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The Ecology of *Mytilus edulis* L. (Lamellibranchiata) on Exposed Rocky Shores

I. Breeding and Settlement

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Summary. The population structure and apparently erratic distribution patterns exhibited by *M. edulis* on many open exposed coasts, are discussed in the light of findings relating to the breeding and settlement of this species. In the absence of previous literature concerning open coast mussels, the reproductive cycle has been described in some detail. These mussels do contribute to the spawning stock, and in the three years from October 1964 — December 1967, the period of spawning was shown to be particularly extended. Spawning occurred mainly from early spring to late summer, though individuals could be found in the spawning condition more or less throughout the year. No marked or consistent differences in the spawning periods of mussels from different local habitats or amongst animals of different size (= age) were recorded. Sexual maturity was attained in the first year of life.

The appearance of larvae in plankton samples confirmed the times of major spawnings recorded from histological preparations of the gonad. Settlement of young mussels (= plantigrades) on existing beds was not direct, there being a period of temporary attachment spent especially upon filamentous substrates. This occurred after about 3—5 weeks of planktonic existence. The majority of plantigrades remained on these primary sites for a period of 4 weeks (i.e. until they measured from 1—2 mm in length), although those settling later in the year often remained there overwinter before migrating on to adult beds. The stimulus to migrate is due to changes in the thigmotactic requirements of small mussels. Whilst filamentous substrates were ideally suitable to early plantigrades, somewhat older individuals preferred the niches and crevices provided on adult beds (especially amongst the byssus threads) and by the small cracks and pits in the rock surface. Since the thigmotactic requirements of all plantigrades were not satisfied at exactly the same time, some migration to adult beds occurred throughout the year, though periods of maximum settlement occurred from 8—10 weeks after spawning. Migration from these extensive "reservoirs" of temporary attachment could account for the sporadic outbursts of settlement recorded on many shores at certain times of the year and which often could not necessarily be predicted on a knowledge of the breeding cycle alone.

Although the extended settlement period is an important contributory factor, it is not thought that this alone could account for the distinctive population structure in this species. At settlement, mussels are particularly gregarious, attraction of plantigrades to adult beds being essentially a thigmotactic response, aided by their ability to attach and detach themselves until favourable situations are

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encountered. Settlement is favoured by roughened, scarred or pitted surfaces and the distribution patterns on many shores could partly be attributed both to the surface texture or topography of the shore (smooth, rapidly draining shores being particularly unsuitable) or the amount of local wave splash.

In a subsequent publication, the population structure and distribution patterns will be examined in the light of growth and mortality rates of this species on exposed shores.

Whilst the literature relating to *Mytilus edulis* L. is particularly extensive, for the most part attention has been directed towards its economic value as food, bait and fouling organism, yet there exist beds of small, often apparently stunted mussels on many of the open, exposed coasts around Britain, and these have received only passing mention in previous literature. Although the biomass (per unit area) of open coast populations may be small in comparison with that of populations from sheltered estuaries and harbours, their densities are almost always very many times greater (densities exceeding 1,000 individuals per 5 cm^2 are not uncommon). In view of such high densities, coupled with the wide occurrence of exposed coastline, these small, exposed forms must constitute the majority of mussels in British waters, and form the basis of an extremely important littoral community.

In an extensive survey of many exposed shores around Britain, Lewis (1964) commented upon the apparently erratic distribution exhibited by *Mytilus* and the uncertainty in predicting which situations would support mussels in quantity (p. 92). In the following investigation relating to local shores (see Fig. 1), initial observations indicated that whereas mussel populations with their associated red algae often dominated barnacles on some exposed shores, other shores which appeared equally suitable, lacked mussels entirely. Even locally, on the same stretch of shore, some areas would be carpeted with mussels whilst adjacent areas would not support a single animal. Observations further suggested that mussels appeared to favour either gently shelving, slow draining platforms, or shores receiving continued wave splash, rather than rapidly draining vertical faces which supported very few animals. On exposed wave beaten shores dominated by small mussels, distribution patterns were far from uniform over the entire shore. Whereas in the upper shore (Fig. 2A) mosaics of apparently old mussels could be found (many being broad and reniform in appearance with exceedingly eroded shells) in the midshore (Fig. 2B) mussels populations usually attained their maximum development, both in terms of biomass and coverage of the shore. Even within these dense beds, however, areas devoid of mussels could still be found, especially around the deep clefts and pot-holes in the rock surface (a characteristic feature of many local shores). Further downshore (Fig. 2C) these dense beds are often replaced by mosaics of smaller, apparently young mussels measuring

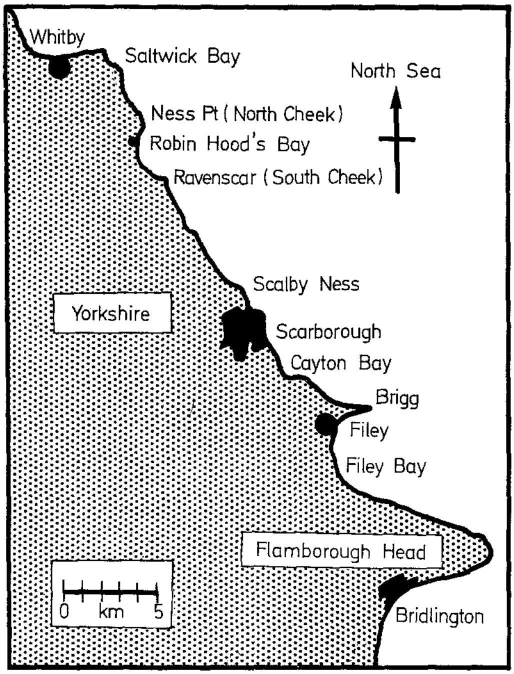

Fig. 1. Map of the region dealt with in the text

up to 2 cms in length. At and around M.L.W.S. these mosaics on many local shores coalesced, resulting in an almost 100% coverage of the shore, whilst just above the laminarian zone their distribution was often abruptly terminated.

Although the varied distribution patterns exhibited by this species might be related to local differences in the physical environment, perhaps a more probable explanation should be sought in terms of variations in the sequential settlement, mortality and recolonisation occuring in the different habitats. In view of this, extensive studies of the breeding cycle, settlement, growth and mortality rates of mussels from a variety of local habitats was undertaken, together with detailed analyses of individual population structures. Whilst the present paper deals exclusively with aspects of breeding and settlement, results relating to growth and mortality will be presented in a later publication.

Analyses of the population structure of many bivalve species have shown length frequency distributions to be polymodal, each mode representing an individual year class. This occurs in those species where new members enter the population over a relatively short time period, and where growth of individuals of each year class is relatively uniform. Of

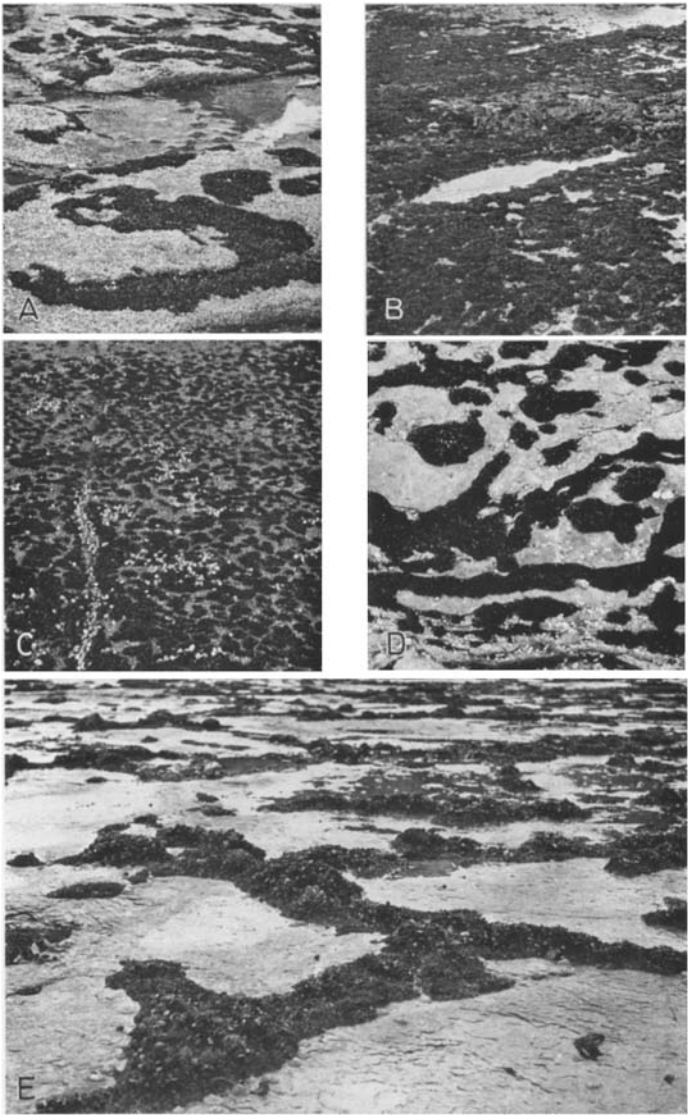

Fig. 2A—E. Distribution patterns exhibited by *M. edulis* on a shore at Ness Point (Yorkshire). A. Mosaics of *Balanus* and *Mytilus* in the upper shore. B. Dense beds of relatively large mussels in the mid shore. C. Mosaics of small mussels in the lower shore. (NB. Large numbers of *Thais lapillus*). D and E. Gregarious settlements of mussels in cracks and pits in the rock surface. NB. How intense settlements amongst existing mussels in E has led to "hummocking"

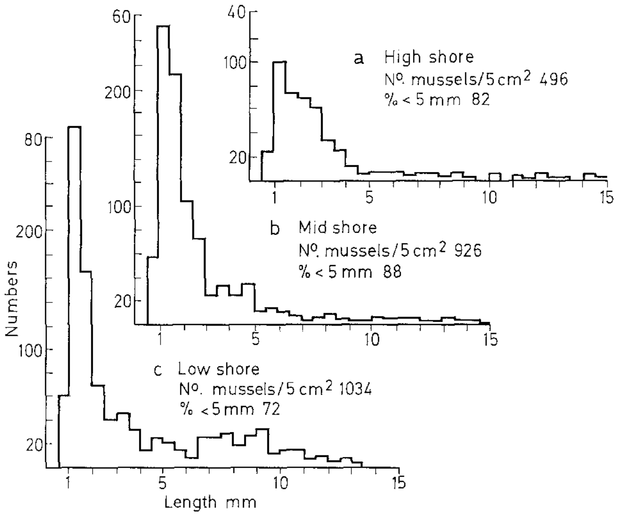

Fig. 3. Population structures of *Mytilus edulis* at three shore levels on an exposed rocky shore at Ness Point. (NB. Mussels over 15 mm, were very few in number and have been ommitted from the graph)

the more recent publications relating to *M. edulis*, Chipperfield (1953) recorded relatively short spawning and settlement periods at five stations around the British Isles. If this is assumed to be a characteristic feature of this species, and if growth rates of individuals within each year class prove to be relatively uniform, length frequency could be expected to be polymodal, and from these, useful data relating to growth, settlement and mortality could be obtained. Actual analyses of populations made in this investigation did not, however, permit the recognition of individual year classes since 60—90% of field populations at any particular time consisted of animals under 5 mm in length (Fig. 3). Although mussels on many open shores frequently attain lengths of 4 cms or more, the numbers exceeding 1.5 cm never accounted for more than 5% of the total population. In younger populations with only two or three year groups present, traces of polymodal length frequency distribution could be found, but their absence from older populations might be explained either by extensive breeding and settlement periods and/or by highly variable individual growth rates.

The following work (started in October 1964) was undertaken with a view to explaining the observed distribution patterns and characteristic population structure of *Mytilus* on local shores. The work relates to populations from the E. Yorkshire coast between Whitby and Filey and although the main emphasis has been directed towards animals situated on open coasts, comparisons have also been made with mussels from less exposed localities such as Whitby harbour, Filey Bay and Robin Hood's Bay.

