

# MORPHOLOGICAL VARIATIONS IN *MYTILUS* FROM THE FRENCH COASTS IN RELATION TO THE OCCURRENCE AND DISTRIBUTION OF *M. GALLOPROVINCIALIS* LAMARCK

by

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## Résumé

*Mytilus edulis* et *M. galloprovincialis* des côtes de France présentent une très grande variabilité, surtout dans la forme de la coquille et ce caractère seul n'aurait pas permis d'identifier un grand nombre des individus. Les sommets terminaux (umbos) de *M. galloprovincialis* sont généralement plus pointus et incurvés et leurs coquilles ne présentent pas de bandes violacées. Dans cette espèce, les empreintes des muscles adducteurs antérieurs ainsi que les plateaux cardinaux sont également de plus petites dimensions et la partie postérieure du manteau est d'un pourpre violacé plus accusé que chez *M. edulis*.

*M. galloprovincialis* est la Moule la plus abondante en Méditerranée. On la trouve également sur la côte atlantique et dans la Manche jusqu'au Cotentin. Quelques individus ont été récoltés sur la côte Ouest du Cotentin mais aucune à l'Est de Cherbourg. Par contre, *M. edulis*, qui existe sur toutes les côtes de la Manche et de l'Atlantique, est plus rare en Méditerranée.

Bien que *M. galloprovincialis* et le type « Padstow » du Sud-Ouest de l'Angleterre soient très variables, en particulier en ce qui concerne la forme de la coquille, la similitude frappante entre des animaux vivant dans des conditions géographiques semblables indique qu'il s'agit de formes de *Mytilus* identiques.

## Introduction

The literature concerning the systematics of *Mytilus edulis* L. and *M. galloprovincialis* Lmk.—the Mediterranean mussel—is particularly extensive, the majority of authorities considering *galloprovincialis* to be a race or subspecies of *M. edulis* (e.g. Bouxin, 1956; Dodge, 1952; Soot Ryen, 1955).

Lewis and Seed (1969) working on mussels collected from a wide variety of habitats in Devon and Cornwall concluded that two quite distinct types of *Mytilus* exist in south-west England, *M. edulis* and a form previously described from this locality as the "Padstow mussel" by Hepper (1957) which accorded closely to earlier descriptions of *M. galloprovincialis*.

More recently, detailed investigations of co-existing populations from the Padstow area (Rock in the sheltered Camel estuary) have further shown that in addition to the various morphological differences between *edulis* and the "Padstow mussel" several other differences exist which strengthen the case for regarding these mussels as distinct

species (Seed, 1971). These include differences in their infection with the parasitic pea-crab, *Pinnotheres pisum* (Penn.), in their reproductive cycles and in the electrophoretic patterns of posterior adductor muscle proteins.

Although two distinct morphological forms can indeed be recognised especially in the Padstow area itself, nevertheless, samples from other localities in south-west England revealed that both forms respond in a similar way to environmental factors to such an extent that in some cases distinction between the "Padstow" and *edulis* types becomes difficult or even impossible in the field, especially in open coast populations. (Plate 1, figures A-C illustrate some of the variation in shell morphology of "Padstow types" from south west England.)

From the literature, Continental *M. galloprovincialis* appears to be equally variable (Bucquoy, Dautzenberg and Dolfus, 1887; List, 1902) but until such variations could be studied in relation to environmental conditions, they did not afford a reliable means of comparison between the two types. However, a limited number of samples of Continental *galloprovincialis* had previously been examined by the author and these showed that both forms were remarkably similar especially in their anterior adductor muscle scars and hinge plates, strongly suggesting that these mussels were indeed identical or very similar forms of *Mytilus*.

During the summer of 1968 an opportunity arose enabling the author to make extensive collections of mussels from a wide variety of habitats on the French coasts. The present paper describes the variations found in these mussels, particularly in relation to the occurrence and distribution of *M. galloprovincialis*.

#### A BRIEF DESCRIPTION OF THE CHARACTERISTIC FEATURES OF *M. EDULIS* AND *M. GALLOPROVINCIALIS*

Whilst descriptions of *M. edulis* and *M. galloprovincialis* can be found elsewhere in the literature, it is felt that a brief description of the salient differences between these mussels should be included at this point.

##### 1) Colour of the mantle edge:

Accepting that identification of some mussels in terms of their mantle edge colour can be rather subjective in that animals of intermediate shades are occasionally encountered, in general the colour of the mantle edge proves to be a very reliable taxonomic character, being deep purple-violet in *galloprovincialis* and yellowish-brown in *edulis*.

##### 2) Anterior adductor muscle scar:

Lewis and Seed (1969) found that the consistently smaller size of this muscle scar in *galloprovincialis* again proved to be a most reliable character. Frequency distributions of values for the ratio scar length/shell

length ( $\times 1,000$ ) were distinctly bimodal in mixed populations. Its greater size in *edulis* is also accentuated by the conspicuous blue prismatic layer which stands out against the surrounding white nacreous layer. In *galloprovincialis*, on the other hand, the prismatic layer is frequently paler and examination under a binocular microscope is usually needed to determine the limits of the much smaller scar. In addition, the scar here tends to be further from the midline of the animal than it does in *edulis* (a consequence of the different shell profiles).

### 3) Size and shape of the hinge plate:

Like the anterior adductor scar the hinge plate too is typically much smaller in *galloprovincialis*. In *edulis* it is usually a gently curving structure [Fig. 1, D (i)] whereas in *galloprovincialis* it describes a much tighter arc with its rear end much more clearly delimited from the adjacent ventral edge of the valve [Fig. 1, D (ii)].

### 4) Raying and general colouration of the shell:

The shells of *M. edulis* typically reveal the presence of longitudinal rays of deeper colour whereas *galloprovincialis* generally lack such rays. However, the colour plates in List's monograph (1902) show raying in some of his *galloprovincialis* and I have previously recorded the presence of rays in 10-15 per cent of otherwise typical *galloprovincialis* from Rock in south west England. Similarly up to 25 per cent of the *edulis* population were without such rays and this figure may be as high as 70-80 per cent in some exposed populations where shells are often badly eroded. After removing the periostracum by boiling in soda, the prismatic layer in *edulis* is usually dark blue whilst in *galloprovincialis* it is purple-violet in colour.

### 5) Shell characteristics:

Although in general the shells of *galloprovincialis* tend to be higher and flatter than *edulis* of similar size and from the same habitat, this character is, nevertheless, subject to considerable variation. The majority of younger specimens of *edulis* are slightly convex on the whole or part of the ventral margin whilst many of the older animals exhibit the concave curvature previously described by Lewis and Powell (1961) and Seed (1968). The ventral margin of the majority of *galloprovincialis* on the other hand is usually fairly straight except for a downturning at the anterior end, but in some cases it is distinctly beaked or incurved. The dorsal margin of the shell in both types varies from some that are gently rounded to others that are markedly angular. Some of the terminology used to describe mussel shells throughout this account is illustrated in Figure 1. A feature found to be very useful in field identification was the transverse profile of the shell. In *galloprovincialis* [Fig. 1, C (i)] the greatest width is generally nearer the ventral margin than it is in *edulis* [Fig. 1, C (ii)] and consequently the ventral part of the animal tends to be much flatter. The anterior end in *galloprovincialis* is usually more pointed and downturned due to the way in which growth increments posterior to the umbo converge on the lunule ventrally and to the position and size of the hinge plate and lunule relative to the umbo itself. In the majority of *edulis* the blunt umbo/lunule curve leads into the curve of the valve edge without any change in profile giving a snub-nosed appearance to the anterior end of the shell. In *galloprovincialis*, the hinge plate is often slightly dorsal to the umbo leaving the anterior end very pointed or slightly beaked, or it may be parallel to it so that the hinge plate and/or the lunule project slightly to form a bulbous swelling which is often rendered more prominent because of the inrolling of the valve edge immediately behind the hinge plate.

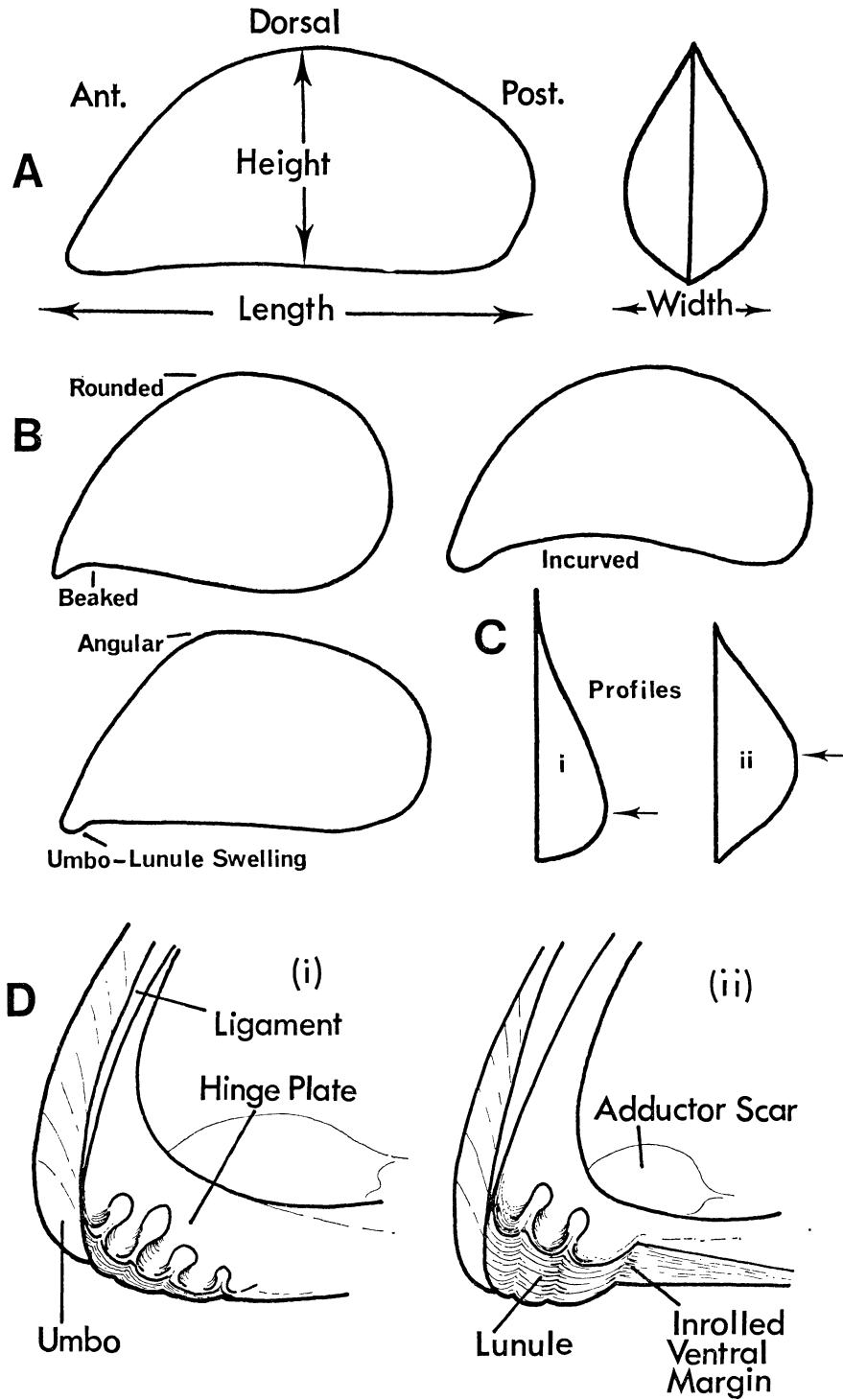


FIG. 1

Diagram illustrating some of the terminology used throughout the text.

Of the above taxonomic characters those involving overall shell shape are perhaps the least reliable since these are most subject to phenotypic variation with the result that animals of almost every conceivable shape can be found. In some populations, however, especially those from low density, low level beds of sheltered harbours and estuaries, the various shell characters can be combined in single animals to produce mussels which are quite distinctive.

### COLLECTION AND TREATMENT OF MATERIAL

Figure 2 shows the localities on the French coast from which samples were collected during this investigation. At each locality, samples were taken from as wide a variety of habitats as possible.

