *edulis*. (The localities in the lower sections of the figure are considered later.)

In the original Rock samples (Fig. 5 and 7), the hinge-plate ratios for the two entities overlapped but the difference in the muscle scar ratios was much more distinct. For these S.W. England sites where few or no *edulis* types were identified the two ratios have values either within the range of the "Padstow type" or even lower, indicating even smaller hinge-plates and muscle scars. This is of particular significance for the open coast samples (Polzeath, Newquay) in providing characters that remain relatively constant (although of doubtful use in the field) when the other shell characters are masked or indeterminate.

In view of the variation in ratio values between different habitats and tidal levels in S.W. England, it is perhaps dubious practice to make comparisons with data from more distant shores. However, the ratio values for *edulis* from five contrasting sites in Yorkshire, together with those from other miscellaneous sample areas, are very much in line with the *edulis* values for Cornwall. The only discordant value —the low muscle scar ratio from Argyll—relates to a population of large and very old, eroded specimens in which some overgrowth of the scar by the nacreous layer made measurements difficult.

The importance and constancy of these differences in ratio values clearly needs testing from further habitats in which both forms grow together in quantity under identical conditions, and where they can be identified by as wide a range of characters as were available at Rock. Present evidence does however suggest that these ratios together with the shape of the hinge-plate are more reliable diagnostic features than any other shell characters.

Thus in the areas of S.W. England so far considered—from Padstow to Penzance—two forms of *Mytilus* appear to exist and the characters recommended for distinguishing the "Padstow type" are as follows (arranged in decreasing order of reliability or wide applicability):

1) the small size of the anterior adductor muscle scar;
2) the purple or violet mantle edge;
3) the shape and small size of the hinge-plate;
4) the pointed, anterior end;
5) the transverse profile and flattening of the ventral surface at and just behind the hinge-plate;
6) the down-turned, anterior end;
7) the rounded, dorsal margin of the shell.

The reason for placing the mantle colour second in this list will appear in the next section.

Although the morphological characteristics of such highly labile animals as mussels cannot be considered without reference to the environment, it seems likely that the maximum expression of their genetic potential will occur in habitats where growth is rapid and free from competitive, physical pressures. Such conditions will be approached most closely in the field in the low density, low-level beds of sheltered estuaries and harbours, and, indeed, it is in the low-level populations of Rock and of Padstow and Newquay Harbours that all of the above seven characters are most frequently combined in single individuals to produce mussels that are quite different from the local *edulis* which one must also assume to be exhibiting the maximum expression of their genetic potential.

Even in such habitats, however, some individuals will be in less favourable positions and may have experienced checks or interference with growth at different times in their lives and accordingly, it is those characters most affected by growth and environmental influence (i.e. gross shell shape and proportions—see Seed, 1968) in which the Rock population shows least constancy and which therefore appear last on our list.

On exposed coasts, where particularly high densities are common, or at high tidal levels, where a high percentage of old animals occur, further variations in shell shape and proportions are imposed, until for most of such populations only the mantle colour and the hinge and muscle scar characters remain as criteria for identification. It must be stressed that the problem of identification on open coasts is not to be dismissed as applying to only a few stunted animals. Because of the large extent of exposed coastline and the high density of small mussels thereon, these forms must constitute the majority of mussels in S.W. England.

THE RELATIONSHIP OF THE MANTLE EDGE COLOUR TO THE HINGE-PLATE AND MUSCLE SCAR RATIOS.

In the foregoing account, separation of doubtful specimens rested ultimately on the colour of the mantle edge and appeared to be confirmed by the hinge-plate and muscle scar ratios. Although separation by colour presented relatively few difficulties in the sites dealt with, we were aware that the colour of *edulis* can range from almost white to dark reddish brown. When the latter shades are viewed in the field against the dark-blue background of the shell, it becomes difficult to decide the point at which they merge into purple or violet. Lewis and Powell (1961) had encountered this difficulty in some specimens from S.W. Ireland, W. Scotland and W. Norway and, although conceding that mantle colour might be one way of separating *edulis* from *galloprovincialis,* had found it of doubtful utility for their particular samples.

Although this problem arose critically only in the Padstow high-level sample, we later obtained further samples—some rather small—from other sites and decided to compare identifications based on colour with those based on the shape of the hinge-plate and the hinge-plate and muscle scar ratios. These results are summarised in Table 2, together with an identification based on overall shell shape, the latter data again demonstrating that even with our increasing experience this criterion was difficult to apply except in the case of the sample from Roscoff. The remaining samples from S.W. England show that identification by colour or by hinge-plate and muscle scar characters does not produce identical results. Some dark mantle types from all sites were found with *edulis* characters, but the opposite combination has so far proved to be very rare. In the Bude high-level sample, the dark, reddish brown appeared too dark for *edulis* but not purplish or violet enough for the "Padstow type" and no identification by colour was made. The difficulty here, which is also reflected in the wide discrepancy of identification by the other means, perhaps reflects some geographical influence and breakdown of differences for at our next more northerly site (Westward Ho!) we found only one dark mantle and no other "Padstow type" characters.