Since work upon reproduction of this species is still in progress, breeding data is given to December 1967, whereas other aspects of the work were discontinued in May 1967.

A. The Reproductive Cycle

Although the breeding cycle in *M. edulis* is well documented (see for e.g. Wilson, 1886; Johnstone, 1898; Scott, 1901; Battle, 1932; Chipperfield, 1953; Savage, 1956) geographical and annual variability necessitated a detailed investigation for this particular locality. Indeed, in the absence of literature relating to open coast mussels, it was not even known at the outset of this investigation whether these populations actually contributed to the spawning stock. Apart from work relating to *M. edulis*, considerable literature also exists for other mytilids, e.g. *M. californianus* (Conrad) (Whedon, 1936; Coe and Fox, 1942; Young, 1946) and *M. galloprovincialis* (Lmk.) (Berner, 1935; Bouxin, 1956; Lubet, 1957). Wilson and Hodgkin (1967) give a comparative account of the reproductive cycles of five species of W. Australian marine mussels, whilst a review of the scanty literature on the physiology of lamellibranch reproduction is given by Giese (1959).

Whilst breeding cycles should ultimately be analysed in the light of both the ecology and the physiology of the animal, the present investigation has been concerned entirely with ecological aspects of mussels reproduction. It is apparent, however, that the complex physiological mechanisms controlling the reproductive cycle, requires further detailed investigation before a complete underständing of this process is forthcoming.

Perhaps the three most pertinent questions relative to the present work are:

i) Do open coast mussels ever attain sexual maturity and contribute to the breeding stock, or are they merely slow growing, non-breeding forms living more or less at their environmental limits, derived from distant stocks living under more favourable conditions ?

ii) If they do contribute to the breeding stock, when and for how long, does spawning occur in any one year ?

iii) In the event of an extended spawning period would this reflect: a) Repeated spawning of individual mussels ? b) Differences in the spawning periods of animals of different ages or from different local habitats (e.g. their vertical position on the shore or degree of exposure to wave action).

These are the basic problems considered in the following investigations.

I. Sampling and Examination of Samples

Attempts to fix the dates of spawning may be accomplished either by direct or indirect methods. The latter include the observation of larval outbursts in plankton samples or the times of maximum settlement of young mussels on the shore, from which it is often possible to infer the times of maximum spawning. However, since fertilization in *Mytilus* is external, and larval stages may be transported considerable distances by water currents, the settlement of young mussels on the shore at any one locality is no true indication that these are the results of spawnings in that particular locality or habitat. Plankton and settlement studies have been made in this investigation (see later) and have served to check data obtained by more direct methods.

Whilst direct observation of spawning in the laboratory is a useful indication of conditions favourable to spawning, it is no guarantee that such conditions operate in nature, where the interaction of many variable factors may have modifying influences on the breeding cycle. Actual field observations of spawning on the other hand, are virtually impossible to obtain.

Perhaps the most useful information concerning the breeding cycle is that obtained from histological preparations of the gonads. Although laborious (probably a major reason for its limited use in previous works) this method, when carried out at regular intervals throughout the year, gives detailed information of the entire reproductive cycle including the actual times of spawning. Most attention has therefore been directed to this method in the present investigation. Initially some use was made of gonad smears, but since these were frequently confusing, and particularly difficult to assess, they were later discontinued. Similarly, estimation of the reproductive condition by macroscopic examinations of the gonads was both difficult and unreliable in as much as "resting" gonads, distended with stored food reserves were frequently mistaken for ripe animals. From October 1964 regular monthly or fortnightly samples were collected from five widely differing local habitats at Filey (Yorkshire). These were:

i) The highest occuring beds from the sheltered bay.
ii) An area at approximately M.L.W.S.; Filey Bay.
iii) The highest occuring beds from the wave-beaten Brigg.
iv) A midshore population; Filey Brigg.
v) An area at approximately M.L.W.S.; Filey Brigg.

Throughout 1966, regular samples were also taken from Whitby harbour (where beds of large, fast-growing mussels could be readily obtained) for comparison with the Filey populations. In order to determine whether spawning varied with age in any one habitat, samples from both Filey (1965) and Whitby (1966) included very small and relatively large individuals. Animals were examined on the day of collection or kept overnight in a cool place in dry polythene bags. The mantle from one valve was removed and the middle third fixed in Bouin's fluid in sea water, then stored in 70% alcohol. Tissues were embedded in Paraplast wax (M.P. 56—57 °C) and sections cut at 10—15 μ, were stained in either Ehrlich's or Delafield's haematoxylin (without counterstain). As many as 10—20 gonads could be embedded, sectioned and stained together, thereby permitting large samples to be taken. Very small mussels (under 5 mm length) were occasionally examined, and these were decalcified in 5% nitric acid in 80% alcohol and sectioned whole.

At various stages throughout the reproductive cycle during 1965, sections were stained for fat (Flemming's osmochromic fixative; 0,5% Oil Red O; Sudan Black) and glycogen content (Periodic Acid Schiff; Best's Carmine). Occasionally, detailed nuclear stains were carried out on a few individuals using the Feulgen reaction for nuclear proteins following 4% formol fixation, and with a light green counterstain.

II. Anatomical Relations and Histology of the Gonad

The sexes in *Mytilus* are separate, and no external signs of sexual dimorphism are apparent. During the breeding season it is sometimes possible to sex individuals by the colour and texture of their gonads, females tending to be pinky-orange, males being more creamy white. Whereas male follicles tend to be rounded, even in size and regularly distributed, female follicles vary in size, having a smoother texture, and being less granular in appearance than the males. During the non-breeding season, on the other hand, it is usually impossible to sex individual mussels, even from histological preparations. Detailed descriptions of the anatomy and histology of the genital system in *Mytilus* are to be found elsewhere (Field, 1922; White, 1937).

Genital tissue invades practically the whole of the body tissues, filling the mantle lobes, mesosoma, the outer surfaces of the digestive gland and the floor of the pericardium. Only the dorsolateral walls of the pericardium, foot, gills and muscles remain free from genital tissue. In the early stages of the reproductive cycle it is frequently difficult to distinguish between males and females. Although the sexes are almost equal in numbers (males slightly outnumbering females) the larger size categories from many localities showed a preponderance of females. Whilst this might be explained in terms of differential growth or mortality, it could also be explained in terms of a sex change during later life, although no traces of intersexuality have been recorded in the large numbers examined.

Sections of animals of all sizes from any locality indicated that maturity was attained during the first year of life, the size at which this occurred depending upon the rate of growth for that locality. Whilst in areas of relatively rapid growth, mussels could be found fully mature at 6—7 mm length, in areas where growth proved to be exceptionally slow, fully mature animals could be found measuring only 2 mms in length. This suggests that sexual maturity is a function not of size but of age, and that the size at which maturity occurs varies according to the growing conditions of the environment. Sections of young mussels indicated that genital development commenced dorsally around the digestive gland, only later extending ventrally into the mantle lobes. The number of follicles present in cross sections of the mantle varied considerably, being more numerous in older mussels.

Oogonia and spermatogonia are budded off from the follicular germinal epithelium, though it was often very difficult to distinguish between these early stages of gametogenesis. During their early development, early oocytes are connected to the epithelium by means of a broad stalk, but this gradually becomes more slender and finally ruptures, leaving the mature ova free within the follicle. Ripe ova have well developed nuclei and nucleoli, measure about 70 μ in diameter, and assume a polygonal configuration due to mechanical pressures exerted within each follicle as these become distended with ripe ova. The presence of abnormal oocytes similar to those illustrated by Wilson and Hodgkin (1967) was not uncommon, but the significance of these is not clear. Spermatogonia give rise, in turn, to spermatocytes and spermatids, whilst in the centre of the follicles are the spermatozoa, usually in the form of lamellae.

III. Arbitrary Scheme of Classification of the Gonad Condition

From the examination of histological preparations it has been possible to assign each mussel in any sample to a particular arbitrary stage, from which the breeding state of the population could be assessed. Schemes of classification of gonad condition have been used previously (Chipperfield, 1953; Lubet, 1957) but the system used in this investigation has been based upon that used by Orton *et al.* (1956) for *Patella vulgata* L.

In any system of arbitrary classification, intermediate stages inevitably occur, resulting in some subjectivity, therefore in order to make the scheme more objective, as many criteria as possible were used in the assesment of each stage. Since there was considerable variation in the degree of genital development, even at the same time and within the same population, it was important to make each sample as large as possible. Before assigning any animal to a particular stage, a whole year's sample was examined so that a more reliable judgement of the changes occurring throughout the year could be made. Although several criteria were considered before assigning any individual to a particular stage, only method id (below) was found to be of any significant value.

a) The Ratio of Genital to Total Mantle Tissue

During the process of maturation, the area of mantle occupied by the gonad in transverse sections, gradually increased, until as much as 95% could be occupied in the fully ripe condition. Even so, considerable variation occurred, both between populations and within the same population, many mussels having only 20—30% of their mantles occupied by genital tissue even in the fully ripe condition.

b) The Relative Thickness of the Mantle of Similar Sized Mussels from the Same Locality

Since recently spawned mussels often had thin, transparent mantles when compared with fully ripe animals, relative mantle thickness appeared to provide a useful method for assessing the state of the reproductive cycle. Yet even within the same population, animals with relatively thin mantles could be found in the fully ripe condition, whilst others with much thicker mantles could be found in relatively early stages of development. Indeed, mantles are often thickest during the resting phase when excessive stores of glycogen and fat are laid down.

c) Total Tissue Weight

As the majority of tissues are invaded by genital tissue, considerable reduction in tissue weight in post spawned mussels is to be expected. Whilst in general this is true, tissue weight was subject to considerable variation, and, as pointed out above (b) was often greatest during the non-breeding period due to the excess amounts of stored food.

d) The Relative Proportions of Early to Late Stages of Gametogenesis within Individual Follicles

In females, actual egg counts could be made, making the assignment to a particular stage more objective than was often possible with males. Since all follicles in any mantle may not be at exactly the same stage, weighted assessments had often to be made.

From the examination of histological preparations, four main stages in the annual cycle could be recognised; developing, ripe, spawning and spent. Developing and spawning stages were further split into four subdivisions, resulting in a total of ten stages into which any animal could be assigned. The mean gonad index, which more or less defines the breeding condition of any sample, was determined by multiplying the number of individuals in each stage by the numerical factor of the arbitrary rating of the stage, and dividing the sum of these products by the grand total of individuals in the sample. The resulting value varies from O, when all individuals in the sample are in the spent or resting condition, to 5 when all individuals are sexually mature.

Scheme of Classification of Gonad Condition

Description of the Gonad

α) The Resting or Spent Gonad. Stage 0 (Fig. 4F): In this stage no trace of sexuality can be observed. It includes virgin animals where the reproductive system is rudimentary, and those animals which have completed spawning. Spent mussels may be thin and transparent, or thick and opaque according to local feeding conditions. During this period, stores of fat and glycogen are accumulated in the connective tissue and this frequently obscures the genital canals.

β) Development Stages. Stage I (Fig. 4 A, 5 A): This stage is characterised by the onset of gametogenesis, islands of germinal tissue appearing in the matrix of dense connective tissue. Very early stages are frequently difficult to separate into males or females. No ova or spermatozoa are present at this stage.

Stage II: Ripe gametes appear in the centre of the follicles although these are occupied mainly by early stages of gametogenesis (small, numerous oocytes attached to the germinal epithelium in the female, and spermatogonia and spermatocytes in the male).

Stage III (Fig. 4B, 5B): Here there is a general increase in the mass of the gonad at the expense of the stored food in the connective tissue. This is a stage of rapid gametogenesis with approximately half of each follicle occupied by ripe gametes, and half with early stages of gametogenesis. The area occupied by genital tissue is about half that of the fully ripe conditions.