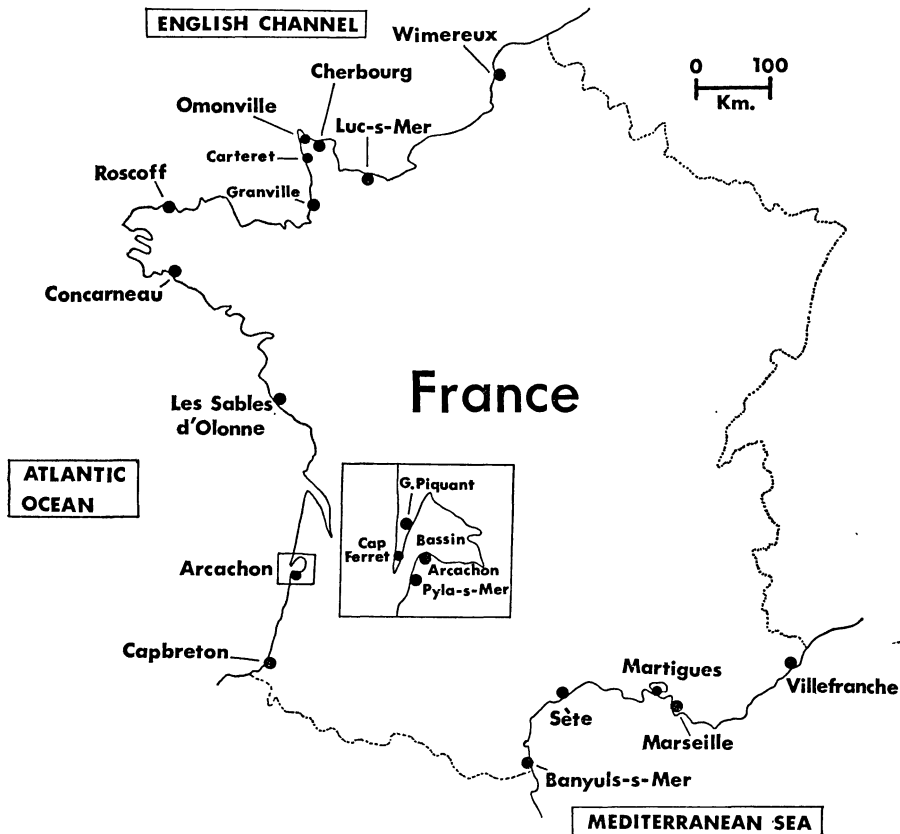


FIG. 2

Map showing the main localities from which mussels were collected.

Animals were opened immediately after collection and separated into three categories; those with purple-violet mantles, those with yellow-brown mantles and those which were intermediate. The flesh was then removed and the shells sealed in plastic bags for subsequent

examination. In the laboratory the shells were boiled in soda to remove the periostracum especially from around the adductor scar and hinge plate. The following measurements were then made; shell length and height, adductor scar and hinge plate lengths, and the following ratios computed, length/height, adductor scar shell length ( $\times 1,000$ ) and hinge plate/shell length ( $\times 1,000$ ). Finally the general shape of the shell (whether pointed, angular, beaked etc.) and the presence or absence of longitudinal rays were noted. On each of these characters it was possible to identify each animal as *edulis*, *galloprovincialis* or uncertain. A final separation into *edulis* or *galloprovincialis* was then made after considering all the available information for each mussel. A summary of these results is given in Tables 1 and 2. Knowing the final identity of each animal it was then possible to assess the percentage of each sample that would have been wrongly identified using the individual characters alone. Such information provides a valuable indicator of the reliability of the various taxonomic characters, not only for each locality but also for *Mytilus* generally. These results are summarised in Table 3.

It should be pointed out that the final separations given in Tables 2 and 3 do not necessarily reflect the *exact* relative abundance of the two types in each locality since the samples were not always collected entirely at random.

## THE RANGE OF VARIATION IN FRENCH MUSSELS

### A) The Channel coast.

1. **Luc-sur-Mer** (Plate 1, D). Although the shores in this region were predominantly sandy, numerous relatively large animals were collected from the rocky outcrops towards low water and beyond. Many mussels were examined in the field and others brought back to the laboratory for more detailed examination but in no instance was *galloprovincialis* found. All mussels were here typical *M. edulis* and showed relatively little individual variation being blunt at the anterior and having straight or slightly convex ventral margins. The majority (94 per cent) were rayed and had elongate shells with gently rounded dorsal margins. Although the hinge plate and adductor scar ratios (Table 1) were rather low, they were, nevertheless, typically *edulis*.

2. **Omonville** (Plate 1, E). *Mytilus* was particularly scarce in this region, a few isolated individuals being found amongst the barnacles on a semi-exposed rocky shore. All except one of these mussels were of the *edulis* type having straight or slightly incurved ventral margins. Shells were small, elongate and generally rounded dorsally and were often badly eroded. Although the umbones were rather pointed these animals were not unlike many growing under similar conditions in British waters. The single *galloprovincialis*, found only after considerable searching, had a much higher shell with pointed,

TABLE 1.  
Shell characteristics of *M. edulis* and *M. galloprovincialis*.

Locality	<i>M. edulis</i>						<i>M. galloprovincialis</i>					
	Shell		L H	(1) A.A.S. L	(2) H.P. L	p. 100 Rayed	Shell		L H	A.A.S. L	H.P. L	p. 100 Rayed
	Length (cm)	Height (cm)					Length (cm)	Height (cm)				
<i>Luc-sur-Mer</i>	5.38	2.50	2.15	88	70	94						
<i>Omonville</i>	2.54	1.34	1.90	120	84	87	2.61	1.70	1.53	54	57	0*
<i>Carteret</i>	2.27	1.24	1.83	118	83	82	2.10	1.16	1.81	86	62	0*
<i>Jullouville</i>	3.09	1.64	1.88	124	84	92	2.21	1.21	1.83	88	70	0*
<i>Roscoff</i>	2.25	1.11	2.03	101	99	54	3.44	1.76	1.95	61	61	6
<i>Concarneau:</i>												
a. Harbour	4.60	2.45	1.88	112	75	94	4.76	2.60	1.83	87	62	17
b. Semi-exposed	3.88	2.10	1.85	104	75	58	3.88	2.09	1.86	86	60	18
c. Exposed	2.80	1.35	2.07	85	76	38	2.93	1.44	2.03	72	57	29
<i>Les Sables</i>	2.98	1.48	2.02	103	70	80	2.72	1.53	1.78	81	62	23
<i>Arcachon:</i>												
a. Sample 1							5.96	2.88	2.07	51	53	17
b. Sample 2	4.66	2.22	2.10	104	75	86	4.47	2.70	1.66	73	56	6
c. Pier	3.17	1.74	1.82	118	85	90	2.73	1.68	1.63	79	58	4
d. Grand Piquant	4.54	2.23	2.04	99	67	100						
e. Pyla-sur-Mer	2.48	1.24	2.00	100	84	73	2.63	1.37	1.92	62	59	8
<i>Capbreton:</i>												
a. Harbour	3.20	1.72	1.90	103	79	100	3.57	1.70	2.10	66	61	3
b. Groins	2.70	1.36	1.99	101	77	81	3.18	1.56	2.04	68	58	4
c. Atlantic Beach	3.94	1.90	2.07	101	66	100	3.72	1.99	1.87	67	56	6
<i>Banyuls-sur-Mer:</i>												
a. Semi-exposed	4.20	2.38	1.76	71	60	0*	4.54	2.32	1.96	52	57	0
b. Buoy chain							3.45	2.08	1.66	58	56	11
c. Jetty							2.86	1.58	1.81	59	54	5
<i>Sète</i>	5.24	2.58	2.03	80	56	65	5.30	2.62	2.02	61	52	0
<i>Martigues</i>	2.80	1.53	1.83	101	77	0*	3.00	1.64	1.82	87	68	2
<i>Marseille:</i>												
a. Les Calanques:												
1. Intertidal							3.10	1.75	1.82	61	55	2
2. Sublittoral							5.60	3.01	1.86	51	51	0
3. Sublittoral reef							4.65	2.59	1.80	54	56	4
b. Ile Riou:												
1. Intertidal							3.76	1.96	1.92	49	62	0
2. Sublittoral							4.64	2.44	1.90	41	60	3
c. Ile Friou:							3.92	2.13	1.84	55	56	12
d. Old Harbour:												
1. Ropes							2.30	1.47	1.56	67	52	0
2. Buoy chain							3.27	1.73	1.89	66	51	0
<i>Villefranche-sur-Mer</i>							4.77	2.65	1.80	54	45	8
<i>Naples</i>							5.09	2.66	1.91	47	53	3
<i>Turkey:</i>												
a. Izmir							4.55	2.44	1.86	56	60	8
b. Amasya							4.30	2.31	1.86	50	59	5
<i>Newquay:</i>												
a. Harbour							5.82	3.07	1.90	45	56	13
b. High exposed							3.02	1.47	2.05	55	65	0
<i>Padstow</i>	5.50	2.89	1.90	1.05	72	76	5.50	3.14	1.75	64	56	12
<i>Polzeath</i>							5.50	2.55	2.16	51	61	0
<i>Westward Ho</i>	3.31	1.69	1.96	95	83	85						

(\*) Based on samples of less than 10 individuals.  
 (1) A.A.S.=Anterior Adductor muscle scar.  
 (2) H.P.=Hinge Plate.

TABLE 2.

Separation of samples on individual characters together with a final separation based upon a weighted assessment of all characters.

Locality	Final p. 100 separation		Separation on Individual Characters (percentage)												
			Shell characters			Rayed	Hinge plate			Adductor scar			Mantle colour		
	ed.	gall.	ed.	♀ (1)	gall	(edulis)	ed.	♀	gall.	ed.	♀	gall.	ed.	♀	gall.
<i>Luc-sur-Mer</i>	100	0	100	0	0	94	100	0	0	100	0	0	100	0	0
<i>Omonville</i>	100	0	95	5	0	87	88	12	0	100	0	0	100	0	0
<i>Carteret</i>	98	2	95	0	5	80	70	25	5	98	0	2	98	2	0
<i>Jullouville</i>	97	3	91	6	3	89	97	3	0	97	3	0	100	0	0
<i>Roscoff</i>	50	50	40	18	42	30	41	13	46	44	9	47	45	10	45
<i>Concarneau:</i>															
a. Harbour	59	41	53	21	26	62	68	9	23	53	4	43	41	0	59
b. Semi-exposed	36	64	20	26	54	33	23	6	71	36	23	41	24	6	70
c. Exposed	32	68	26	30	44	32	17	12	71	11	37	52	18	17	65
<i>Les Sables</i>	57	43	52	31	17	56	42	16	42	50	24	26	44	12	44
<i>Arcachon:</i>															
a. Sample 1	0	100	0	59	41	17	0	0	100	0	0	100			
b. Sample 2	49	51	49	0	51	45	49	0	51	49	0	51	49	0	51
c. Pier	64	36	62	12	26	59	63	1	36	62	2	36	62	0	38
d. Grand Piquant	100	0	100	0	0	100	100	0	0	100	0	0	100	0	0
e. Pyla-sur-Mer	40	60	48	21	31	34	33	4	63	41	4	55	36	4	60
<i>Capbreton:</i>															
a. Harbour	10	90	17	31	52	13	11	13	76	9	3	88	13	0	87
b. Groins	30	70	43	21	36	27	23	7	70	22	10	68	23	0	77
c. Atlantic Beach	50	50	50	17	33	53	50	7	43	50	7	43			
<i>Banyuls-sur-Mer:</i>															
a. Semi-exposed	4	96	11	31	58	0	4	14	82	0	10	90	16	48	36
b. Buoy chain	0	100	62	15	23	11	0	0	100	0	0	100	13	0	87
c. Jetty	0	100	1	44	55	5	3	4	93	0	0	100	8	0	92
<i>Sète</i>	18	82	48	17	35	12	18	21	61	7	24	69	46	0	54
<i>Martigues</i>	8	92	27	47	26	2	8	5	87	19	48	33	3	0	97
<i>Marseille:</i>															
a. Les Calanques:															
1. Intertidal	0	100	0	25	75	2	0	2	98	0	5	95	11	0	89
2. Sublittoral	0	100	3	34	63	0	0	2	98	0	3	97	2	0	98
3. Sublittoral reef	0	100	7	37	56	4	0	7	93	0	4	96	11	0	89
b. Ile Riou:															
1. Intertidal	0	100	12	25	63	0	0	13	87	0	2	98	17	49	34
2. Sublittoral	0	100	26	14	60	3	0	9	91	0	0	100	17	0	83
c. Ile Friou	0	100	8	39	56	12	7	0	93	0	2	98	4	0	96
d. Old Harbour															
1. Ropes	0	100	0	30	70	0	0	0	100	0	0	100	0	0	100
2. Buoy chain	0	100	59	24	17	0	0	17	83	2	37	61	22	0	78
<i>Villefranche-sur-Mer</i>	0	100	24	24	52	14	4	6	90	0	8	92	14	0	86
<i>Naples</i>	0	100	0	13	87	3	0	0	100	0	0	100			
<i>Turkey:</i>															
a. Izmir	0	100	0	15	85	8	0	0	100	0	0	100	0	10	90
b. Amasya	0	100	0	17	83	8	0	0	100	0	0	100	0	8	92
<i>Newquay:</i>															
a. Harbour	0	100	7	2	91	13	0	9	91	0	0	100	0	0	100
b. High exposed	0	100	3	47	50	0	0	3	97	0	3	97	0	23	77
<i>Padstow</i>	50	50	49	11	40	44	50	10	40	50	10	40	50	0	50
<i>Polzeath</i>	0	100	25	37	38	0	0	22	78	0	0	100	0	17	83
<i>Westward Ho!</i>	100	0	100	0	0	85	100	0	0	100	0	0	100	0	0

(1) Individuals of uncertain identity.