TABLE 2

Locality	Sample size	Method of identification						
		Mantle colour		Shell shape			Hinge and add. scar	
		'Padstow'	*edulis*	'Padstow'	uncertain	*edulis*	'Padstow'	*edulis*
Roscoff (h.e.)	100	50	50	42	15	43	52	48
Penzance Harbour	20	9	11	2	5	13	6	14
St. Ives (h.e.)	62	62	—	25	10	27	53	9
Bude (l.e.)	44	44	—	11	20	13	36	8
Bude (h.e.)	70	?	?	18	11	41	52	18
Filey (l.e.)	100	29	71	—	—	—	—	100

(h.e.=high level exposed site; l.e.=low-level exposed site)

In Penzance Harbour, the situation was more complex. Only 9 of a random sample of 100 possessed dark mantles (only a few of the light types were kept for later examination, hence the eleven *edulis* in Table 2). Of these nine the two most like "Padstow mussels" in shell shape had *edulis* ratio values and five of the six animals with "Padstow type" ratios had confidently been identified as *edulis* on the basis of shell shape.

The ratio values for these samples are shown in the middle section (B) of Fig. 8. Since identification here rested on the characters being measured, good separation of the two forms was expected, and was realised with the Roscoff sample. The poorer separation and variation in *edulis* values for the other sites may reflect the small numbers in these samples.

The final evidence relating to the reliability of mantle edge colour, or illustrating the difficulties that can be encountered, is contained in the last entry in Table 2 referring to a sample from Filey, Yorkshire. The existence, on this coast, of small numbers of mussels with very dark mantles, had been known by us for some time and a specific investigation has now shown that they can form up to 29 p. 100 of some low-level populations. The shape of the hinge-plate and the hinge-plate and muscle scar ratios reveal no significant difference between the dark and light coloured types, values for both groups falling between the two sets of Filey Brigg values shown in Fig. 8. We found it totally impossible to distinguish visually between the colour of these dark Filey mussels and similar sized animals from Cornwall. It could perhaps be argued that this data from North Sea coasts, where there is no suggestion of the Padstow type occurring, has little relevance to the present problem. We take the view that this example reinforces the uncertainties illustrated by the other samples in Table 2 and that the colour of the mantle edge should therefore take second place to the adductor scar ratio when these two characters conflict.

This does not mean, however, that all individuals can be identified with certainty by the muscle scar ratio alone. Although the mean values and standard deviations for a particular sample may not overlap, a few individuals usually exist in which the scar length either cannot be measured accurately or gives a value more appropriate to the other type (as in Fig. 7, where, if no other criteria had been available, about 15 p. 100 of the sample would not have been identifiable). Thus we have been unable to find a single character which permits certain identification for all individuals. In some cases (e.g. Rock, Newquay Harbour), a weighted consideration of all the characters listed on page 241, and especially items 1-4, gives separation with a high degree of accuracy. However, since all characters vary in their expression in any one habitat and since, in many habitats, certain characters cease to have diagnostic value (especially those lowest on our list) the situation can arise in which the balance of uncertain or opposing characters may not permit an identification to be made.

THE RELATIONSHIP OF THE 'PADSTOW MUSSEL' TO *M. GALLOPROVINCIALIS*

Although there now appear to be more morphological criteria for distinguishing between the majority of *M. edulis* and the "Padstow type", confirmation from reproductive and biochemical studies is still awaited. These however will not resolve the practical problems of field identification. The relationship between the "Padstow type" and *M. galloprovincialis* also requires further study of continental mussels but there are now further grounds for believing that the two entities are similar.

We have demonstrated the wide range of shell shape in the "Padstow type" in S.W. England, and the literature relating to *M. galloprovincialis* (especially the illustrations by List, 1902 and Bucquoy *et al.*, 1887) shows equally wide variation in this form (Fig. 9), as do some continental samples that we possess. Vorobiev (1938), quoted in Kiseleva (1966), found that the shape of Black Sea mussels varied so greatly that it was difficult to find similar specimens in different habitats. The most constant feature throughout the literature, appears to be the pointed anterior end, the contrast between this and the blunt end of Mediterranean *edulis* being well brought out by Bucquoy *et al.* The dark mantle colour is also widespread but there appears to be no recurring feature of shell shape or proportion and it is notable