Stage IV: Maximum proliferation of genital tissue is almost attained. There is a preponderance of ripe gametes in each follicle, with a general reduction in the earlier stages of gametogenesis. Gametogenesis is, however, still in progress.

Stage V (Fig. 4C, 5C): Here the gonad attains its fully ripe condition. It differs from developing stage IV only in the greater reduction of early stages of gametogenesis (a few small oocytes in the germinal epithelium of the female, and a narrow band one or two cells deep, of spermatogonia and spermatocytes in the male). These correspond to the "gamètes de réserves" referred to by Lubet (1957). Ova are compacted into polygonal configuation, whilst in the males the follicles are distended with morphologically ripe spermatozoa. The time taken from morphological to physiological ripeness, varies from a few weeks to a few months.

γ) Spawning Stages. Stage IV: The follicles are still relatively full of ripe gametes, but active discharge of these is now in progress. This is

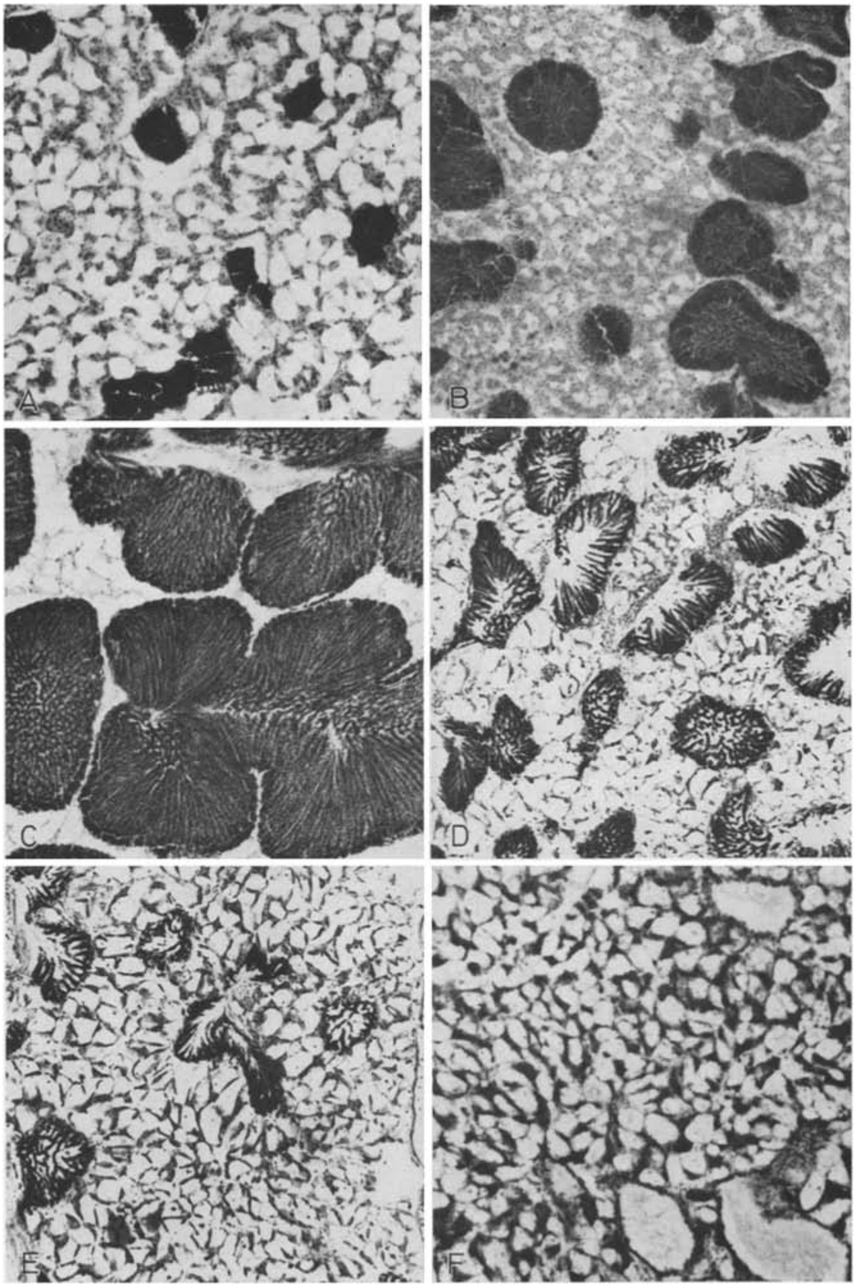

Fig. 4 A—F. Photomicrographs of male gonads at various stages in the sexual cycle (× 60). A. Stage I developing. B. Stage III developing. C. Stage V developing (fully ripe). D. Partially spawned Stage III. E. Partially spawned Stage I. F. Resting or spent gonad. No traces of sexuality evident

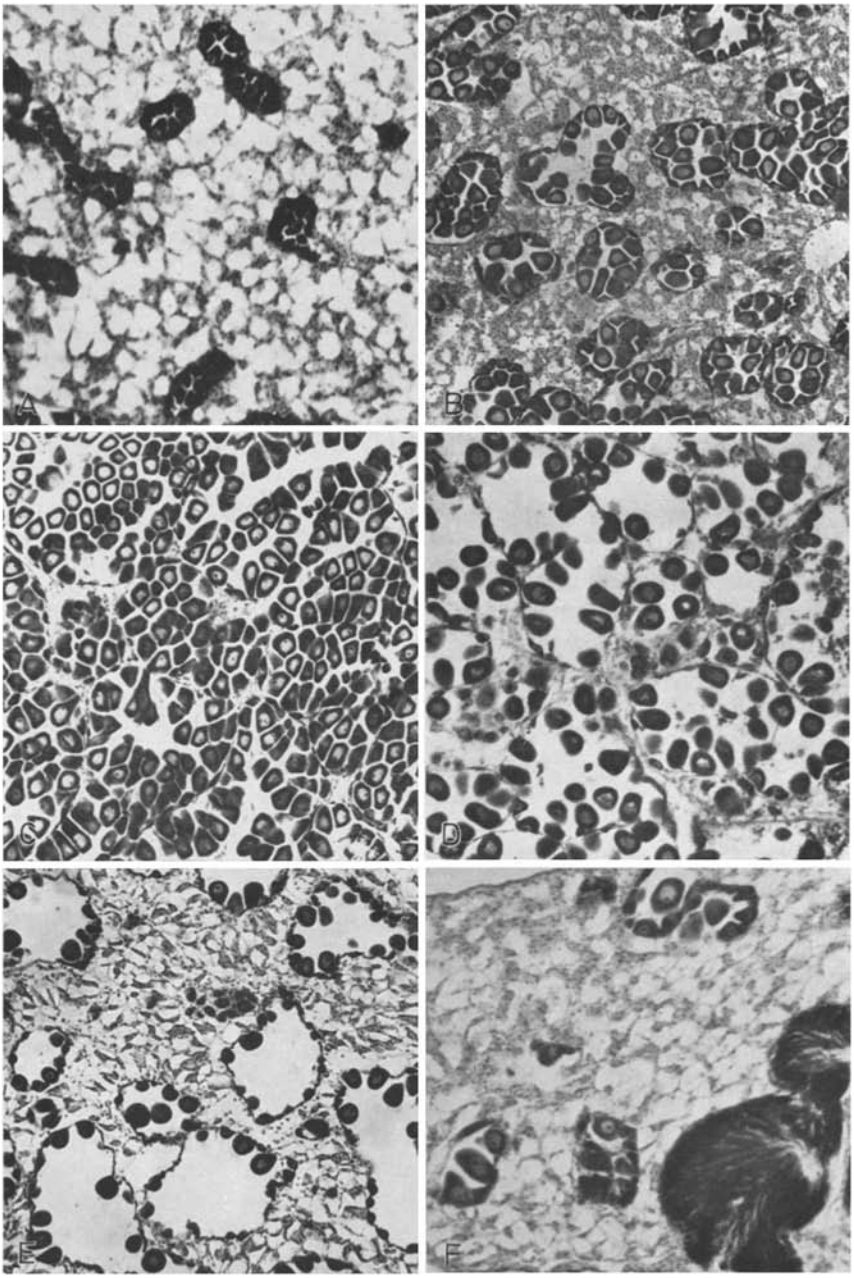

Fig. 5 A—F. Plate 3. Photomicrographs of transverse sections through female gonads at various stages in the reproductive cycle. Preparations stained with Ehrlich's haematoxylin (× 60). A. Stage I developing (NB. dense connective tissue). B. Stage III developing. C. Stage V developing (Fully ripe). D. Partially spawned Stage III. E. Partially spawned Stage I. F. Hermaphrodite gonad

obvious from the general reduction in density of spermatozoa, and the rounding off of the remaining ova as the pressure within the follicles is reduced following partial emission.

Stage III (Fig. 4D, 5D): This stage is similar in some ways to developing stage III in as much as the follicles are approximately half full of mature gametes. Here, however, unlike developing stage III, relatively few early stages of gametogenesis are present. In the female, the ripe eggs are rounded rather than polygonal in appearance. There is a general reduction in the area of mantle covered by genital tissue.

Stage II: At this stage the follicles are considerably less than half full of mature gametes. There is still further general reduction in the area occupied by genital tissue.

Stage I (Fig. 4E, 5E): Residual spermatozoa and ova are still present in the follicles and can often be seen undergoing cytolysis by amoeboid phagocytes (these are eosinophilic and their nuclei stain intensely with haematoxylin). Takatsuki (1934) reviews the properties and functions of bivalve amoebocytes in some detail. The centre of the follicles is often filled with a yellow-brown matrix — the result of cytotysis of the residual gametes.

Thus the criteria that exist for separating spawning and developmental stages are undoubtedly a little subjective and often difficult to assess quantitatively, with all intermediate stages present. Yet with considerable experience in the examination of gonads throughout the year in animals from each locality, it became possible to recognise each stage with confidence. During 1965 and 1966, a period of partial spawning during the spring months (see later) was followed by a redevelopment of the gonads, and it was in the separation of spawning and redeveloping stages that most subjectivity in assessment occurred. In the female, redevelopment is characterised initially by the presence of rounded eggs in the follicle, with large numbers of developing oocytes around the periphery. Later, the production of more ova causes them to assume the characteristic polygonal configuration. In redeveloping males, the centre of the follicles often has residual spermatozoa, whilst the peripheral band of spermatogonia and spermatocytes is of considerable width.

IV. The Annual Cycle

Breeding data for Whitby and Filey mussels is given in Tables 1—6 as numbers in each of the arbitrary stages (sexes being considered separately) together with the index of gonad condition for each sample. Fig. 6 illustrates the breeding cycles (as defined by the gonad index) in the 5 widely differing Filey habitats, whilst in Fig. 7A the total percentages in the spawning, developing and resting conditions for these same habitats are considered collectively.