TABLE 3.

Percentages of animals in each sample which could not be positively identified, or which were incorrectly identified on individual characters.

Locality	Final separation (per cent)		Misidentified using individual characters (percentage)				
	ed.	gall.	Shell characters	Hinge plate	Adductor scar	Raying	Mantle colour
<i>Luc-sur-Mer</i>	100	0	0	0	0	6	0
<i>Omonville</i>	100	0	5	12	0	13	0
<i>Carteret</i>	98	2	3	28	0	18	2
<i>Jullouville</i>	97	3	6	3	3	8	3
<i>Roscoff</i>	50	50	21	17	15	26	10
<i>Concarneau:</i>							
a. Harbour	59	41	22	12	37	11	28
b. Semi-exposed	36	64	38	21	43	27	20
c. Exposed	32	68	36	21	45	40	44
<i>Les Sables</i>	57	43	46	31	33	21	21
<i>Arcachon:</i>							
a. Sample 1	0	100	59	0	0	17	—
b. Sample 2	49	51	0	0	0	10	0
c. Pier	64	36	12	1	2	8	2
d. Grand Piquant	100	0	0	0	0	0	0
e. Pyla-sur-Mer	40	60	39	17	13	16	9
<i>Capbreton:</i>							
a. Harbour	10	90	44	22	10	3	6
b. Groins	30	70	36	11	12	9	9
c. Atlantic Beach	50	50	17	7	7	3	—
<i>Banyuls-sur-Mer:</i>							
a. Semi-exposed	4	96	47	15	10	4	60
b. Buoy chain	0	100	38	0	0	11	13
c. Jetty	0	100	45	7	0	5	8
<i>Sète</i>	18	82	59	33	27	6	55
<i>Martiques</i>	8	92	65	8	60	10	9
<i>Marseille:</i>							
a. Les Calanques:							
1. Intertidal	0	100	25	2	5	2	11
2. Sublittoral	0	100	37	2	3	0	2
3. Sublittoral reef	0	100	44	7	4	4	11
b. Ile Riou:							
1. Intertidal	0	100	37	13	2	0	66
2. Sublittoral	0	100	40	9	0	3	17
c. Ile Friou	0	100	47	7	2	12	4
d. Old Harbour							
1. Ropes	0	100	30	0	0	0	0
2. Buoy chain	0	100	83	17	39	0	22
<i>Villefranche-sur-Mer</i>	0	100	48	10	8	14	14
<i>Naples</i>	0	100	13	0	0	3	—
<i>Turkey:</i>							
a. Izmir	0	100	17	0	0	8	8
b. Amasya	0	100	15	0	0	8	10
<i>Newquay:</i>							
a. Harbour	0	100	9	9	0	13	0
b. High exposed	0	100	50	3	3	0	23
<i>Padstow</i>	50	50	12	11	8	18	0
<i>Polzeath</i>	0	100	62	22	0	0	17
<i>Westward Ho!</i>	100	0	0	0	0	15	0
<b>Means:</b>			31	10	10	10	14

downturned umbones and a beaked ventral margin. The mantle edge was brownish but all other characters were typically *galloprovincialis*.

3. **Carteret** (Plate 1, F). In general, the shores in this region were sandy but isolated patches of mussels were found amongst the barnacles on the rocky outcrops in the mid and upper shore. These mussels were all rather small and many badly eroded. The majority were typical *edulis* with straight or slightly incurved ventral margins and blunt umbones and the dorsal shell margins varied from rounded to slightly angular. *M. galloprovincialis* made up about 2 per cent of the population, and although the mantle edge of these was no more than reddish-brown they were fairly typical *galloprovincialis* on other characters. Their shells were distinctly angular, pointed and slightly beaked.

4. **Jullouville** (Nr. Granville) (Plate 1, G). As at Carteret, the shores here were mainly sandy and mussels were again rather scarce being restricted to rocky outcrops where they occurred in cracks and pools. The majority were typical *edulis* and were of a relatively uniform shell shape. Many were straight ventrally, some slightly convex and about 8-10 per cent incurved. The umbones were blunt and the dorsal shell margins rounded though a few were slightly angular. The mean adductor scar ratio for this sample was the highest recorded throughout this investigation. Of this sample 3 per cent were tentatively assigned as *galloprovincialis* types. These had somewhat higher, almost triangular shaped shells which were purplish-blue in colour and lacked longitudinal rays. The anterior end was more pointed and the ventral margin straight. Adductor scar and hinge plate ratios were significantly lower than for most of the *edulis* types, but even so were still rather high to be regarded as typically *galloprovincialis*. In addition, the mantles were yellowish-brown in colour.

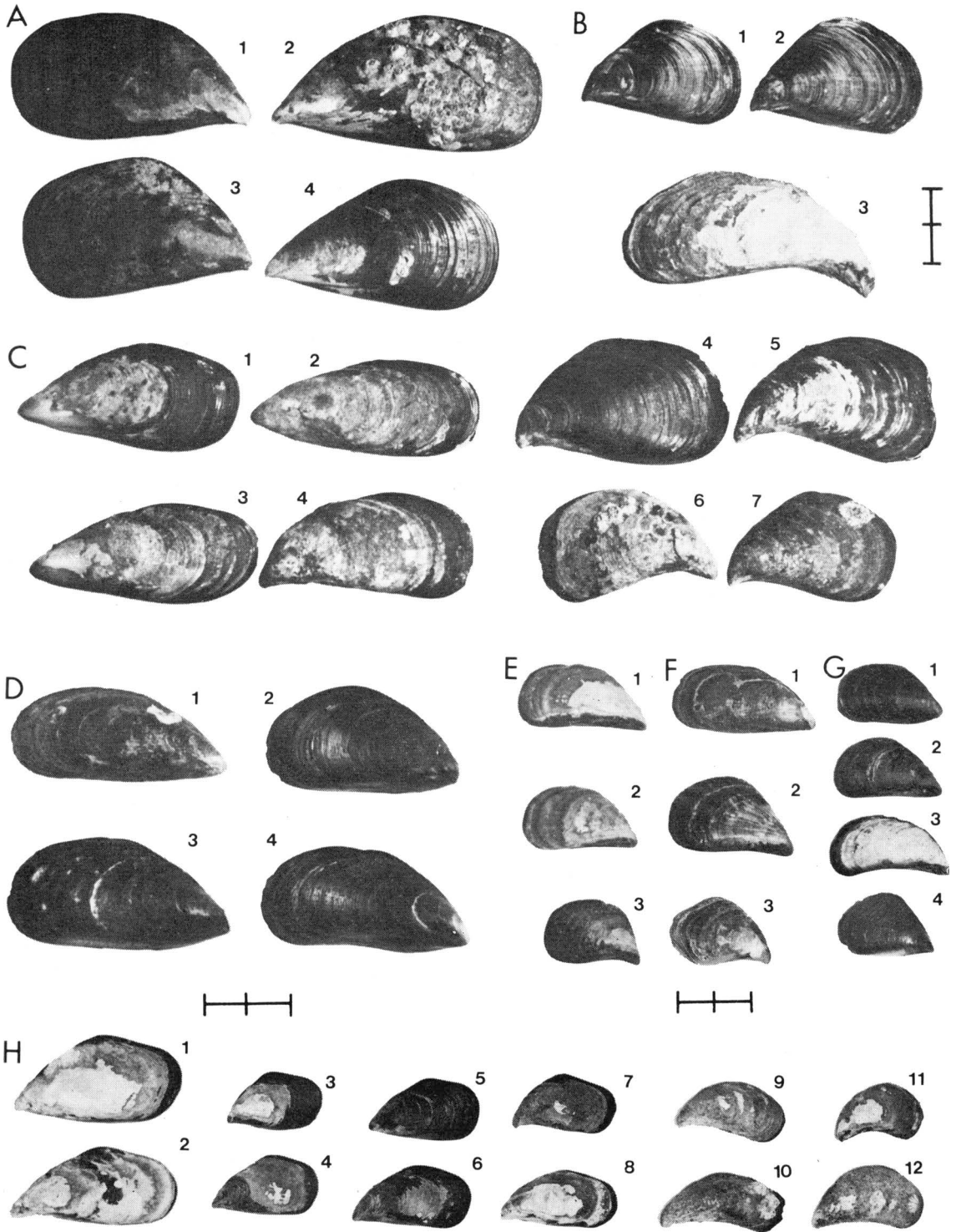
5. **Roscoff** (Plate 1, H). Here, mussels were collected from the mid and upper levels of a relatively exposed wave-swept rocky shore. The majority were badly eroded and there was considerable variation in shell shape; some were high and angular whilst others were elongate and rounded. The *edulis* types were generally blunter when compared with the more pointed and frequently beaked *galloprovincialis*. Even so it was sometimes quite difficult to separate *galloprovincialis* from old, incurved *edulis* types. In this particular sample it was noticeable that the larger mussels were all *galloprovincialis*. From Table 1 it will be seen that the hinge plate and adductor scar ratios are considerably higher in *edulis* and frequency distributions of these values, especially the latter, are distinctly bimodal (Fig. 3, 7).

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PLATE 1

*Mytilus* from south-west England (A-C) and from the Channel coast of France.