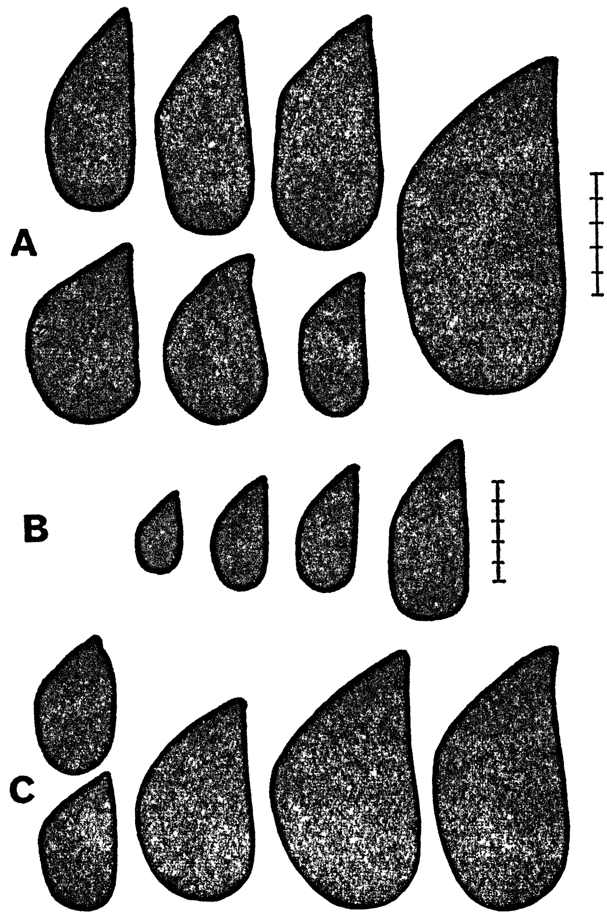


FIG. 9

Silhouettes of *M. galloprovincialis* based on plates by Bucquoy *et al.* (1887): A; Lubet (1959): B; List (1902): C. (Scale in cm.)

that the high, rounded dorsal margin allied to anterior beaking is not often in evidence. It will be recalled that this combination, which is common at Padstow and which Hepper illustrated, appears to be associated mostly with sheltered low-level sites and it may be more widespread in the Mediterranean than the literature suggests if this type of habitat were investigated. For the present however, these characters appear to be rather local, perhaps centred on S.W. England and N. France and superimposed upon mussels that otherwise tend to possess the same form of hinge-plate and the same relative sized hinge-plates and anterior adductor scars as the Mediterranean mussel. The hinge-plate and muscle scar ratios for four samples supplied to us as local representatives of *M. galloprovincialis* are shown in the lower section (C) of Fig. 8. These values are slightly smaller than those of most of the "Padstow types" but this closeness, coupled with the great similarity of hinge-plate shape, leads to the tentative conclusion that the Padstow and Mediterranean mussels will prove to be identical or very similar forms of *Mytilus*.

CONCLUSIONS

The reported existence of a distinctive "Padstow mussel" (possibly *Mytilus galloprovincialis* Lmk.) is re-examined in the light of the extreme range of environmental variation in the shell shape of *Mytilus edulis* L.

In the Padstow area itself, two distinct forms can indeed be recognised but even here, the "Padstow type" is considerably more variable than previously reported. This variation in shell shape and some new diagnostic features that appear rather more reliable, are described in detail and compared with the locally occurring *M. edulis*. In other similar habitats in S.W. England, the "Padstow facies", with further variation, is again fairly easily recognisable. However, at high-tidal levels, where many old animals occur and in the distinctive growing conditions of the high-density populations typical of exposed shores, the external shell characters of the two forms merge until criteria for separation are reduced to differences in the form and relative sizes of the hinge-plate and anterior adductor muscle scar and in the colour of the mantle edge. The latter can be a very subjective criterion while the two shell characters are of little practical use in the field and, in a few cases, do not permit positive separation even after laboratory analysis.

Although biochemical and reproductive studies may establish further differences, perhaps of specific rank, these practical problems of field identification will still remain, especially in the widespread open coast populations.

The shell shape of continental *M. galloprovincialis* appears, from the literature, to be very variable and, until such variations can be studied in relation to environmental conditions, does not afford a reliable means of comparison with the "Padstow type". However, both forms show marked similarity in the shape of the hinge-plate and in the relative sizes of the hinge-plate and adductor scar and may, pending other biochemical and reproductive studies, be tentatively assigned to the same form of *Mytilus*.

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Summary

The recorded existence of a distinctive mussel, the "Padstow type" in S.W. England has been re-examined in view of the variations in shell shape found recently in *M. edulis.*

In harbours and sheltered localities, two distinct types can be easily recognised, but the "Padstow type" is more variable than previously recorded. A wide range of shell characteristics is described and their value for identification purposes is discussed. In other localities, however, e.g. exposed coasts, it becomes more difficult to distinguish the two types of mussels.

Whilst Continental *M. galloprovincialis* also appears to show considerable variations, it would seem that the "Padstow type" and *M. galloprovincialis* are probably identical forms of mussel.

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