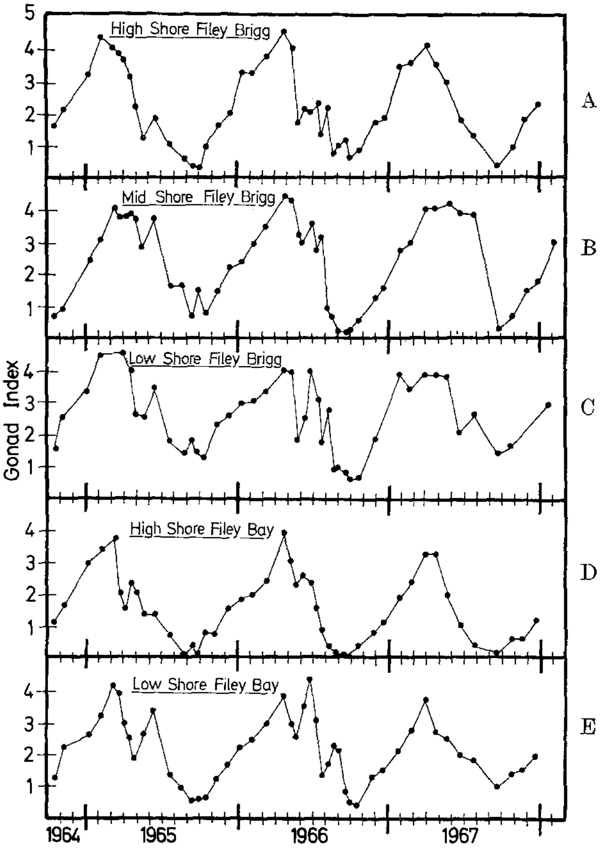

Fig. 6. The breeding cycle of *M. edulis* from 5 widely differing populations at Filey (Yorkshire), as defined by the mean gonad index

From these figures and tables it will be noted that the cycle is subject to variation, both annually and from habitat to habitat, although in 1965 and 1966 the general basic pattern was remarkably similar. Redevelopment of the resting gonad commences during October or November, and rapid gametogenesis occurs over the winter, until by the following early spring the gonad is fully ripe. During the spring (March-May) in 1965 and 1966 a period of partial spawning occurred, when the follicles of the majority of animals became partly emptied. This was followed, in certain populations, by a further period of rapid gametogenesis, until by June the gonads were once again fully ripe. Whereas in mussels growing under favourable environmental conditions (e.g. in the low shore) the gonad index frequently attained a value comparable with that earlier in the year (Fig. 6C and E), in those animals situated high in the littoral,

Table 1. *Distribution of gonad stages in samples of M. edulis from the high shore Filey Brigg*

Date	No.	Male									Spent	Female									Index
		Developing					Spawning					Developing					Spawning				
		I	II	III	IV	V	IV	III	II	I	0	I	II	II	IV	V	IV	III	II	I	
1964																					
14 Oct.	24	3	4	3	2	—	—	—	—	—	4	5	2	1	—	—	—	—	—	—	1.67
5 Nov.	29	1	6	2	2	2	—	—	1	—	1	9	2	—	2	1	—	—	—	—	2.24
1965																					
5 Jan.	26	—	—	1	4	5	—	—	—	—	—	6	1	3	6	—	—	—	—	—	3.27
5 Feb.	72	—	—	4	9	19	—	—	—	—	—	—	2	3	8	23	—	4	—	—	4.40
4 Mar.	86	—	—	—	4	28	3	4	5	—	—	—	2	2	4	15	5	9	5	—	4.02
18 Mar.	86	—	—	4	10	25	0	1	4	—	3	—	—	6	4	10	5	13	1	—	3.88
1 Apl.	71	—	—	3	—	15	7	1	—	—	6	—	—	—	3	13	12	7	4	—	3.79
14 Apl.	172	—	—	10	7	30	13	7	13	—	22	—	3	4	—	18	18	12	12	3	3.20
29 Apl.	48	—	1	6	—	—	2	3	4	4	3	2	5	5	—	2	2	3	4	2	2.35
14 May	163	—	—	—	—	3	5	9	18	12	66	—	—	3	1	2	10	4	6	24	1.35
11 June	179	—	—	12	12	2	—	13	15	18	46	—	—	2	10	6	12	4	6	21	1.95
19 July	270	—	—	12	4	2	—	—	16	46	105	—	—	6	—	—	4	12	42	21	1.17
25 Aug.	63	—	—	—	—	—	—	—	6	12	39	—	—	—	—	3	—	—	—	3	0.67
10 Sept.	31	—	2	—	1	—	—	—	—	1	24	—	1	—	—	—	—	—	—	2	0.42
24 Sept.	22	—	—	—	—	—	—	—	1	2	16	1	1	—	—	—	—	—	—	1	0.36
9 Oct.	33	9	2	1	—	2	—	1	—	1	13	2	—	—	—	1	—	—	—	1	1.15
11 Nov.	24	4	5	3	—	—	—	—	—	—	4	4	2	—	2	—	—	—	—	—	1.67
12 Dec.	35	4	8	7	—	1	—	—	—	1	3	5	—	3	2	1	—	—	—	—	2.06

1966																					
9 Jan.	52	—	2	8	20	4	—	—	—	—	—	6	2	6	2	2	—	—	—	—	3.35
5 Feb.	77	—	—	—	6	16	3	—	—	—	4	8	9	8	12	8	—	—	—	2	3.32
11 Mar.	35	—	—	2	8	11	—	—	—	—	—	—	3	4	5	—	—	1	—	1	3.83
21 Apl.	42	—	—	1	1	15	3	—	—	—	1	—	—	1	2	16	1	1	—	—	4.57
5 May	68	—	—	—	2	6	16	6	—	—	—	—	—	2	4	16	12	2	2	—	4.15
20 May	37	—	2	2	1	1	—	3	4	2	8	1	8	1	—	—	—	—	1	3	1.68
3 June	40	—	—	8	2	1	—	4	3	3	4	1	3	3	1	—	—	1	3	3	2.25
21 June	74	—	2	10	4	—	—	—	12	2	6	4	10	2	4	4	—	—	4	10	2.11
6 July	81	—	—	10	13	11	—	3	2	6	12	8	7	2	—	—	—	—	3	4	2.39
18 July	78	—	6	2	2	8	—	—	—	9	35	—	6	2	—	—	—	—	5	3	1.36
2 Aug.	68	—	3	—	9	8	—	2	—	6	12	2	7	—	2	—	4	—	7	6	2.26
16 Aug.	71	—	—	—	—	—	—	—	6	6	33	7	8	—	—	—	—	—	5	6	0.80
31 Aug.	46	—	—	—	—	4	—	2	—	4	27	—	—	—	—	—	1	2	3	3	1.01
15 Sept.	52	2	—	—	1	7	—	1	3	4	24	5	—	—	—	—	—	—	1	4	1.25
28 Sept.	39	1	—	—	—	1	—	—	3	—	23	6	—	—	—	—	1	—	—	4	0.67
13 Oct.	49	—	—	—	—	2	—	—	3	4	21	12	—	—	—	—	—	2	3	2	0.94
29 Nov.	60	6	13	5	—	—	—	2	—	—	10	8	11	3	2	—	—	—	—	—	1.67
13 Dec.	67	—	9	13	3	—	—	—	—	1	8	17	11	5	—	—	—	—	—	—	1.85
1967																					
29 Jan.	59	—	—	—	14	8	—	5	2	6	—	—	4	7	7	6	—	—	—	—	3.53
27 Feb.	66	—	—	6	14	14	—	—	2	—	—	3	8	5	6	2	—	6	—	—	3.55
30 Mar.	59	—	—	3	4	14	—	2	—	—	—	—	—	9	6	16	3	2	—	—	4.24
26 Apl.	85	—	—	4	4	15	6	7	—	—	2	—	—	—	2	14	8	9	8	6	3.61
25 May	92	—	—	6	4	18	5	4	7	2	8	—	—	2	—	11	3	5	10	7	3.01
26 June	38	—	1	2	4	1	1	4	3	—	12	3	2	3	—	—	—	—	1	1	1.84
27 July	44	—	1	1	—	—	—	2	6	4	15	4	—	1	3	—	—	2	2	3	1.34
20 Sept.	42	1	—	—	—	—	—	—	1	5	27	8	—	—	—	—	—	—	—	—	0.38
20 Oct.	51	2	3	1	—	2	—	1	2	1	22	13	4	—	—	—	—	—	—	—	0.99
16 Nov.	45	4	5	6	4	—	—	1	—	2	3	8	9	—	1	—	—	—	—	2	1.88
18 Dec.	38	1	3	7	7	1	—	—	—	1	—	10	6	1	1	—	—	—	—	—	2.39

Table 2. *Distribution of gonad stages in samples of M. edulis from the mid shore Filey Brigg*

Date	No.	Male									Spent	Female									Index
		Developing					Spawning					Developing					Spawning				
		I	II	III	IV	V	IV	III	II	I	0	I	II	III	IV	V	IV	III	II	I	
1964																					
14 Oct.	11	5	—	—	—	—	—	—	—	—	3	3	—	—	—	—	—	—	—	—	0.73
5 Nov.	19	6	2	—	—	—	—	—	—	—	4	6	1	—	—	—	—	—	—	—	0.95
1965																					
6 Jan.	154	8	24	21	16	9	—	—	2	—	3	22	27	7	6	7	—	—	2	—	2.55
5 Feb.	201	—	12	22	26	12	—	4	5	2	—	10	32	30	32	10	—	2	2	—	3.13
4 Mar.	230	—	—	10	40	66	2	4	8	2	—	—	6	22	22	36	—	2	8	2	4.12
18 Mar.	224	—	—	5	23	55	—	6	2	4	2	4	—	7	10	51	2	19	20	14	3.80
1 Apl.	248	—	—	—	14	90	8	4	—	—	18	—	—	—	8	36	12	30	22	6	3.83
14 Apl.	249	—	—	4	24	72	4	10	6	—	9	—	—	6	22	40	4	26	20	2	3.89
29 Apl.	250	—	—	4	6	66	16	10	—	2	8	—	—	—	6	54	10	30	26	12	3.80
14 May	364	—	—	12	4	30	34	54	60	12	22	—	30	30	20	20	4	10	14	8	2.94
11 June	244	—	—	8	50	28	28	6	—	—	14	—	8	22	34	34	2	6	14	—	3.82
19 July	222	—	—	10	4	—	14	16	16	30	62	—	—	—	—	4	8	16	22	20	1.69
25 Aug.	64	—	—	—	—	4	—	5	4	—	26	—	—	—	—	8	—	3	3	10	1.75
10 Sept.	68	—	—	—	—	8	—	2	—	2	50	—	—	—	—	—	—	—	2	4	0.76
24 Sept.	33	—	—	—	—	5	—	—	3	5	14	2	—	—	—	2	—	—	—	2	1.51
9 Oct.	105	—	3	—	—	8	—	—	9	—	78	—	—	—	—	3	—	4	—	—	0.87
10 Nov.	55	5	9	2	—	4	—	—	—	2	11	12	5	3	—	—	—	—	—	2	1.53
9 Dec.	55	2	11	4	4	4	—	—	2	—	2	17	2	—	3	2	—	—	2	—	2.26
1966																					
9 Jan.	78	9	7	12	17	2	—	—	—	2	—	15	9	5	—	—	—	—	—	—	2.40
5 Feb.	69	2	3	13	12	4	—	—	—	—	—	4	14	11	4	2	—	—	—	—	3.00
11 Mar.	70	2	7	—	11	17	—	—	—	—	—	4	9	5	6	4	3	2	—	—	3.48