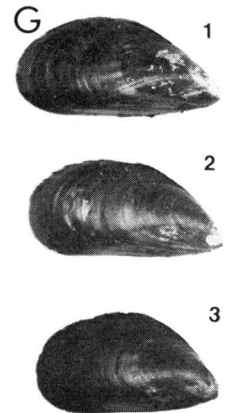
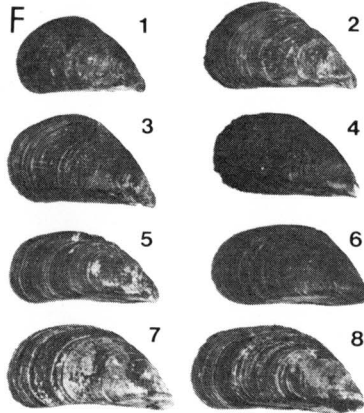
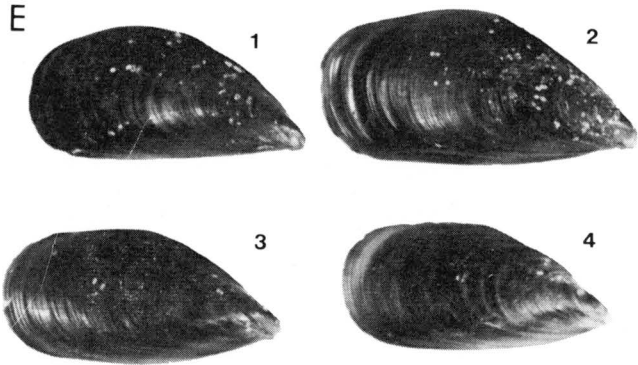
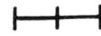
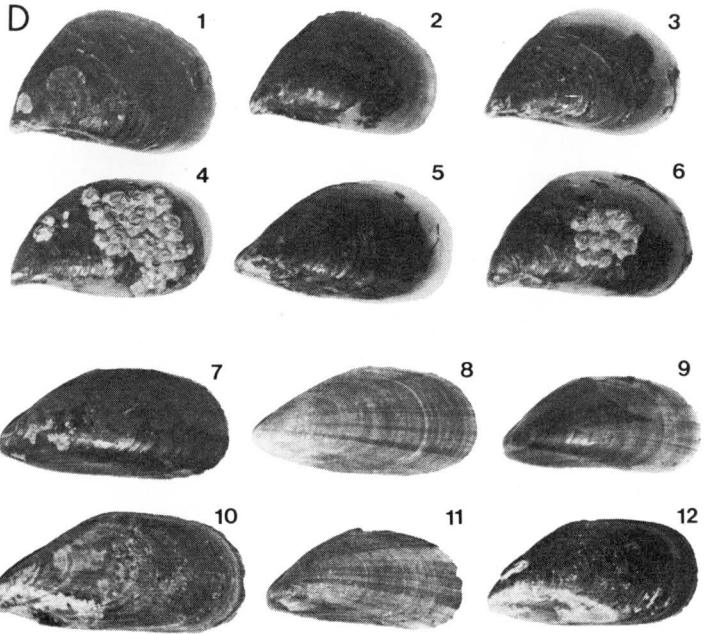
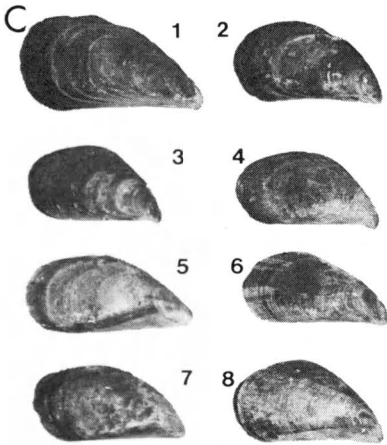
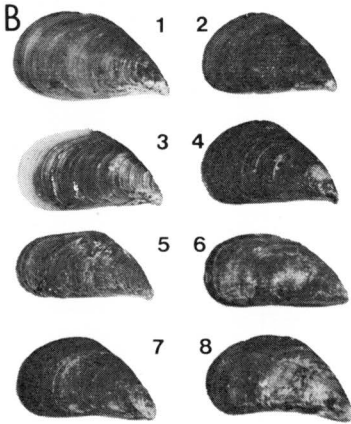
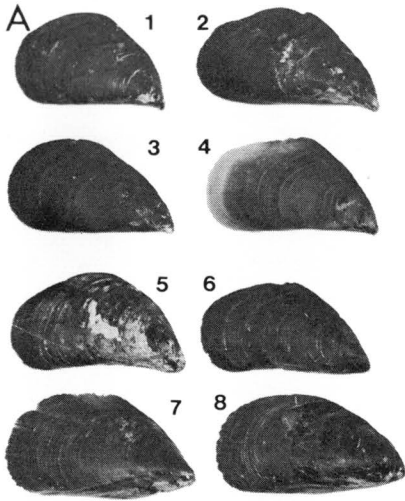
A, B, C - *M. galloprovincialis* (« Padstow types ») respectively from Newquay Harbour, Padstow and Polzeath. D - *M. edulis* from Luc-sur-Mer. E - Omonville; 1 and 2, *edulis*; 3, *galloprovincialis*. F - Carteret: 1 and 2, *edulis*; 3, *galloprovincialis*. G - Jullouville: 1-3, *edulis*; 4, *galloprovincialis*. H - Roscoff: 1-8, *galloprovincialis*; 9-12, *edulis*.



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PLATE 1



R. SEED.

**B) The Atlantic coast.****1. Concarneau.**

a) *The Harbour* (Plate 2, A). Dense clusters of large mussels, some over 7 cm in length, were found growing on the supporting structures of a small bridge in the very sheltered waters of the harbour. Identification of these mussels was not always easy since many animals appeared to show a combination of both *edulis* and *galloprovincialis* characters. Many *edulis* had convex ventral margins sloping upwards to rather blunt umbones but others varied from straight—apart from a tendency towards a slightly bulbous umbo/lunule swelling—to distinctly incurved. The dorsal margin was either rounded or slightly angular and over 90 per cent were rayed, some quite heavily. The main difference in shell shape between the two mussels was in the more pointed anterior end and absence of rays in the majority of *galloprovincialis*. Approximately 30 per cent of the latter showed slight ventral beaking especially just behind the downturned umbones but many were fairly straight apart from a distinct umbo/lunule swelling. Although the shells of most of the *galloprovincialis* were here somewhat more purple-violet in colour than *edulis*, approximately 15 per cent were greyish tinged with yellow-orange especially around the shell margin—a feature found in many *galloprovincialis* further south in the region of Arcachon.

b) *Semi-exposed shore* (Plate 2, B). Mussels were collected from all levels of this shore which was situated a few kilometers north west of Concarneau on the outside of a small harbour. In the low shore, animals were densely crowded and tended to be rather elongate in shape, but where isolated individuals were found attached to stones and shingle, these generally had higher more angular shaped shells. In the upper shore, many obviously older incurved mussels were restricted to shallow pools and cracks in the rock surface. Whilst the majority of animals could be identified without too much difficulty there was again considerable shell variation and many intermediate forms were found. The majority of *edulis* were straight or slightly incurved but a few (about 7 per cent) were convex and although generally rather blunt with rounded or slightly angular shells, over 40 per cent lacked rays. In *galloprovincialis* the ventral margin varied from some that were incurved through many that were straight apart from a distinct umbo/lunule swelling, to yet others (about 30 per cent) that were beaked, especially just behind the umbones. The umbones were here more pointed and in some cases were very pointed indeed. The shells were again more purply-blue than in *edulis* and the numbers

## PLATE 2

*Mytilus* from the Atlantic coast of France.

A, B, C from Concarneau. A - The Harbour: 1-4, *galloprovincialis*; 5-8, *edulis*. B - Semi-exposed shore: 1-4, *galloprovincialis*; 5-8, *edulis*. C - Exposed shore: 1-4, *galloprovincialis*; 5-8, *edulis*. F - Les Sables-d'Olonne: 1-4, *galloprovincialis*; 5-8, *edulis*. D, E, G from the Bassin d'Arcachon. D - Sample 2: 1-6, *galloprovincialis*; 7-12, *edulis*. E - Sample 1: *galloprovincialis*. G - Grand Piquant: *edulis*.

with greyish shells tinged with yellow-orange here rose to over 25 per cent.

c) *Exposed shore* (Plate 2, C). This site to the south of Concarneau supported dense beds of mussels that were generally much smaller than those in the previous two sites in this region. In the mid and low shore mussels were densely crowded and appeared to be fairly young and fast-growing whereas those in the upper shore were considerably smaller and more stunted and occurred in mosaics which were restricted to damp cracks and shallow pools. Characteristic *edulis* and *galloprovincialis* could still be identified but on individual characters alone it was even more difficult to separate the two types than at the previous sites. Many of the shells were badly eroded and the mantle colour varied from yellowy-brown to deep violet through all intermediate shades. Many *edulis* had elongate, rounded or slightly angular shells with straight or incurved ventral margins and downturned umbones typical of old mussels. Of the *galloprovincialis* only 10-15 per cent were beaked, the majority being either slightly incurved or straight, apart from the anterior umbo/lunule swelling. Most of the shells were again more purple-violet than *edulis* and between 7-10 per cent light grey in colour.

Thus whilst relatively characteristic *edulis* and *galloprovincialis* exist around Concarneau there are many intermediate forms and considerable misidentification would have been made on individual characters. Table 3 shows that even as many as 40-45 per cent of these populations would have been misidentified on adductor scar ratios or mantle edge colour—characters which have elsewhere proved to be very reliable.

2. **Les Sables-d'Olonne** (Plate 2, F). Here, the shore was essentially sandy but dense beds of rather small but fast-growing mussels carpeted the rocky outcrops in the lower shore. Both types were present but their separation, as at Concarneau, again frequently proved difficult due to the occurrence of many intermediate forms. *Edulis* shells were predominantly elongate, rounded or slightly angular with very blunt umbones. The ventral margins were either straight or slightly incurved and the majority were rayed. Many of the *galloprovincialis*, on the other hand, had higher more angular shells with the dorsal angle often further back along the shell than in *edulis*. This in fact was a feature not uncommon in *galloprovincialis* and appeared to be due to the larger ligamentary region in this species. The anterior end was more pointed and there was tendency for the umbones either to be downturned, or to form a pronounced bulbous umbo/lunule swelling. The ventral margin varied from slightly incurved in some to straight in the majority. As many as 23 per cent were rayed, but the shells were again generally more purple-violet than the darker blue shells of *edulis*. Between 15-20 per cent were greyish-blue tinged with yellow-orange.

### 3. Bassin d'Arcachon.

a) *Arcachon Pier*, (Plate 3, A). Due to unfavourable tides whilst at Arcachon no collections were here made from the very low shore. This particular sample was collected at about M.T.L. from the support-

ing structures of Arcachon Pier. Although not very large, these mussels were nevertheless very distinctive and no problems of identification were encountered. Here, *edulis* was quite typical, having dark blue shells with straight or slightly convex ventral margins and very blunt umbones. They were rather elongate, rounded or slightly angular. The striking external feature of *galloprovincialis* from this locality was the relative absence of pigment in the shell. The majority were pale grey in the anterior part changing through yellowish-orange to become almost translucent around the posterior margin. Some were tinged with violet but only a few (under 5 per cent) were rayed. The shells were much higher and more angular than *edulis* and in profile the ventral region was very flat. (Table 1 shows that the mean length/height ratio of 1.63 for this sample was one of the lowest recorded). The ventral margin was generally straight and associated with a prominent umbo/lunule swelling giving the shell a slightly beaked appearance.

b) *Grand Piquant*, (Plate 2, G). Despite prolonged searching along the outer and inner shores of the predominantly sandy Cap Ferret peninsular the only mussels found were those at Grand Piquant which, perhaps quite suprisingly, all proved to be quite typical *edulis*. They were elongate, slightly angular with very blunt umbones and ventral margins which were either straight or slightly convex. All were heavily rayed.

c) *Pyla-sur-mer*, (Plate 3, C). This sample was collected from the concrete and wooden groins just south of the mouth of the Bassin. Here dense clusters of small mussels of both types occurred but these proved more difficult to identify than those from the Bassin especially on external shell characters on which up to 40 per cent of the population would have been misidentified. *Edulis* shells were generally darker blue and the majority were rayed. They were elongate, rounded or slightly angular with straight or convex ventral margins and rather blunt umbones. *Galoprovincialis* shells were here pale in colour—usually greyish-blue—although some were slightly yellowy-orange like those at Arcachon. A few were tinged with violet but the majority lacked rays. Apart from these colour differences and perhaps a tendency towards a slightly more pointed anterior end associated with an umbo/lunule swelling these mussels were otherwise very similar to *edulis* in their external appearances.

In addition to the collections made during the course of this investigation two further samples from the Bassin region had previously been supplied by the Director of the Arcachon laboratory. Although the *exact* location of these mussels within the Bassin is not known, a brief description of them will be included for the sake of completeness.

d) *Sample 1*, (Plate 2, E). It is believed this sample of *galloprovincialis* was taken sublittorally from the buoys marking the access channels to Arcachon harbour. These mussels were large (up to 7 cm in length) rather elongate with very brittle, apparently fast-growing shells. The majority were either rounded or slightly angular whilst the ventral margins varied from straight to markedly convex. The anterior end was not especially pointed but there was often a pronounced umbo/lunule swelling present. The shells were yellowish in

colour, frequently tinged with purple but rays were generally absent. The hinge plate and adductor scar ratios of these mussels were amongst the lowest recorded.

e) *Sample 2*, (Plate 2, D). In view of their remarkable similarity to the mussels from Arcachon Pier, apart from their larger size, it seems quite probable that these animals were collected from a similar locality within the Bassin (possibly from lower down the shore or sublittorally). The two types were very distinctive and provided no problems of identification. *M. edulis* varied from light to dark blue in colour with deeper blue rays. They were elongate, rounded or slightly angular with a straight or convex ventral margin sloping upwards to a very blunt anterior end. By contrast *galloprovincialis* had higher, flatter almost triangular shaped shells. The majority were markedly angular but a few were rounded and closely resembled those previously described by Hepper (1957). The shells were brownish-orange tinged with violet, and whilst the ventral margins of some were straight, apart from the prominent umbo/lunule swelling, the majority exhibited some form of beaking associated with the very pointed downturned umbones.

#### 4. Capbreton.

a) *The Harbour*, (Plate 3, B). Dense clusters of rather small mussels were found attached to the supporting structures of the jetty at the entrance to Capbreton harbour. These showed considerable variation in their external shell characters and, as shown in Table 3, many misidentifications would have been made on these characters alone. The majority of *galloprovincialis* shells were of a similar colour to those at Arcachon whereas *edulis* were predominantly dark blue. Although there were no marked differences between the two types in external form many of the *galloprovincialis* were somewhat more pointed and either had a prominent umbo/lunule swelling or showed some traces of beaking, though the latter was not always easy to distinguish from the overall ventral incurvature of some *edulis*.

b) *Groins*, (Plate 3, D). Running across the predominantly sandy beach were a series of wooden/concrete groins which supported dense clusters of mussels. Both types were present and the main obvious external difference between them was again the colouration of the shells and the relative absence of rays in *galloprovincialis*. In their general shell shape the two were remarkably similar and although *galloprovincialis* was here not particularly pointed at the anterior end there was often a fairly pronounced umbo/lunule swelling which was not usually in evidence in *edulis*. These shells, like those from the harbour, were rather elongate, rounded or slightly angular dorsally

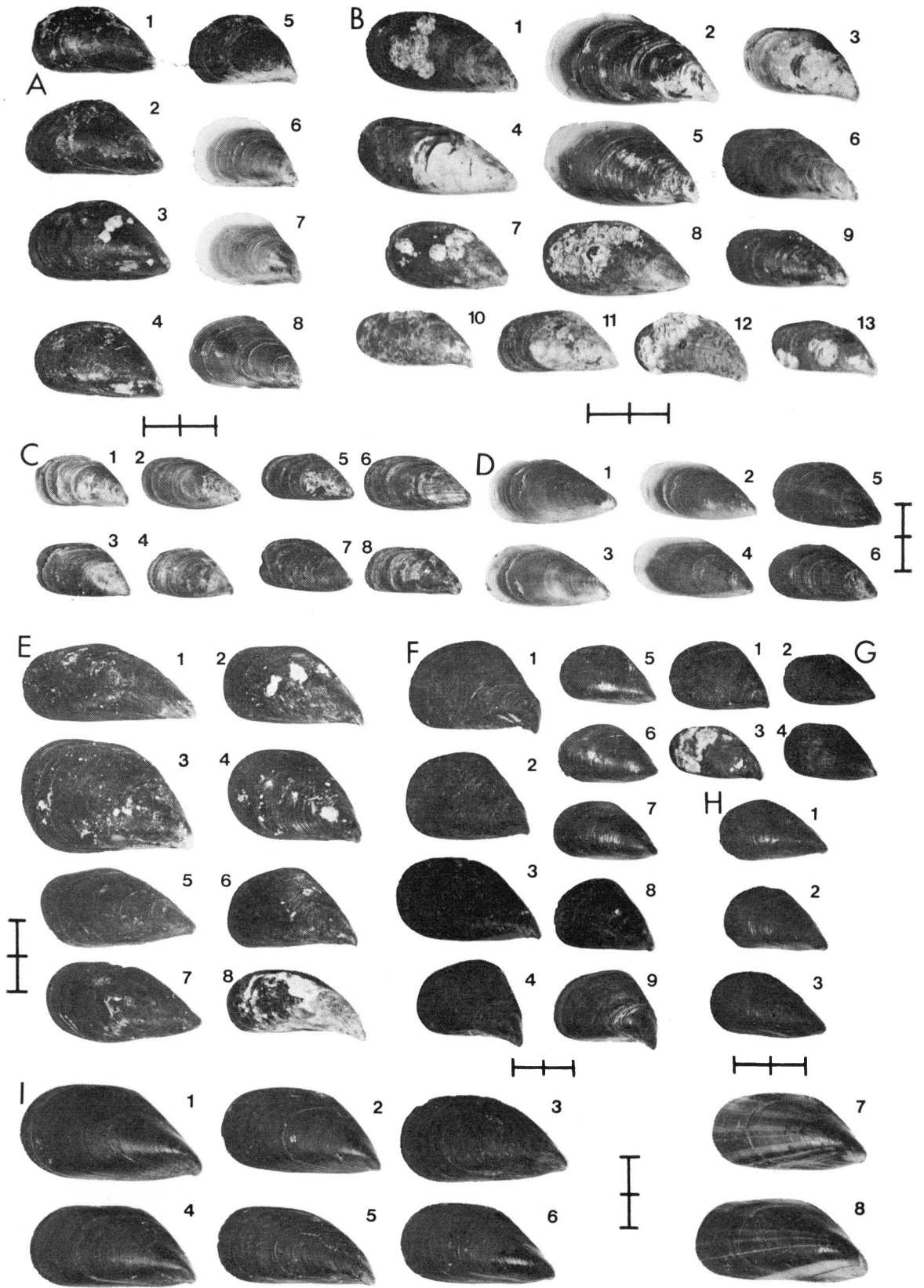
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#### PLATE 3

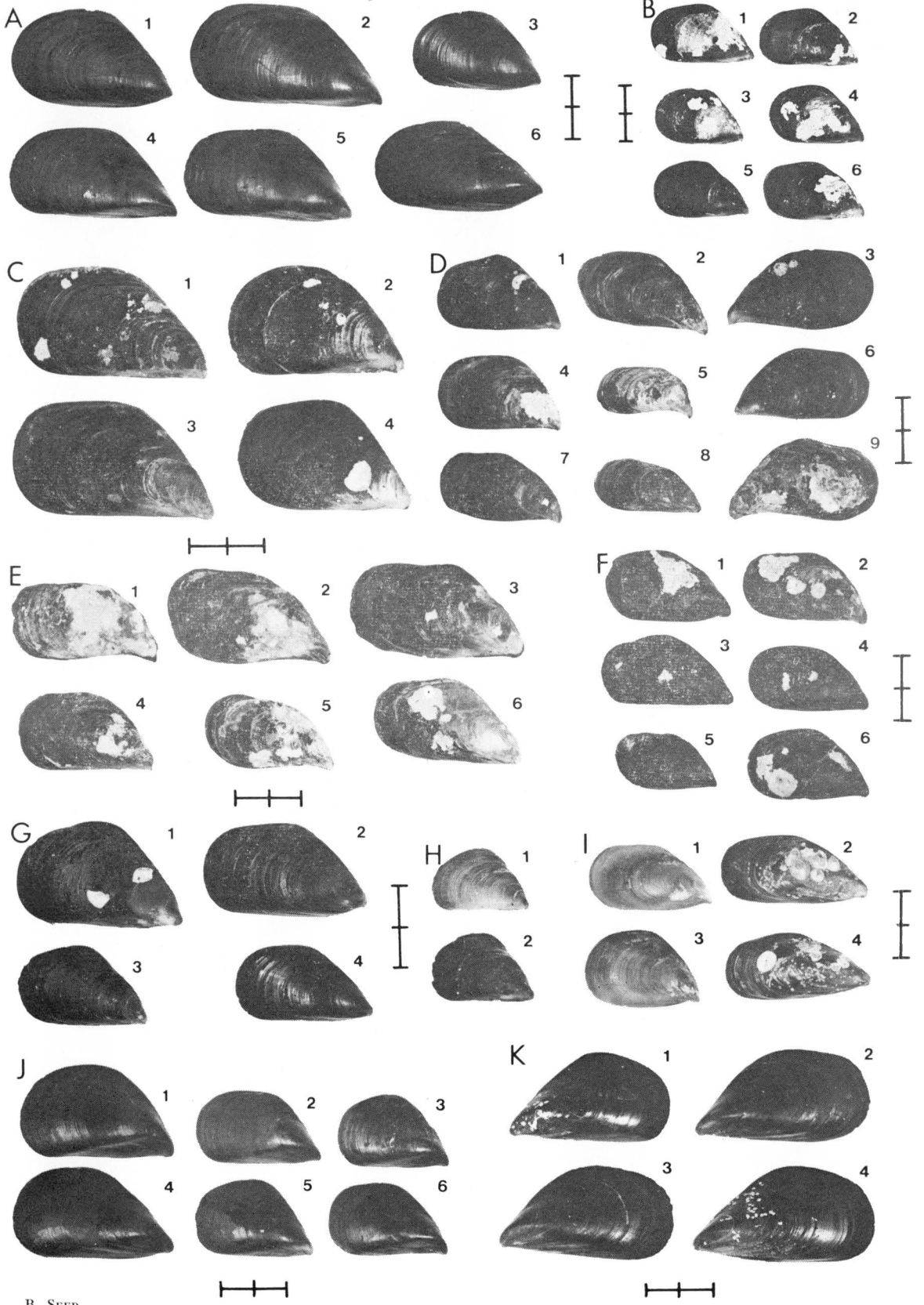
*Mytilus* from the Atlantic (A-D) and Mediterranean (E-I) coasts of France.

A - Arcachon Pier: 1-4, *edulis*; 5-8, *galloprovincialis*. B - Capbreton Harbour: 1-6, *galloprovincialis*; 7-13, *edulis*. C - Pyla-sur-Mer: 1-4, *galloprovincialis*; 5-8, *edulis*. D - Capbreton groins: 1-4, *galloprovincialis*; 5 and 6, *edulis*. E, F, G - *M. galloprovincialis* from Banyuls-sur-Mer. E - Semi-exposed shore. F - Buoy Chains. G - Jetty. H - *M. galloprovincialis* from Martigues. I - Sète: 1-6, *galloprovincialis*; 7 and 8, *edulis*.





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R. SEED.

and with a ventral margin which in the majority was straight or somewhat convex.

c) *Atlantic Beach*. In addition to the mussels from Capbreton a further sample was collected from Atlantic Beach a few kilometers further south. Apart from their larger size, these mussels were very similar to those from Capbreton.

### C) The Mediterranean coast.

#### 2. Banyuls-sur-Mer.

a) *Semi-exposed open rock*, (Plate 3, E.) This sample was collected from a small semi-exposed reef immediately to the south of Banyuls. It would be impossible to attempt to describe the enormous variation in the external shell morphology of these mussels since practically every conceivable shape was found even in mussels from the same part of the reef. The dorsal shell margin varied from some that were distinctly rounded through many that were slightly angular to others which were markedly angular. The ventral margin showed a similar degree of variation and although the majority were straight, some were slightly convex and others distinctly beaked or incurved. The anterior end in most individuals was pointed and downturned but some had the umbo/lunule swelling and a few were quite blunt. None were rayed and most had deep violet coloured shells, but as in many of the Mediterranean mussels the flat, ventral part of the shell was often light brown. Even after considerable searching no typical *edulis* were found but a few (4 per cent of this sample) were tentatively identified as such in view of their light coloured mantles, shell shape and hinge plate characteristics. In addition to the variation in shell morphology a striking feature of mussels from this site was the variability in mantle edge colour, on which character alone up to 60 per cent of the population would probably have been incorrectly identified. Many of these mussels were quite large and had badly eroded shells often covered with encrusting organisms. Some individuals gave the appearance of being quite, if not exceedingly old.

b) *Banyuls Bay* (Buoy chain), (Plate 3, F). These constantly submerged, apparently fast-growing mussels were all finally identified as *galloprovincialis* after a weighted consideration of all characters. The shells were here basically of two types. A few of the smaller mussels (3 cm in length) were rather *edulis*-like in shape being slightly angular with ventral margins varying from slightly to exceedingly convex, and having rather bulbous umbones. The larger mussels were again fairly uniform in their shape but had much

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#### PLATE 4

##### *M. galloprovincialis* from the Mediterranean coast.

A, B, C - respectively from the immediate sublittoral, intertidal and sublittoral reef regions of Les Calanques (Marseille). D and E - from the intertidal and sublittoral regions of Ile Riou respectively. F - Ile Friou. G and H - respectively from the buoy chains and mooring ropes in Marseille's Old Harbour. I - Black Sea (Amasya, Turkey). J - Villefranche-sur-Mer. K - Naples.