21 Apl.	81	—	—	2	7	46	—	2	—	—	—	—	—	5	4	10	3	—	2	—	4.53
5 May	64	—	—	—	2	26	4	—	—	—	2	—	—	—	—	16	6	6	2	—	4.37
20 May	34	—	1	3	1	7	1	1	4	—	—	—	3	—	—	6	1	3	1	2	3.33
3 June	43	—	—	7	8	1	—	3	1	—	—	—	10	8	5	—	—	—	—	—	3.09
21 June	40	—	—	1	7	4	3	4	1	—	1	—	1	—	4	7	2	2	2	1	3.73
6 July	74	—	2	15	8	3	2	7	6	4	—	—	2	17	—	—	—	—	2	6	2.78
18 July	69	—	—	—	—	32	—	3	—	2	10	—	3	—	3	4	—	2	6	4	3.33
2 Aug.	39	—	—	—	—	2	—	2	2	5	22	—	—	—	—	—	1	1	2	2	0.97
16 Aug.	37	—	—	—	—	3	—	—	2	2	26	—	—	—	—	—	—	—	1	3	0.70
31 Aug.	70	—	—	—	—	2	—	—	2	2	62	—	—	—	—	—	—	—	—	2	0.26
15 Sept.	43	5	—	—	—	1	—	—	—	1	35	1	—	—	—	—	—	—	—	—	0.28
28 Sept.	40	3	—	—	—	1	—	—	1	3	32	1	—	—	—	—	—	—	—	—	0.34
13 Oct.	56	22	4	—	—	—	—	—	—	—	24	4	—	—	—	—	—	—	—	—	0.63
29 Nov.	25	3	4	3	—	—	—	—	—	—	4	9	2	—	—	—	—	—	—	—	1.32
13 Dec.	27	1	13	—	—	—	—	—	—	—	1	10	2	—	—	—	—	—	—	—	1.55
1967																					
29 Jan.	58	—	4	14	12	2	—	—	—	—	—	6	6	8	4	2	—	—	—	—	2.68
27 Feb.	74	—	3	7	13	11	—	—	—	—	3	9	12	7	9	—	—	—	—	—	3.02
30 Mar.	66	—	2	—	19	18	—	—	—	—	2	—	3	2	8	12	—	—	—	—	4.15
26 Apl.	91	—	—	—	16	30	—	—	—	—	—	—	—	6	10	14	—	15	—	—	4.14
24 May	109	—	—	—	3	37	15	5	—	—	—	—	—	—	—	17	15	11	3	3	4.21
26 June	41	—	—	—	1	9	1	2	—	1	2	1	1	1	—	11	7	1	2	1	3.87
27 July	38	—	—	—	—	10	9	4	1	—	3	—	—	—	—	7	2	—	2	—	3.86
20 Sept.	36	—	—	—	1	—	—	—	—	5	28	2	—	—	—	—	—	—	—	—	0.30
20 Oct.	34	2	2	—	1	—	—	—	—	2	16	10	—	—	—	—	1	—	—	—	0.76
16 Nov.	34	7	4	2	1	1	—	—	—	3	5	8	2	—	—	1	—	—	—	—	1.47
18 Dec.	34	3	7	5	2	—	—	—	—	—	2	9	6	—	—	—	—	—	—	—	1.80
1968																					
1 Feb.	53	2	—	6	10	2	3	1	1	—	—	2	12	8	5	1	—	—	—	—	3.00
28 Feb.	46	—	—	4	6	11	2	1	—	—	1	3	1	11	5	1	—	—	—	—	3.59

Table 3. *Distribution of gonad stages in samples of M. edulis from the low shore Filey Brigg*

Date	No.	Male									Spent	Female									Index
		Developing					Spawning					Developing					Spawning				
		I	II	III	IV	V	IV	III	II	I	0	I	II	III	IV	V	IV	III	II	I	
1964																					
14 Oct.	38	3	12	5	—	—	—	—	—	—	2	7	9	—	—	—	—	—	—	—	1.58
5 Nov.	33	2	2	3	6	3	—	—	—	1	6	—	4	3	2	1	—	—	—	—	2.58
1965																					
6 Jan.	36	—	4	1	5	8	—	—	—	2	—	—	4	6	3	2	1	—	—	—	3.42
5 Feb.	33	—	2	1	7	10	—	—	—	—	—	—	—	2	3	9	—	—	—	—	4.46
1 Apl.	84	—	—	3	7	32	—	—	—	—	—	—	—	8	10	24	—	—	—	—	4.54
14 Apl.	83	—	—	—	4	24	2	4	5	—	—	—	2	2	4	16	4	10	6	—	4.00
29 Apl.	93	—	—	—	—	12	—	16	12	4	5	—	4	11	—	4	—	5	16	4	2.66
14 May	111	—	2	9	8	—	14	12	8	—	8	—	8	22	4	—	—	—	4	12	2.61
11 June	112	—	—	9	14	20	—	23	4	—	4	—	—	8	4	14	2	—	8	2	3.54
19 July	216	—	—	11	8	—	8	5	28	16	44	—	4	8	4	12	—	4	28	36	1.83
25 Aug.	57	—	—	—	2	1	3	2	5	5	13	2	3	—	—	2	—	2	1	16	1.54
10 Sept.	40	—	—	—	—	5	1	—	1	1	22	—	—	—	—	7	—	1	—	2	1.80
24 Sept.	66	—	—	—	—	10	—	—	8	2	32	—	—	—	—	4	—	—	—	10	1.48
9 Oct.	33	—	—	—	—	3	—	3	—	3	17	—	—	—	—	2	—	—	1	4	1.30
11 Nov.	74	—	—	3	7	9	6	3	2	12	16	10	—	—	—	6	—	—	—	—	2.38
9 Dec.	75	6	7	10	12	15	—	—	—	3	17	—	—	3	—	2	—	—	—	—	2.60
1966																					
9 Jan.	117	—	6	14	18	16	—	—	—	4	7	13	12	20	4	3	—	—	—	—	2.88
5 Feb.	112	—	6	10	2	18	2	4	—	—	10	14	6	12	10	8	—	—	—	—	3.00
11 Mar.	175	—	8	11	45	20	—	—	9	—	4	—	12	5	18	20	—	12	3	8	3.40

24 Apl.	74	—	—	2	—	24	5	—	—	2	4	—	3	—	5	19	4	2	2	2	4.01
5 May	65	—	—	—	3	23	3	4	—	—	2	—	—	2	—	12	8	—	6	2	3.91
20 May	70	—	14	6	—	—	—	—	8	8	—	10	14	4	—	—	—	—	2	4	1.81
3 June	131	—	3	13	16	10	3	3	—	—	6	4	25	16	9	—	—	—	6	7	2.57
21 June	98	—	6	—	—	18	4	—	5	—	—	—	2	—	8	23	—	6	3	—	4.00
6 July	151	—	—	5	27	23	11	8	17	3	4	—	8	25	5	—	—	—	12	3	3.18
16 July	80	—	6	6	—	—	2	2	8	2	12	12	14	—	2	—	—	2	6	6	1.69
2 Aug.	117	—	—	—	—	8	22	9	5	—	15	4	—	—	13	9	—	13	9	6	2.81
16 Aug.	130	—	—	—	—	—	6	5	6	7	69	4	13	—	—	—	—	4	6	9	0.93
31 Aug.	52	—	—	—	—	2	1	4	2	4	29	—	—	—	—	—	—	4	5	4	1.00
15 Sept.	92	—	—	—	—	8	—	2	6	6	60	20	—	—	—	—	—	—	4	4	0.83
28 Sept.	38	4	—	—	—	1	—	—	1	—	20	11	—	—	—	—	—	—	—	1	0.61
15 Oct.	56	2	—	—	—	3	—	—	—	2	29	15	—	—	—	—	—	—	2	3	0.73
29 Nov.	30	3	5	5	2	—	—	—	1	—	—	11	2	1	—	—	—	—	—	—	1.87
1967																					
29 Jan.	34	—	—	7	7	2	—	—	—	1	—	4	1	4	3	4	—	—	—	—	3.90
27 Feb.	71	—	—	5	7	17	3	—	—	—	8	2	4	5	7	5	—	6	2	—	3.38
30 Mar.	74	—	—	2	6	17	—	2	—	—	1	—	3	14	19	8	—	2	—	—	3.93
26 Apl.	107	—	—	—	13	39	2	7	4	—	5	—	4	—	6	10	—	15	2	—	3.88
24 May	103	—	—	2	10	19	2	3	—	2	4	—	—	—	3	26	8	19	2	3	3.86
26 June	39	—	7	6	1	—	—	1	—	3	1	8	4	2	1	2	—	—	1	2	2.10
27 July	34	—	—	3	2	3	—	—	3	1	4	1	5	4	4	1	—	2	1	—	2.68
21 Sept.	50	7	—	—	—	8	2	—	—	4	18	7	—	—	—	1	—	—	2	1	1.52
20 Oct.	54	15	6	1	—	6	—	—	—	2	6	13	1	1	—	1	—	1	—	1	1.65
1968																					
17 Jan.	76	1	3	7	20	7	1	—	1	1	1	9	12	10	3	—	—	—	—	—	2.93

Table 4. *Distribution of gonad stages in samples of M. edulis from the high shore Filey Bay*

Date	No.	Male									Spent	Female									Index
		Developing					Spawning					Developing					Spawning				
		I	II	III	IV	V	IV	III	II	I	0	I	II	III	IV	V	IV	III	II	I	
1964																					
14 Oct.	36	8	4	1	—	—	—	—	—	—	7	9	6	1	—	—	—	—	—	—	1.19
5 Nov.	28	3	9	3	1	—	—	—	—	—	1	8	3	—	—	—	—	—	—	—	1.71
1965																					
6 Jan.	49	—	3	4	2	9	1	2	—	—	4	7	3	6	5	3	—	—	—	—	3.00
5 Feb.	77	4	7	8	6	15	—	—	2	—	—	—	6	2	9	12	—	2	4	—	3.42
4 Mar.	72	—	2	4	8	18	—	4	4	—	2	—	—	2	6	12	—	6	4	—	3.80
18 Mar.	129	—	4	13	—	—	—	9	19	18	3	6	10	12	4	—	—	6	15	—	2.00
1 Apl.	168	—	6	—	—	—	—	—	18	15	39	12	36	6	—	—	—	18	12	6	1.48
14 Apl.	234	—	15	23	30	9	—	—	33	—	68	—	23	9	5	21	8	—	—	—	2.39
29 Apl.	173	—	18	7	12	13	—	—	7	12	51	—	12	7	22	—	6	—	6	—	2.11
14 May	176	—	—	23	4	—	—	—	—	29	54	—	6	5	—	4	—	—	17	34	1.40
11 June	179	—	—	—	6	6	3	—	11	12	99	—	—	—	2	19	—	6	6	9	1.40
19 July	147	—	—	—	—	4	—	—	12	7	103	—	—	—	—	8	—	—	4	9	0.73
25 Aug.	46	—	—	—	—	—	—	—	—	—	46	—	—	—	—	—	—	—	—	—	0.00
9 Sept.	52	6	—	—	—	—	—	—	2	2	42	—	—	—	—	—	—	—	—	—	0.43
24 Sept.	72	4	—	—	—	—	—	—	—	—	64	4	—	—	—	—	—	—	—	—	0.11
10 Oct.	34	11	3	1	—	—	—	—	—	—	10	9	—	—	—	—	—	—	—	—	0.85
10 Nov.	42	6	8	—	—	—	—	—	—	—	16	12	—	—	—	—	—	—	—	—	0.81
9 Dec.	52	6	18	4	—	—	—	—	—	—	2	18	4	—	—	—	—	—	—	—	1.58

1966																				
9 Jan.	42	5	4	8	2	1	—	—	—	—	4	10	7	—	1	—	—	—	—	—	1.86
5 Feb.	53	5	8	10	5	—	—	—	—	—	4	13	3	3	2	—	—	—	—	—	1.98
11 Mar.	68	—	4	3	10	7	—	—	3	—	9	12	7	4	4	2	—	—	3	—	2.47
21 Apl.	70	—	—	—	4	17	2	6	—	2	1	—	2	—	—	21	2	7	6	—	3.99
5 May	71	—	—	7	—	12	2	2	9	—	3	—	4	2	—	8	3	5	9	5	3.04
20 May	101	—	2	13	—	—	3	6	8	8	6	5	11	10	—	4	4	7	9	5	2.28
3 June	62	—	4	11	6	2	—	1	4	1	5	—	7	10	4	1	—	1	2	3	2.61
21 June	87	—	—	9	4	12	—	3	7	5	10	3	—	—	—	—	3	7	16	8	2.37
6 July	72	—	6	4	4	4	—	3	6	6	23	—	4	—	—	—	—	—	2	10	1.51
18 July	35	—	2	4	1	—	—	—	2	3	22	—	—	—	1	—	—	—	—	—	0.91
2 Aug.	37	—	1	—	1	1	—	—	1	—	32	—	—	—	—	—	—	—	1	—	0.41
16 Aug.	78	—	—	—	—	2	—	—	2	—	74	—	—	—	—	—	—	—	—	—	0.18
31 Aug.	57	—	—	—	—	1	—	—	—	1	54	—	—	—	—	—	—	—	1	—	0.14
15 Sept.	48	—	—	—	—	—	—	—	—	4	43	—	—	—	—	—	—	—	—	—	0.10
28 Sept.	38	—	—	—	—	—	—	—	1	1	36	—	—	—	—	—	—	—	—	—	0.08
13 Oct.	51	5	—	—	—	—	—	—	2	2	32	10	—	—	—	—	—	—	—	—	0.41
29 Nov.	25	2	6	—	—	—	—	—	—	1	7	9	—	—	—	—	—	—	—	—	0.96
13 Dec.	48	2	16	2	—	—	—	—	—	2	10	16	—	—	—	—	—	—	—	—	1.21
1967																					
29 Jan.	75	3	13	16	6	—	—	—	—	—	—	30	4	3	—	—	—	—	—	—	1.97
27 Feb.	35	2	5	8	2	5	—	—	2	—	1	4	4	4	—	—	—	1	—	—	2.43
30 Mar.	71	—	2	4	19	10	—	2	2	—	—	6	9	13	4	—	—	—	—	—	3.37
26 Apl.	93	5	3	3	9	21	—	3	—	3	5	5	5	—	4	16	4	4	3	—	3.38
26 May	122	—	5	11	3	9	5	9	9	5	25	—	—	—	—	—	11	—	9	21	2.07
26 June	34	—	—	—	—	1	—	1	1	1	19	—	—	—	—	1	2	1	2	5	1.01
27 July	34	—	—	—	—	—	—	—	1	3	27	—	—	—	—	1	1	—	1	—	0.47
20 Sept.	47	—	—	—	—	—	—	1	1	—	44	—	—	—	—	—	—	1	—	—	0.17
19 Oct.	39	6	—	1	—	—	—	—	—	1	17	13	—	—	—	—	—	—	—	1	0.62
16 Nov.	43	5	1	—	1	—	—	—	—	1	21	13	—	—	—	—	—	—	—	1	0.60
18 Dec.	36	5	6	—	2	—	—	—	—	—	8	11	2	2	—	—	—	—	—	—	1.27