*Scales throughout show cm.*

higher, flatter shells which were distinctly angular and rather beaked. Many appeared to have encountered a marked change in their growth patterns when measuring about 1.5-2 cm in length. The shells were again of a deep violet colour becoming distinctly brown along the flatter ventral region.

c) *Banyuls Bay (Jetty)*, (Plate 3, G). This sample was collected from the end of the jetty in front of the Marine Station where dense clusters of small mussels were found carpeting the rocks. Although a few were superficially *edulis*-like in their shell proportions the majority were rather pointed and had either a slight umbo/lunule swelling or showed some signs of beaking. Again all were finally identified as *galloprovincialis*.

2. *Sète* (Plate 3, I). Here large mussels were obtained from the commercial beds of the "étangs". Considerable difficulties were experienced in identifying these mussels as Table 3 indicates. Many would have been regarded as *edulis* on shell characters but others were more pointed often with a quite pronounced umbo/lunule swelling. The latter were not dissimilar to those *galloprovincialis* originally sent from Arcachon (sample 1) apart from their colour which in these mussels was predominantly deep purple-violet except for the ventral region which was light brown. Some of the mussels in this sample, however, had much blunter umbones, were browner in colour and frequently heavily rayed. Table 3 shows that in this sample 18 per cent were finally regarded as *edulis*, but these were found only after examining a much larger sample. In a purely random sample these *edulis* types would account for no more than 5 per cent of the Sète population. Although finally identified as *edulis* it is perhaps worth noting that the mean adductor scar and hinge plate ratios of these mussels were the lowest on record for *edulis*.

3. *Martigues* (Plate 3, H). This sample was collected from the canal leading into Martigues harbour where dense clusters of small, fast-growing mussels were found covering the wooden mooring stakes. Their shells were deep violet in colour apart from the brownish ventral region and raying was not generally in evidence. On external appearances many would have been regarded as *edulis* having elongate, rounded or slightly angular shells and straight or convex ventral margins. Others, however, had the umbo/lunule swelling characteristic of many *galloprovincialis* and in some cases this was quite pronounced. Although 8 per cent were finally regarded as *edulis* this figure is again probably somewhat high since, as at Sète and Banyuls, exhaustive searches were made for typical *edulis* types.

4. *Marseille*. Several sites were sampled in the immediate vicinity of Marseille and although there was considerable variation in these mussels, in the final analysis it was concluded that *M. edulis* was absent from this part of the Mediterranean.

a) *Les Calanques*. Three fairly distinct habitats were sampled in these creeks in front of the Marine Station.

1) *Intertidal*, (Plate 4, B). In the restricted intertidal region mussels of up to 4 cm in length were not uncommon. These were

relatively uniform in shape with rather angular shells and straight ventral margins. The anterior end was distinctly pointed and usually associated either with a distinct umbo/lunule swelling or some form of beaking especially just behind the umbones. These mussels generally lacked rays and were deep violet in colour with noticeably brown ventral margins.

2) *Immediate sublittoral*, (Plate 4, A). This sample was taken from the shallow sublittoral region of the creek and consisted of large fast-growing mussels with very brittle shells. They were rather angular, and although the ventral margins varied from straight to exceedingly convex, the umbones were, nevertheless, quite pointed. Beaking, however, was not generally in evidence. In shell colour and absence of rays they were similar to the previous sample.

3) *Sublittoral reef*, (Plate 4, C). A final sample from this locality was collected from the seaward side of a submerged reef off the entrance to the creeks. The majority of these mussels were distinctly angular with straight ventral margins associated with a marked downward projecting umbo/lunule swelling. Others had rather blunt umbones and in shell shape might have been regarded as *edulis*, but in colour and absence of rays were typically *galloprovincialis*. Many were remarkably similar to mussels from Naples which I had previously examined.

b) *Ile Riou* :

1) *Intertidal*, (Plate 4, D). This sample came from the relatively exposed end of the island where barnacles extended as much as 6-8 feet above low water. Here mussels varied considerably in their shell shape (and age?) and whilst the umbones in a few instances were blunt, in the majority they were pointed and associated with some form of beaking or ventral incurvature. A striking feature of these animals was the great variability in mantle colour from some that were dark brown, through many intermediate shades, to others which were distinctly deep purple-violet.

2) *Sublittoral*, (Plate 4, E). Many of these mussels were very distorted and badly eroded, often covered with encrusting organisms. There was again considerable variation in shell shape and on this character alone several would unquestionably have been regarded as *edulis*. The majority, however, had rather pointed umbones and ventral margins that were either straight or slightly beaked, but a few (probably very old individuals) were extremely pointed and incurved.

c) *Ile Friou*, (Plate 4, F). Like Riou this is a relatively small exposed offshore island several kilometers from Marseille. Most of the mussels here were rather angular with a straight or slightly beaked ventral margin associated with rather pointed downturned umbones. Even so, quite a number would have been misidentified solely on shell characters. Although the colour of these shells was predominantly dark blue tinged with purple, a few (c. 5 per cent) were yellowy-orange especially around the posterior margin.

d) *Marseille's Old Harbour*. Two samples were collected from this region, one from an old mooring rope within the harbour, and another from the anchorage chains of a large buoy outside the harbour entrance.

1) *Mooring ropes*, (Plate 4, H). The most distinctive feature of these fairly small mussels growing individually along the length of the rope was their very high, triangular shaped shells (mean length/height, 1.56) and whilst some of them might have been regarded as *edulis* on external characters, all other characters were typically *galloprovincialis*.

2) *Buoy chain*, (Plate 4, G). Unlike the previous sample these mussels were very densely packed and their shells were more elongate (mean length/height, 1.89). Some of them measured over 4 cm and their very thin brittle shells suggested rapid growth. In their appearance many strongly resembled the mussels from Martigues. Their ventral margin varied from straight to quite markedly convex, sloping upwards to a rather bulbous umbo/lunule swelling. None were rayed, and although a few (2 per cent) were brownish-orange in colour the majority were purple-violet with brown ventral margins.

5. *Villefranche-sur-Mer* (Plate 4, J). Some of these mussels were distinctly *edulis*-like in shape but others showed a striking resemblance to many of the *galloprovincialis* illustrated by List (1902) and to the Naples mussels which I had previously examined. They had angular shells with straight or slightly convex ventral margins associated with a distinct umbo/lunule swelling. Neither beaking nor ventral incurvature was in evidence, and whilst 15 per cent were rayed these were exceedingly faint.

## DISCUSSION

From the foregoing account and from Plates 1-4, it is evident that both *M. edulis* and *M. galloprovincialis* from the French coasts exhibit considerable variation in external shell morphology. Of the two, *galloprovincialis* seems to be slightly the more variable, but without detailed information concerning the growth rates and environmental conditions in the various localities it is impossible to know with certainty to what these variations are due. It seems probable, however, that they are related, at least in part, to the age of the animals and the local conditions under which they are grown as shown for *M. edulis* on the north east coasts of England (Seed, 1968). Table 3 indicates that over 30 per cent of all the mussels examined during this investigation would have been misidentified on external characters alone. Similar problems of identification were previously encountered in mussels from south west England (Lewis and Seed, 1969).

In densely crowded situations mussels tend to be elongate whilst those growing individually or in less dense conditions were usually higher and more angular. Mussels from the higher shore levels, especially on exposed shores, apart from being generally smaller, can in the absence of major predators, live much longer. Consequently many of these animals show features associated with old age, i.e. they are wider rather than high, have overall ventral incurvature and pointed divergent umbones, and are often badly eroded. In such habitats iden-

tification on external shell characters becomes even more difficult. The range of habitats in the relatively atidal Mediterranean was more limited, and although there was still considerable variation in shell shape, it is perhaps significant that basically similar morphological types recurred in many localities (e.g. Plate 3, H and I; Plate 4, C, G and J). These mussels also showed striking similarities to those previously examined from Naples and the Black Sea (Plate 4, K and I).

Perhaps the most consistently recurring external morphological feature was the more pointed anterior end in *galloprovincialis*. This was usually associated either with some form of beaking of the ventral margin or, especially in Mediterranean mussels, with a prominent umbo/lunule swelling. In contrast, the majority of *edulis* were rather blunt with relatively straight or convex ventral margins, but many of the older animals were more pointed and distinctly incurved (e.g. Plate 1, E 1, G 3, H 9-12; Plate 3, B 10 and 12). Sometimes, such forms could be difficult to separate from *galloprovincialis*.

Table 1 shows that in any one locality *galloprovincialis* had somewhat higher shells than *edulis* as indicated by their lower length/height ratios. These values, however, varied considerably from one sample to another, with ranges of 1.82-2.15 for *edulis* and 1.56-2.10 for *galloprovincialis*. Even greater variation occurred amongst individual animals with values for *galloprovincialis* ranging from 1.4-2.4.

Shell colour in both was subject to considerable individual variation but the majority of *galloprovincialis* were distinctly more violet than the darker blue *edulis*. Many of the *galloprovincialis*, especially from the Atlantic coast, were predominantly greyish-blue tinged with yellow-orange and becoming almost white around the posterior shell margin. In certain localities these colour differences often proved to be the only external means of identification (e.g. Plate 3, D). The presence of longitudinal rays in *edulis* and their absence in *galloprovincialis* (a feature also noted by Lubet (1959) gave an initial identification which proved to be correct for about 90 p. cent of the mussels.

Previous literature, especially the illustrations of List (1902) and Bucquoy, Dautzenberg and Dolfus (1887) also clearly indicates considerable variation in external morphology of *M. galloprovincialis*. Bucquoy *et al.* further comment upon the difficulties in separating the two species on external characters alone, « ... il existe des formes étroites et allongées du *M. galloprovincialis* qui se rapprochent du *M. edulis* et des formes courtes et larges du *M. edulis* qu'il est difficile de distinguer du *M. galloprovincialis* ». Dautzenberg (1897) also comments upon the variability in *M. edulis* according to the conditions in which the animals are grown, and describes *M. galloprovincialis* as « ... une forme plus large et plus triangulaire que le *M. edulis*. Sa coloration d'un noir plus pur et moins bleuâtre ne représente pas de rayons comme celle de la moule commune ». Ricci (1957) considers that the major difference between *galloprovincialis* from Tunis and *edulis* (from Germany?) was in the length/height ratios of their shells.