Table 5. *Distribution of gonad stages in samples of M. edulis from the low shore Filey Bay*

Date	No.	Male									Spent	Female									Index
		Developing					Spawning					Developing					Spawning				
		I	II	III	IV	V	IV	III	II	I	0	I	II	III	IV	V	IV	III	II	I	
1964																					
14 Oct.	14	4	1	—	—	—	—	—	—	—	—	6	3	—	—	—	—	—	—	—	1.29
5 Nov.	42	4	8	10	2	—	—	—	—	—	—	7	7	3	—	1	—	—	—	—	2.21
1965																					
6 Jan.	61	4	9	16	4	—	2	—	—	—	—	7	2	13	4	—	—	—	—	—	2.62
5 Feb.	52	—	—	2	8	10	—	—	—	—	—	12	2	6	12	—	—	—	—	—	3.27
4 Mar.	56	—	—	—	4	22	2	3	—	—	1	—	—	3	6	6	4	—	4	1	4.20
18 Mar.	79	—	2	5	12	18	—	4	—	—	—	4	3	3	8	13	4	3	—	—	3.92
1 Apl.	195	—	5	—	7	24	13	15	10	18	14	—	10	3	12	26	12	3	8	15	3.02
14 Apl.	91	—	5	—	3	4	12	10	6	3	10	—	12	5	7	—	3	—	7	4	2.55
29 Apl.	85	—	12	5	4	—	—	1	10	8	8	—	12	4	2	—	—	—	15	4	1.93
14 May	113	—	6	16	8	1	6	10	9	2	14	—	1	10	24	1	—	2	—	3	2.77
11 June	166	—	—	8	45	15	7	12	1	6	15	—	2	4	15	27	2	2	1	4	3.39
19 July	174	—	—	—	—	12	3	3	12	36	78	—	—	—	—	3	5	10	9	3	1.33
25 Aug.	32	—	—	—	—	1	1	1	4	5	15	—	—	—	—	—	1	—	—	4	1.03
10 Sept.	52	—	—	—	—	2	—	—	4	7	34	—	—	—	—	—	—	—	—	5	0.58
24 Sept.	60	5	—	—	—	—	—	—	4	9	33	7	—	—	—	2	—	—	—	—	0.65
9 Oct.	30	2	4	—	—	—	—	—	1	5	14	3	—	—	—	—	—	—	—	1	0.70
9 Nov.	22	2	1	1	1	—	—	1	1	6	7	2	—	—	—	—	—	—	—	—	1.23
9 Dec.	51	2	13	6	2	—	—	—	—	—	4	11	11	—	—	—	—	—	—	2	1.73

1966																					
8 Jan.	64	—	16	19	2	—	—	—	—	—	—	8	14	5	—	—	—	—	—	—	2.31
5 Feb.	62	4	11	18	8	—	—	—	—	—	—	6	12	3	—	—	—	—	—	—	2.44
11 Mar.	73	—	8	17	11	8	—	—	—	—	—	2	18	3	6	—	—	—	—	—	3.00
21 Apl.	73	—	—	2	7	24	—	—	—	4	2	—	3	5	3	10	7	—	2	4	3.79
5 May	75	—	2	9	—	2	4	11	4	—	2	—	10	15	4	2	5	2	—	3	2.90
20 May	75	—	9	11	2	—	2	4	4	2	—	—	25	11	—	—	—	—	3	2	2.47
3 June	47	—	1	8	13	1	2	2	—	—	—	—	3	6	9	2	—	—	—	—	3.55
21 June	84	—	—	—	8	30	—	9	4	—	—	—	—	—	12	21	—	—	—	—	4.41
6 July	73	—	—	—	11	6	3	7	10	—	5	—	—	—	—	6	4	15	6	—	3.15
18 July	36	—	—	—	—	3	—	2	6	5	13	—	—	—	—	—	2	—	1	4	1.44
2 Aug.	35	—	—	—	—	4	3	1	3	5	12	—	—	—	—	1	—	—	2	4	1.69
16 Aug.	70	—	—	—	—	14	—	4	2	8	24	—	—	—	2	8	—	4	2	2	2.29
31 Aug.	45	—	—	—	—	7	3	4	1	2	19	—	—	—	—	5	—	1	1	2	2.11
15 Sept.	40	—	—	—	—	1	—	3	2	2	29	—	—	—	—	2	—	1	—	—	0.83
28 Sept.	33	—	—	—	—	—	—	—	4	1	21	—	—	—	—	—	—	—	2	5	0.58
13 Oct.	54	—	—	—	—	4	—	—	2	—	48	—	—	—	—	—	—	—	—	—	0.44
29 Nov.	54	9	12	8	—	—	—	—	2	—	16	5	2	—	—	—	—	—	—	—	1.30
13 Dec.	48	10	12	8	—	—	—	—	—	6	4	8	—	—	—	—	—	—	—	—	1.50
1967																					
29 Jan.	58	—	5	9	6	2	—	—	—	4	4	10	13	5	—	—	—	—	—	—	2.17
27 Feb.	71	—	—	15	17	3	—	2	2	—	3	5	8	10	4	—	—	2	—	—	2.83
30 Mar.	74	—	2	6	23	16	—	2	—	—	—	3	9	4	3	6	—	—	—	—	3.72
26 Apl.	86	—	11	29	7	3	—	—	—	—	2	2	12	17	—	—	—	3	—	—	2.77
24 May	114	—	2	29	4	7	4	6	11	—	5	—	2	10	—	3	—	10	9	12	2.69
26 June	38	4	1	5	4	—	1	2	2	1	5	1	3	6	—	—	—	—	2	1	2.05
27 July	42	—	—	1	—	4	1	3	3	5	11	1	—	—	—	4	—	—	5	4	1.95
21 Sept.	41	3	—	—	—	4	—	2	1	3	23	1	—	—	—	—	—	—	2	2	1.00
19 Oct.	43	11	4	4	1	1	1	—	1	—	8	11	—	—	—	—	—	1	—	—	1.39
16 Nov.	54	10	10	4	3	—	—	1	1	—	2	22	1	—	—	—	—	—	—	—	1.54
18 Dec.	31	2	2	9	1	—	1	—	—	—	—	8	5	3	—	—	—	—	—	—	2.02

Table 6. *Distribution of gonad stages in samples of M. edulis from Ca. M.L.W.S. Whitby harbour*

Date	No.	Male									Spent	Female									Index
		Developing					Spawning					Developing					Spawning				
		I	II	III	IV	V	IV	III	II	I	0	I	II	III	IV	V	IV	III	II	I	
1966																					
8 Feb.	33	3	4	4	5	2	—	—	—	—	—	5	4	6	—	—	—	—	—	—	2.55
22 Feb.	32	—	—	5	5	2	—	—	—	—	—	—	8	12	—	—	—	—	—	—	3.03
9 Mar.	39	—	—	11	5	2	—	—	—	—	2	—	4	7	—	6	—	2	—	—	3.29
22 Mar.	52	—	—	3	12	6	2	—	—	—	—	—	3	4	9	13	—	—	—	—	4.30
8 Apl.	28	—	—	—	2	16	—	—	—	—	—	—	2	—	4	4	—	—	—	—	4.57
25 Apl.	29	—	—	—	1	8	1	—	—	—	—	—	—	—	2	16	1	—	—	—	4.83
8 May	44	—	—	—	—	18	—	2	4	—	—	—	—	—	—	18	—	—	2	—	4.50
25 May	44	—	—	7	—	—	—	15	4	—	—	—	5	10	—	—	—	3	—	—	2.80
4 June	30	—	—	6	4	3	—	—	1	—	—	—	3	9	2	—	—	—	1	1	3.17
22 June	43	—	—	—	3	10	1	3	3	—	—	1	—	—	4	7	2	—	3	6	3.56
7 July	35	—	—	—	—	5	3	2	3	4	6	—	—	—	1	3	—	—	3	5	2.37
21 July	40	—	—	—	—	2	—	2	—	6	24	—	—	—	—	—	—	—	—	6	0.70
8 Aug.	54	—	—	—	—	—	—	—	—	6	45	—	—	—	—	—	—	—	3	—	0.22
20 Sept.	36	—	—	—	—	—	—	—	—	14	18	—	—	—	—	—	1	1	—	2	0.69
14 Oct.	44	9	7	—	—	—	—	—	—	—	24	4	—	—	—	—	—	—	—	—	0.61
29 Nov.	54	5	9	4	—	—	—	—	—	2	6	23	3	2	—	—	—	—	—	—	1.33
1967																					
30 Jan.	83	—	—	4	22	7	3	6	—	3	7	—	1	2	7	13	1	1	—	2	3.38
27 Feb.	37	—	1	4	6	8	—	—	1	—	—	—	1	5	4	7	—	—	—	—	4.00

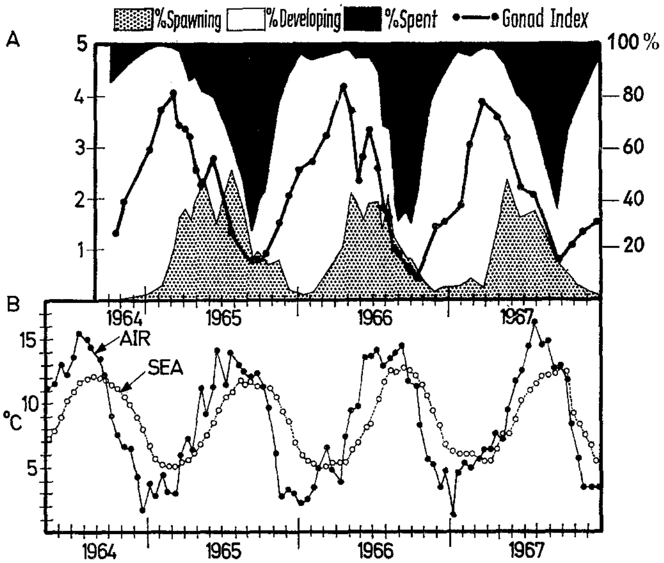

Fig. 7. A. The breeding cycle of all Filey mussels considered together showing a) mean gonad index b) the percentages in the developing, spawning and spent conditions. B. Mean fortnightly air and sea temperatures at Filey and Longstones Lighthouse respectively

full reripening was often accomplished only by a minority of the population (Fig. 6A and D) and consequently the index never reached its earlier spring value. This is doubtless a direct consequence of the considerably reduced feeding time available to these animals. During July and August (1965 and 1966) complete evacuation of ova and spermatozoa occurred, so that by late August to September, the gonad index in all localities reached its lowest value, as the majority of individuals entered the spent or resting condition. Throughout late August, September, and early October, the connective tissue became fattened with varying amounts of glycogen and fat.

That two peaks of spawning occurred in most local populations during 1965 and 1966 was confirmed, in females at least, by actual counts of ripe ova and early oocytes present in the follicles. Several counts per unit area, over a wide area of mantle tissue were made for each animal, and an average taken. Indication of a secondary period of rapid gametogenesis was shown by the relative increase in numbers of early oocytes during the early summer.

The breeding cycle during 1967 differed from the two previous years in that it appeared to lack two distinct spawning periods. Whilst this could possibly be a reflection of the less frequent sampling over this period, it is perhaps significant that the winter of 1966/67 was particularly mild. The relationship between the breeding cycle, and both sea and air temperature is illustrated in Fig. 7 B. The air temperatures given are those for Filey, whilst the surface sea temperatures relate to the Longstones Light House in the Farne Islands well to the north, 55°39'N; 1°37'E. (I am particularly indebted to the Meteorological Office for providing the basic data from which this graph has been compiled). Although these sea temperatures are generally very similar to our limited records for inshore waters at Robin Hood's Bay, it should be noted that the latter generally both fall slightly below, and rise slightly above the Longstones temperatures.

Perhaps the most significant feature of the annual spawning season in this locality, particularly relevant to this investigation, is its duration. From Fig. 7 A it will be seen that although never more than 50% of the total Filey population was in the spawning condition at any particular time, the period over which 25% were spawning extends over about 4—6 months of the year. Whilst extended spawning has previously been recorded in *Mytilus*, many of these records have been based upon systematic plankton observations and these often cannot be taken as a true reflection of the breeding cycle of animals in those localities. Records of extended spawning periods from direct gonad examinations are, however, afforded by Johnstone (1898); Havinga (1929) and Battle (1932). Bruce (1926) and Chipperfield (1953) on the other hand, record short spawning seasons in *Mytilus*. Evidence for a single spawning period each year is given by Wilson (1886) and Chipperfield (1953), whilst repeated spawnings have been recorded by Johnston (1898), Williamson (1907) and Battle (1932).

Although too close a comparison between the results of the present investigation and the spawning periods recorded by previous workers should not be made, both in view of the different methods used (e.g. histology of the gonad versus larval abundance and periods of settlement) and the annual and geographical variations, it does appear that many previous records agree with the findings here reported. Whilst generalisations are difficult, the extensive literature suggests that mussels from more southerly waters generally spawn prior to those from colder northern waters.

The present investigation showed that males were frequently somewhat more advanced in gametogenesis at any one time than the females, yet this is probably a consequence of the arbitrary scheme of classifying gonad condition rather than any chronological differences in the rates of development, since females in fact often appeared to spawn slightly before the males. It is not improbable, however, that production of spermatozoa would occur faster than the production of ova with their large reserves of yolk.

Apart from a general tendency for certain populations situated higher in the intertidal to spawn slightly before those further down the shore, no marked or consistent habitat differences, were recorded, contrary to initial expectations. Mussels situated on the extremely wave swept Brigg at Filey showed spawning patterns similar to populations from Filey Bay or from Whitby harbour. Neither were there any differences in the spawning periods of small and large mussels from Filey (1965) or Whitby (1966), though the gonad index in samples including very small individuals was usually somewhat lower at any particular time, due to the presence of virgin animals or those with a rudimentary genital system.

V. Spawning Stimuli

Whilst a wide variety of stimuli, including temperature, mechanical shock, chemicals and lunar cycles have been suggested as being important in inducing spawning, results have been both confusing and even conflicting. Perhaps some confusion has arisen in the search for one particular factor, since in any process as complex as reproduction, interactions of factors are perhaps to be expected. Direct correllations between spawning and exogenous factors, could be misleading, yet invariably controlled experimental data is lacking.

Correllations between neurosecretory and breeding cycles have been shown by Lubet (1955, 1956) who found that maximum spawning to external stimuli coincided with periods of evacuation of neurosecretory material from cerebral ganglia. He concludes therefore, that neurosecretion has an inhibitory effect on spawning, and only after neurosecretory cells have been emptied of their secretion, does the animal become sensitive to external factors, thus evoking spawning.

Although much attention has been given to the act of spawning, relatively little has been directed to factors influencing the entire reproductive cycle. These aspects are, however, basically physiological problems, and as such will not be dealt with in the present ecological investigation.

B. Larval Life and Settlement

The settlement of certain larval forms (including *M. edulis*) in connection with the problems of fouling and commercial exploitation, is of particular economic importance. Even so, relatively little literature exists upon larval behaviour and settlement for this species, though particular attention is drawn to the publications of Maas Geesteranus (1942), Verwey (1952), Savage (1956), De Blok and Geelen (1958) and Bayne (1964, 1965).

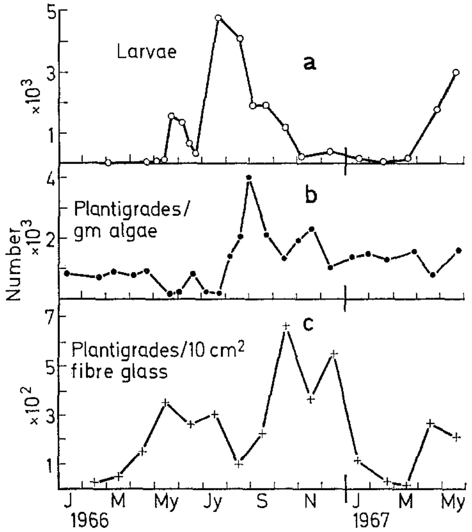

Fig. 8a—c. The occurrence of three stages of *M. edulis* during 1966 and early 1967. a Late larvae per 20 minute plankton haul, Saltwick Bay. b Early plantigrades per gram dry wt. *Polysiphonia,* Ness Point. c Late plantigrades per 10 cms² fibre glass panel, Ness Point

The regular monitoring of *Mytilus* larvae in plankton hauls, and their settlement on the shore, not only served as a check on the breeding data recorded from histological preparations, but also gave valuable information on times of larval recruitment to parent stocks. The latter is particularly important in any population study, but has proved to be even more important in the present study where growth rates have proved to be particularly slow.

I. Occurrence of Larvae in the Plankton

A survey of the literature reveals that in general, *Mytilus* larvae are particularly abundant over the spring and summer in British waters. For the present investigation it will suffice to note that there exists considerable diversity in the seasons of maximum larval abundance, and this is to be compared with the variability in the spawning periods previously recorded for this species in different geographical locations. Of particular significance to the present work are those records of the presence of larvae over a considerable part of the year (Kändler, 1926; Jørgensen, 1946; Raymont and Carrie, 1964).

In order to observe the distribution of larvae, regular plankton samples (each of 20 minutes) were taken, using a guage 25N Nylon plankton net towed at 1—2 knots against the tide, in the surface waters of Saltwick Bay (south of Whitby). Although strong currents and rough seas lead to a thorough mixing of the water, samples were taken, wherever possible, over the same ground and at approximately the same state of the tide. Samples brought back to the laboratory were fixed in 4% formalin and examined for larvae at a later date. Results, expressed as numbers per 20 minutes haul, are illustrated in Fig. 8a.

Identification of bivalve larvae is particularly difficult especially in their early stages, though detailed descriptions are afforded in the literature (see for e.g. Stafford, 1912; Rees, 1950). Only larvae over 175 μ in length could be identified to species with any degree of certainty, though many of the earlier larvae (trocophores and "D" shaped veligers) abundant at certain times of the year, were almost certainly *M. edulis*. Fig. 8a shows that although some larvae were present over a considerable part of the year during 1966, maximum numbers were recorded in late May to mid June, and more especially from July through until October.

The length of time spent in the plankton prior to their settlement on the shore probably varies with temperature and local food supply. In the absence of suitable substrates for attachment, however, mussels are known to be able to delay their settlement (Bayne, 1965). The literature indicates that from 3—10 weeks may elapse between fertilization and settlement though 3—4 weeks appears to be the more usual duration of planktonic existence.

II. Settlement on the Shore

Perhaps the major criticism against many of the earlier works relating to settlement of *Mytilus* has been the failure by many authorities to distinguish between the settlement of young mussels on filamentous algae and hydroids (primary settlements) and that of somewhat older animals on established beds or virgin rock surfaces (secondary settlements). In view of this, many previous records, both of the time taken from spawning to settlement, and the actual dates of settlement, even for the same geographical localities, have been particularly variable, and frequently conflicting. In accordance with Carriker (1961) primary settlement stages will be termed early plantigrades, and secondary settlement stages late plantigrades.

1. Primary and Secondary Settlement

Associations of recently settled mussels with filamentous substrates have been recorded many times in the literature (reviewed by Bayne, 1964). Wilson (1886) attributed the presence of small mussels (ca. 250 μ long) on zoophytes and seaweeds, to a process of passive interception of the larvae. De Blok and Geelen (1958), however, found that young mussels were not directed onto existing beds, but rather onto filamentous substrates from which they subsequently disappeared, and experiments with artificial substrates indicated a distinct preference for filamentous surfaces by early plantigrades. Later plantigrades on the other hand, were shown by Maas Geesteranus (1942) to exhibit a marked preference for the niches afforded on adult beds.

More recently, Bayne (1964) demonstrated that mussels pass successively from the plankton, to sites of temporary attachment on filamentous algae, and from there to sites of more permanent attachment near adult beds. He suggests that this primary phase of attachment is a natural prelude to final settlement, and not wasteful settlement on unsuitable substrates. Thorson (1957) discusses the difficulties that newly settled bivalves have in competition with adults, and suggests that a primary attachment away from adult stocks, during which time they can grow, could have survival value.

a) Settlement on Filamentous Algae

Observations during 1965 revealed the presence of dense populations of early plantigrades on certain algae (especially species of *Polysiphonia, Ceramium* and *Enteromorpha)* at various times of the year, whilst at other times their numbers were considerably reduced. Even so, relatively large numbers of plantigrades could be found attached to these algae almost throughout the year. In this respect the clear cut appearance of early plantigrades on filamentous algae at certain times of the year, and their complete disappearance at other times shown by Bayne (1964) was not fully supported in this investigation. Associations of plantigrades with other algae such as *Fucus*, *Gigartina*, *Laminaria* and *Corallina* were also observed. Throughout 1966 and early 1967, regular samples of *Polysiphonia* were collected from the mid-low shore from a wave beaten locality between Robin Hood's Bay and Ness Point, and examined for early plantigrades. After removal of these plantigrades, the alga was dried to constant weight. Results obtained, expressed as numbers per gram dry weight of alga, are shown in Fig. 8b, indicating that whilst from January—April (1966) relatively large numbers of plantigrades were present, during May these fell quite sharply. Their increase during June was again followed by a marked drop in July, whilst in August and early September, numbers rose dramatically with up to 4,000 plantigrades/gram. Although numbers decreased during September, many could still be found on the algae throughout winter. It was noted that whilst the fine terminal axils of the algae generally supported newly settled plantigrades, animals from lower, and coarser axils were generally of a larger average size. From the times of maximum spawning (July—August), and the subsequent settlement on the algae, it would appear that larvae in this locality must spend between 3—5 weeks in the plankton. Settlement on the algae occurred when plantigrades measured about 300 μ in length.