A sample of mussels from Naples examined by the author and illustrated in Plate 4, K showed remarkable similarities in shell morphology to mussels illustrated by List (1902)—they were quite high and rather angular with straight ventral margins and marked

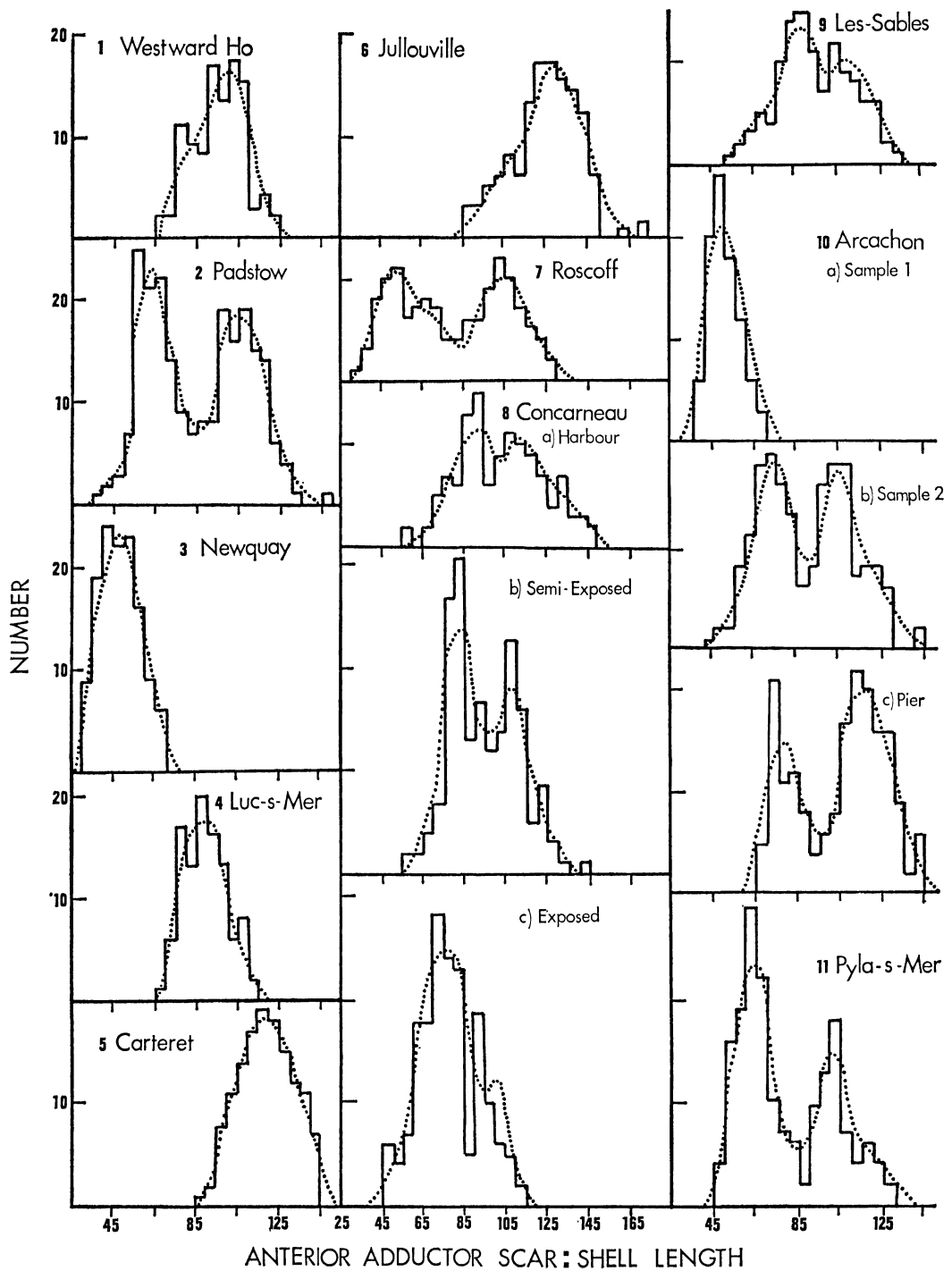


FIG. 3

Histograms showing the frequency distributions of values for the ratio anterior adductor muscle scar length/shell length ( $\times 1,000$ ) in *Mytilus* from the localities investigated. The dotted line was obtained by using a standard smoothing technique.



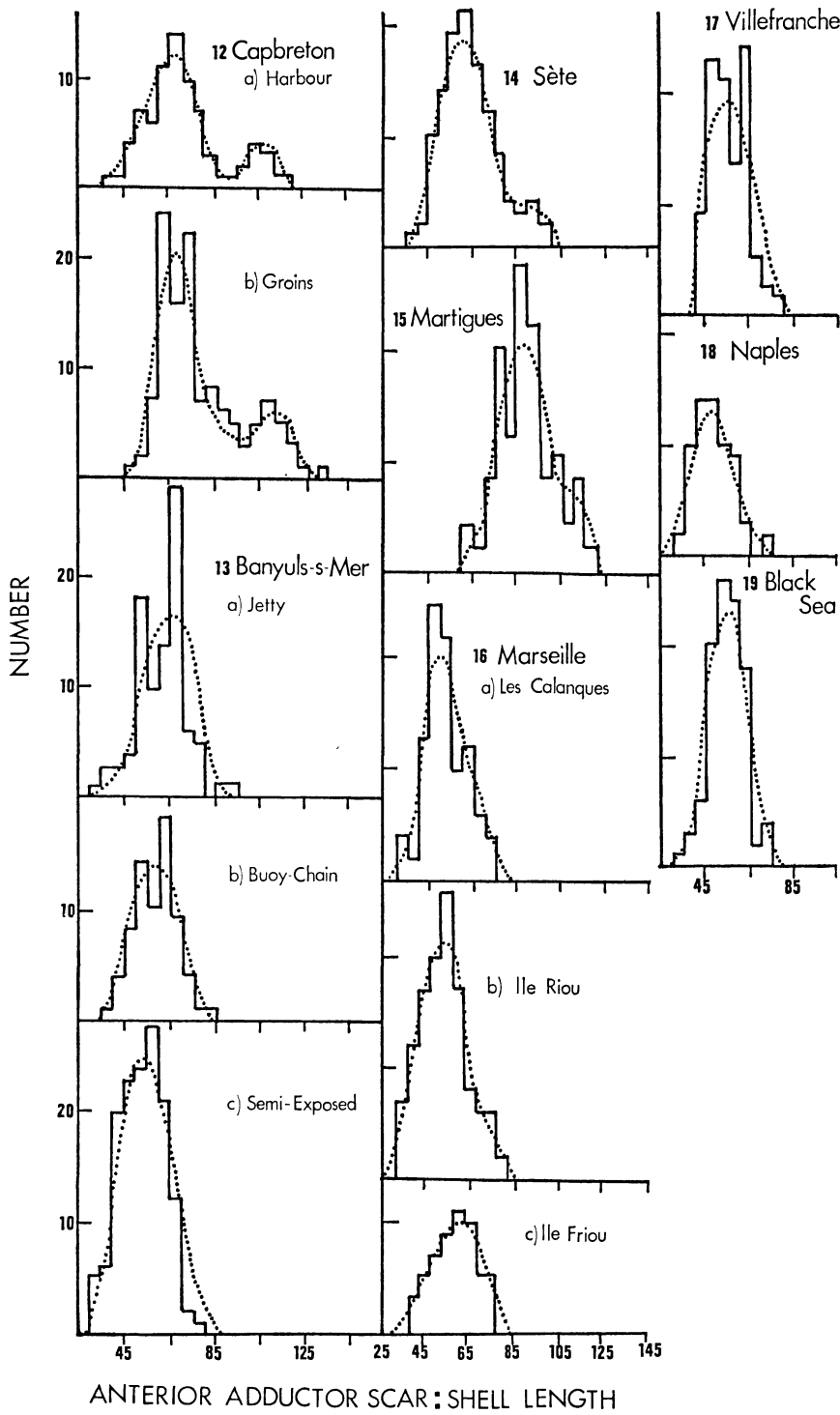


FIG. 3

umbo/lunule swellings. Further samples from the Mediterranean and Black Sea coasts of Turkey (Plate 4, I) were basically similar apart from being somewhat more elongate (1).

As in mussels from south-west England, the size of the anterior adductor scar and hinge plate ratios generally proved to be reliable taxonomic characters, values for *galloprovincialis* (particularly those from the Mediterranean) being consistently lower than those for *edulis*. Whilst considerable variation in the mean adductor scar ratios occurred from one locality to another, Table 1 shows that there was very little overlap in the mean values for *edulis* and *galloprovincialis*, 80-124 and 41-87 respectively. Figure 3 illustrates the frequency distributions of values for the ratio scar length/shell length ( $\times 1,000$ ) at most of the sites visited. The first three histograms relate to populations in south-west England—Westward Ho! and Newquay Harbour, where populations consisted entirely of *edulis* and *galloprovincialis* respectively and Padstow where both species occur in approximately equal numbers. At the latter locality the frequency distribution is distinctly bimodal as it is for the majority of stations on the French coasts where both species occur together. However, in the regions around Concarneau and Les Sables-d'Olonne (Fig. 3, 8-9) there is considerable overlap in the values, and distributions are not as markedly bimodal. Whilst this could possibly reflect some local breakdown in the values of the adductor scar as a taxonomic character it could be due to a higher incidence of hybrid forms since other characters too were here generally much less reliable than elsewhere (Table 3). In this respect it would be interesting to know the breeding patterns of the two mussels in this particular region since at Arcachon to the south, and at Padstow in south-west England, both localities where these mussels are morphologically distinct, the reproductive cycles are known to be different (Seed, 1971). The possible preclusion of cross fertilisation in these localities could perhaps result in the two populations remaining relatively genetically isolated, but if in the Concarneau - Les Sables regions there was considerable overlap in the spawning periods, then one might expect to find a higher incidence of intermediate forms.

In all the Mediterranean samples, distribution of scar ratios were unimodal except at Sète and Martigues (Fig. 3, 14-15) where the presence of a few *edulis* types gave these graphs a distinct skew. The situation at Sète, however, was rather peculiar since animals were grown commercially and considerable relaying of animals took place (even apparently from the Atlantic coast). Certainly, some difficulties of identification were encountered in these regions and also in the sample from outside Marseille harbour as indicated in Table 3. The mean scar ratio of 87 for the Martigues sample was the highest recorded for *galloprovincialis* and was much higher than in any of the other Mediterranean samples.

The smaller size of the anterior adductor scar in *M. galloprovincialis* has been noted by previous authors (e.g. Barsotti and Meluzzi, 1968; List, 1902) and Soot-Ryen (1955) comments upon the higher, flatter forms with small adductor scars named *M. galloprovincialis*

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(1) Since this work was carried out, I have also found mussels similar in shape to those at Naples in samples from North Africa.

in the Mediterranean and *M. edulis diegensis* Coe in California. A sample of the latter examined by the author showed remarkable similarities to Mediterranean *galloprovincialis*, not only in their small adductor scars but also in their hinge plates and absence of longitudinal rays, and in their general shell shape (a marked umbo/lunule swelling, straight ventral margin and rather high angular shells). Possibly the smaller hinge plates and adductor scars in *galloprovincialis* may have arisen in relation to the less wave-swept conditions of the Mediterranean, and in this respect the relative restriction of *M. edulis diegensis* to bays and inlets (Coe, 1946) is perhaps significant.

Unlike the adductor ratios, frequency distributions of the value hinge plate length/shell length ( $\times 1,000$ ) were generally unimodal (Fig. 4) and the degree of overlap such that identity of individual mussels on size alone, without any reference to the shape of the hinge plate, would be uncertain except where the value was either very high (*edulis*) or very low (*galloprovincialis*). In a few localities, however (Arcachon Pier, Pyla-sur-Mer, Capbreton and Roscoff) the differences between the two mussels on this character were somewhat more marked and distributions of hinge plate ratios were distinctly skewed.

Although mantle edge colour varied from almost white in some individuals, through all shades of brown, reddish-brown and purple to deep violet in others, for the majority of mussels this proved to be generally a reliable taxonomic character. Table 3 shows that only about 15 per cent of all mussels examined would have been misidentified on mantle colour alone. The distribution of these « misidentifications » is, however, rather interesting. In the Concarneau-Les Sables region between 20-45 per cent of the population would have been misidentified on this character, supporting the contention that perhaps here considerable hybridisation and intermingling of characters occurs, but no satisfactory explanation can be given for the apparent breakdown in the value of this character in samples from Banyuls, Sète and Riou where over 60 per cent of the population might have been incorrectly identified.

In most localities in the Mediterranean where samples were taken, only *galloprovincialis* was present. *M. edulis* was recorded in samples from Banyuls, Sète and Martigues but many of these showed a mixture of characters and few could be regarded as typical *edulis*. It should also be stressed that extensive searches were in fact made for this species in the Mediterranean and the samples in which it is recorded cannot therefore be regarded as entirely random. In none of the above three sites did *edulis* account for more than 5 per cent of the total mussel population.

*M. galloprovincialis* was present along the whole of the Atlantic coast and extended into the Channel as far as the Cotentin. Whilst a few individuals were found on the west shores of the Cotentin none occurred east of Cherbourg despite prolonged searching. Between Luc-sur-Mer and Wimereux large numbers of mussels were examined in the field but no *galloprovincialis* were found. *M. edulis* on the other hand was abundant at all stations along the Channel and Atlantic coasts but few positive identifications were made in the Mediterranean.

The conclusions that can be drawn from this investigation concerning the distribution of these two mussels on the French coasts generally appear to be supported by previous reports that exist on this subject.

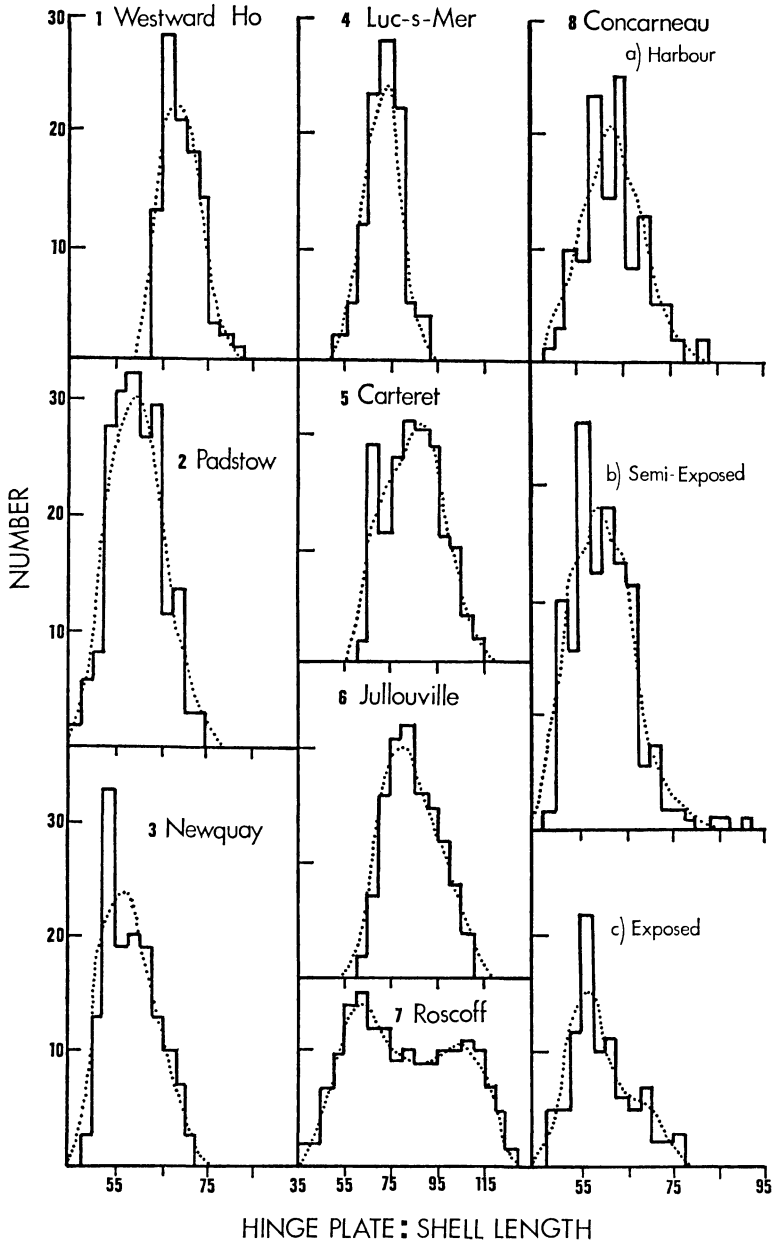


FIG. 4

Histograms showing the frequency distributions of values for the ratio hinge plate length/shell length ( $\times 1,000$ ) in *Mytilus* from the localities investigated. The dotted line was obtained by using a standard smoothing technique.

Bucquoy et al. (1887) found *galloprovincialis* throughout the Mediterranean, Adriatic and Black Seas and less abundantly along the Atlantic coast. It was also found at Cherbourg but they suggest

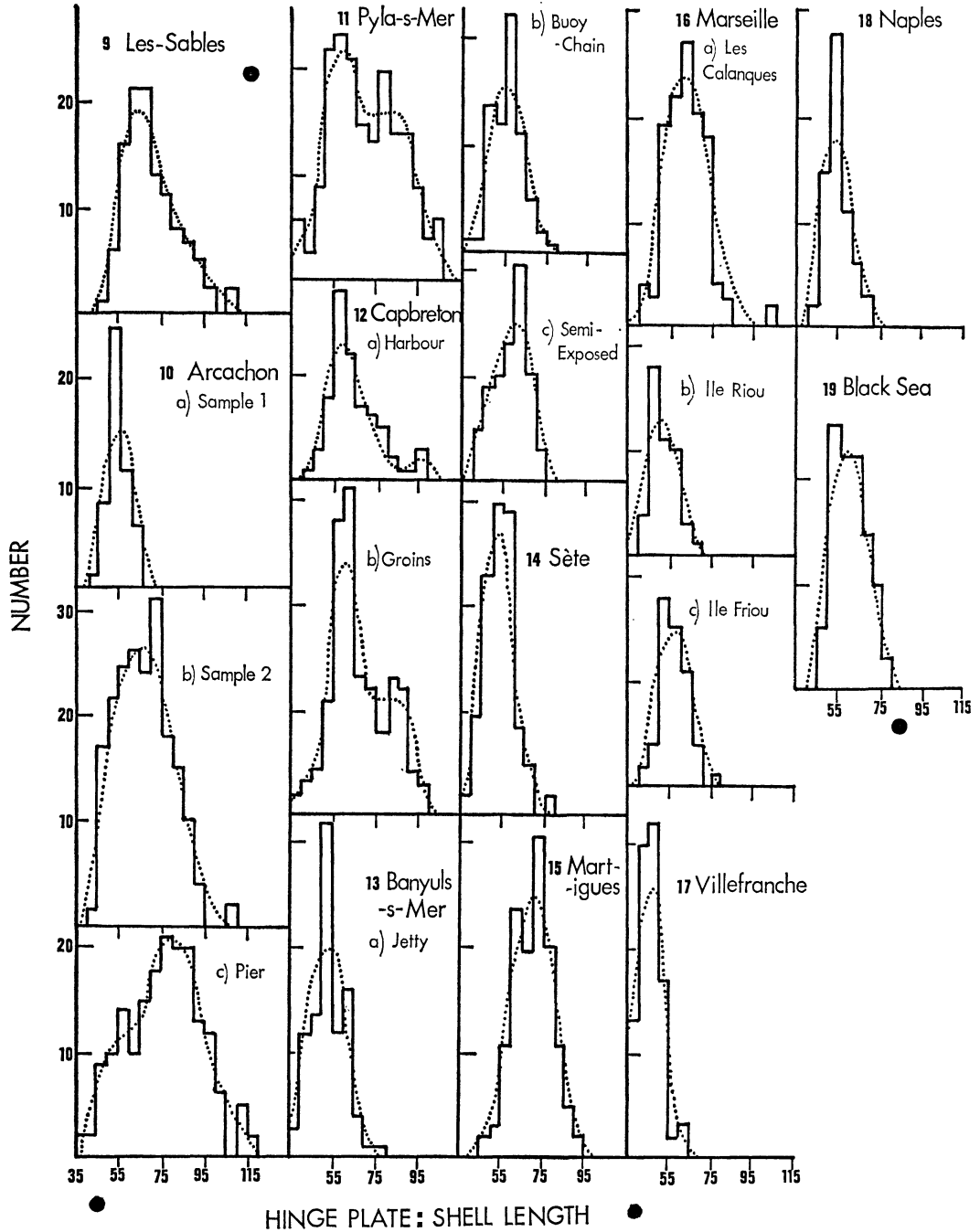


FIG. 4

that it may have been introduced there on boats coming from the Mediterranean. The distribution of *edulis* was equally extensive, occurring along all the oceanic coasts of Europe, but these authors are of the opinion that its presence in the Mediterranean is perhaps doubtful.

Berner (1935) concludes that whilst *edulis* occurs from the Arctic as far south as Spain, *galloprovincialis* is predominantly restricted to shores bordering the Mediterranean (including the Adriatic and Black Seas). He comments on the possible harmful influence of tides on *galloprovincialis* but believes that another factor is probably involved (as yet unknown)—the same factor that prevents *edulis* from becoming "acclimatised" at Marseille.

According to Dodge (1952), *edulis* is found on both sides of the Atlantic from Arctic waters to Gibraltar and North Carolina, as well as on the west coast of America as far south as San Diego.

Molinier and Picard (1957) have recorded *M. edulis* in the Mediterranean only as far as Motril (east of Gibraltar) but even here it was restricted to shaded overhangs and cracks in the rock surface. *M. edulis* has, however, been recorded from Marseille (Marion, 1883—quoted in Berner) and *M. galloprovincialis* from the Schleswig-Holstein region of Germany (List, 1902) but in the earlier literature there appears to have been some confusion over *M. galloprovincialis* and *M. angulatus* and several authorities, including List, seem to be of the opinion that these two forms are synonymous. *M. angulatus* is, however, perhaps best regarded as a distorted form of *edulis* as originally suggested by Linnaeus (1758). Certainly, Lamarck (1819) must have been fully aware of both these forms when describing *M. galloprovincialis*. The record of this species in the Schleswig-Holstein is therefore perhaps rather questionable. Dr. Ziegelmeier (pers. comm.) who has worked extensively on the macrobenthos in the southern North Sea has apparently never found *M. galloprovincialis* in that region.

Fischer (1929) remarks on the scarcity of mussels around the Cotentin (also noted during this investigation) but points out that the mussels to the east of the Cotentin at Grandcamp-les-Bains were *edulis* types whereas those in the region of Saint-Malo and Granville appeared to be *M. galloprovincialis*. He regards *edulis* as a predominantly northern form whose distribution extends to the Baie d'Isigny (nr. Grandcamp) but which is also found further south for example at Esnandes and Lisbon.

An interesting discussion of the probable phylogeny of *M. edulis* and *M. galloprovincialis* is given by Barsotti and Meluzzi (1968).

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### Summary

Both *M. edulis* and *M. galloprovincialis* on the coasts of France showed considerable variability, especially in shell shape, and on this character alone many individuals would undoubtedly have been misidentified. However, the majority of *galloprovincialis* could generally be identified by their somewhat more pointed and downturned umbones, frequently associated with some form of beaking or with a prominent umbo/lunule swelling.

The dark colour of the mantle edge, absence of longitudinal rays on the shell and the small size of the anterior adductor muscle scar and hinge plates generally proved to be more reliable taxonomic characters than external shell morphology.

*M. galloprovincialis* is the dominant mussel in the Mediterranean. It also extends along the length of the Atlantic coast of France and into the Channel as far as the Cotentin. A few individuals were recorded on the west coast of the Cotentin but none were found east of Cherbourg. *M. edulis* on the other hand, occurred at all the stations on the Channel and Atlantic coasts but very few positive identifications were made in the Mediterranean.

Although both *M. galloprovincialis* and the « Padstow mussel » from south-west England exhibit wide variations, particularly in their shell morphology, the striking similarity between animals from similar environmental conditions indicates quite conclusively that these mussels are synonymous forms of *Mytilus*.

### Resumen

*Mytilus edulis* y *M. galloprovincialis* de las costas de Francia son muy variables sobre todo en la forma exterior de sus conchas y según este carácter hubiera sido imposible identificar varios especímenes. Las puntas anteriores (umbos) en *M. galloprovincialis* las más veces son más agudas y más encorvadas y las conchas no tienen rayas purpúreas longitudinales. La huella de los músculos anteriores aductores y las conyunturas (hingeplates) son también más pequeñas en esta especie y la región posterior del manto (mantle) es más purpúrea que en *M. edulis*.

*M. galloprovincialis* es la almeja más abundante en el Mediterráneo. Se halla también en la costa del Atlántico y en el canal de la Mancha hasta el Cotentin. Unos especímenes fueron coleccionados en la costa del oeste de Cotentin pero ningunos al este de Cherbourg. Sin embargo *M. edulis* se halla en todos los sitios del canal de la Mancha y de la costa del Atlántico, pero en el Mediterráneo esta especie es más rara.

Aunque *M. galloprovincialis* y el « tipo Padstow » del sud-oeste de Inglaterra son muy variables sobre todo en cuanto a la morfología de la concha, la semejanza entre los animales de ambientes similares indica que estas almejas son formas sinónimas de *Mytilus*.

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