Generally, early plantigrades remained upon the red algae until they measured between 1—2 mms length (the time taken to attain this size depending upon individual growth rates). Four weeks, however, seemed to be the average time spent by the majority of plantigrades on filamentous algae in this locality (cf. Bayne (1964), 30 days; De Blok and Geelen (1958), 18—28 days). The stimulus to leave the algae is primarily due to changes in the ecological requirements of the plantigrades. Whilst filamentous substrates satisfy early plantigrades, such habitats do not apparently satisfy the somewhat older (larger) stages. On the other hand, dense settlements of animals 1—2 mms in length between mussels on adult beds (especially amongst the byssus threads) at certain times of the year, suggested that these habitats were particularly suitable to later plantigrades. Settlement on red algae during late autumn, when conditions for further growth are unfavourable, may result in early plantigrades remaining on these sites over winter, leaving only with the resumption of more favourable conditions for renewed growth in the following spring. This would explain the appearance of spat on adult beds during early spring, which could not be explained solely from a knowledge of the breeding cycle. Since migration from sites of temporary attachment is due to changes in the ecological requirements of the mussels, it might be expected that some animals would migrate earlier than others, depending both on individual growth rates, and on the nature of the primary sites of attachment. For example, coarser algae such as *Corallina* or *Gigartina* might satisfy early plantigrades for longer periods than the extremely fine filamentous species. Certainly plantigrades up to 3—4 mm in length have been found, not only on these coarser algae but even amongst the coarser basal branches of *Polysiphonia*. It is possible therefore, that sites of temporary attachment could provide extensive "reservoirs" of plantigrades, from which varying numbers might be migrating at almost any time throughout the year for their more permanent attachment on adult beds. This, together with the "liberation" of plantigrades as algae die back at various times of the year, could explain the sporadic outbursts of settlement which are known to occur on some shores, and which could not be predicted solely from a knowledge of the breeding cycles. Nevertheless, periods of maximum settlement on filamentous substrates, followed by correspondingly dense settlements on adult beds, can usually be forecast from a knowledge of the times of maximum spawning.

b) Settlement on Adult Mussels Beds

Observations at Filey during November 1964 indicated that a particularly heavy settlement had recently occurred, since large numbers of small mussels (mean length 1.67 mm) were to be found carpeting what previously must have been bare rock surfaces. Similar dense settlements of young mussels were also noted amongst populations of *Balanus balanoides* (especially in the grooves on the shells, and between individual barnacles). Adult mussels 3—4 cm long could also be found covered with as many as 6—700 late plantigrades. Heavy settlements were again recorded in the autumn and early winter of 1965 and 1966. Quantitative investigations of the settlement of late plantigrades were carried out in two separate ways.

α) *Experimental Panels.* A variety of experimental panels of varying surface texture have been tried in order to find which surfaces were most attractive to searching plantigrades. These included smooth, rough or pitted Tufnol, slate, asbestos, roughened perspex, concrete or mortar, raw wood, fibreglass and rubberised hair, each panel measuring 10 cm^2.

Initial experiments at Filey and Robin Hood's Bay in 1965 met with little success, mainly due to severe damage to panels by rough seas. The panels in these early experiments were attached to the shore by means of Rawlplugs and stainless steel screws. In February 1966, however, panels were set out at three shore levels at Ness Point, anchored by means of stout Rawlbolts, and countersunk into the rock so that their surfaces were level with the ground. In this way they remained *in situ* for up to twelve months. Prior to their attachment, panels were naturalized in running sea water in laboratory tanks for two weeks.

Smooth surfaces attracted very few plantigrades, maximum settlement being recorded on the rougher surfaces such as rubberized hair, fibre glass and conrete. Edges of inset panels and any pits, cracks or scratches in the surfaces proved exceptionally attractive. Settlement was particularly gregarious, earlier settled plantigrades forming loci for those arriving later. For the monthly monitoring of settlement, fibre glass panels were set out at regular monthly intervals.

Whilst settlements in February and March 1966 were fairly low (Fig. 8C) numbers increased steadily from April to July, declined during August, and became very heavy from September to December. Early spring settlements were due, in the main, to recruitment from the overwintering stocks on the red algae. Early summer recruitments from primary sites of attachment were supplemented by plantigrades resulting from the spring spawning, whilst the heavy spatfalls from September to December were a direct consequence of the main spawning periods during July and August. Although no quantitative data is available, the relatively earlier major spawning in 1967, was reflected in dense settlements of late plantigrades during August. Thus it would appear that in general a period of approximately 8—10 weeks elapses between spawning and the appearance of plantigrades on adult beds, in this locality.

Panels set out on wave swept shores such as Ness Point collected more plantigrades than those set out in the relatively calm waters of Whitby harbour. Whilst this could be a direct influence of the greater volume of water passing over the panels in more turbulent waters, transport of many larvae out of the harbour could occur by the fresh water currents of the River Esk. Heavy settlements at the mouth of the harbour, where there was moderate wave action and some degree of eddying, were in fact recorded. High densities of spat were also found at the head of Filey Bay, into which plantigrades were probably funnelled by prevailing onshore winds.

Whilst large numbers of plantigrades were recorded on panels at M.L.W.S. at Ness Point, very few survived on panels in the mid and high shore, even though dense mussel beds existed in these habitats. This is probably due to the rapid dessication of the panels, whilst plantigrades settling on adjacent beds, found local moisture both amongst the byssus threads of adult mussels, and in cracks or depressions in the rock surface. The upward extension of *Mytilus* on any given shore will therefore depend largely upon local conditions such as surface texture of the rock or the amount of wave splash. The importance of constant wetting during byssus secretion is also probably very important.

In June 1965, sandblasted perspex panels were attached to a Dexion framework, and set out under Keppel Pier, Millport, covering the tidal range from + 8.5 to — 1.0′ Chart Datum. At the bottom of the frame, a wire guard was fitted to keep off predators (mainly *Asterias rubens*). By October 1965 heavy settlements of *Mytilus* had occurred, not only on the panels but also on nearby ropes, the Dexion framework itself, and other roughened or scarred surfaces. Whereas naturally occurring mussels could be found amongst barnacles at + 8.5′ C.D., no plantigrades were present on panels above + 6.5′ C.D. (i.e. approximately M.T.L.). Again this doubtless reflects the retention of moisture amongst the barnacles, thus permitting mussels to survive higher in the intertidal than is possible on the relatively quick draining panels. Between M.L.W.N. and M.L.W.S., the number of plantigrades found attached to the panels increased markedly, maximum numbers occurring at and below M.L.W.S. On the actual pier supports, however, no mussels could be seen below M.L.W.S., a result of the heavy starfish predation. A similar framework put out in Whitby harbour in 1966 gave comparable results, maximum numbers setting at and just below M.L.W.S. with few surviving on panels at M.T.L.

On exposed shores, where the lower levels are frequently dominated by laminarians, the lower limits of *Mytilus* are often quite sharp. The presence of large areas of smooth *Lithothamnia* covered rock in this region may prove particularly unsuitable for settling plantigrades, though their absence might also be attributed to the sweeping effects of

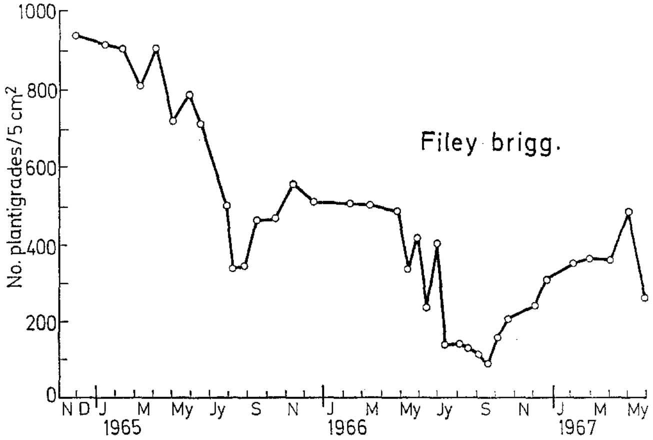

Fig. 9. The occurrence of young mussels (< 3 mm in length) per 5 cms², from the midshore Filey Brigg

the laminarian fronds. The abundance of predators in the lower shore could also be a major factor in setting the lower limits of mussel distribution on many exposed shores.

β) Population Studies. By taking regular replicated 5 cm² samples from the newly established population (autumn 1964) on Filey brigg and counting the total numbers of small mussels (< 3 mm in length) further indication of the periods of maximum settlement was obtained. This method does not, however, give a true quantitative representation of settlement since it does not take into account the processes of mortality or growth out of the size categories sampled. Aspects of growth and mortality will, however, be dealt with in a subsequent publication. Fig. 9 shows that during the winter, in the absence of major mortality factors, and when growth is particularly slow, populations remained relatively stable. During the spring and summer, heavy mortality and rapid growth lead to excessive losses in the numbers of small mussels. At certain times of the year however, these were offset by recruitment of late plantigrades, spring and early summer recruitments coming from both the early spawning period, and the migration of overwintering plantigrades. Numbers of late plantigrades increased through September to December (the results of the July, August spawnings) and then remained relatively stable until the following spring. Fig. 9 therefore, represents a balance between recruitment of plantigrades and their subsequent loss through mortality or growth out of the size categories sampled. Increase in numbers occurs when recruitment exceeds loss, whilst decrease indicates losses of small mussels from the population.

III. Behaviour of Plantigrades at Settlement

Field observations have indicated a preference by mussels for those shores which are either slowly draining, or those receiving constant wave splash. Fewer mussels were recorded on rapidly draining vertical faces although dense clusters of mussels on pier supports or harbour walls indicated that such habitats were not entirely excluded to them (though in these situations they were usually restricted to the lower levels). Observations of field populations and of settlement on artificial panels, showed that whilst some settlement will occur on almost any stable substrate, preference was given to those surfaces which were roughened, pitted or scarred in some way. Mussels then attached themselves with their umbones projecting into the discontinuity and their inhalent siphons directed outwards. Moisture retaining pits and cracks (Fig. 2D) were particularly favourable, and the presence of such habitats often permitted mussels locally to extend further upshore. Many local shores, consisting of smooth shales, frequently lacked mussels entirely except in places where some fault in the rock surface occurred (Fig. 2E). Ropes or cables, barnacles, cockle and limpet shells, have all been seen supporting dense settlements of small mussels, their grooved surfaces being ideally suitable to late plantigrades (densities of up to 3,000 plantigrades/5 cm^2 have been found amongst barnacles at Filey).

At settlement, mussels are particularly gregarious and dense settlements can be found around the edges and in between individual mussels in existing populations. In established patches of mussels, the oldest animals are frequently found in the centre, with progressively younger mussels arranged around them. Gregarious behaviour probably has some adaptive significance since *Mytilus* is essentially a littoral species, and as such, is subject to the mechanical forces of wave crash, especially on the open coast. The reduced surface area exposed to mechanical forces, of individuals within a population, together with the mutual support of neighbouring animals, makes groups of mussels better adapted at withstanding wave action than isolated individuals. The wedge-shaped profile also makes the mytilid form particularly well suited to animals living in dense clusters. Plantigrades onse settled, provide loci for further settlement, and so the colony gradually extends. Although sparser settlements can sometimes be found amongst barnacles in the upper shore, this region on local shores is more usually characterised by isolated patches of animals (Fig. 2A) which have been able to become established through local survival in damp cracks or crevices. On yet other shores which permit the full vertical range of mussels to become developed, the upper limits of distribution can often be very sharp.

In an extensive series of laboratory experiments (Seed, 1967) giving late plantigrades various alternative sites in which to settle, results have shown that gregarious behaviour (observed in the field) is primarily a response to their thigmotactic requirements rather than to any chemotactic attraction. Numbers settling were directly proportional to the amount of suitable substrate available to them. Byssus secretion, and subsequent attachment was favoured by surface discontinuities and such requirements would undoubtedly be most ideally satisfied amongst individuals on adult beds. Plantigrades reach adult beds through their ability to attach and detach themselves from unsuitable substrates until they eventually encounter surfaces that satisfy their thigmotactic requirements. In this respect these experiments confirmed the findings of Maas Geesteranus (1942).

Once established, mussel beds increase in dimensions both through gregarious recruitment, and growth of individuals in the population. Yet relatively slow growth, and extremely heavy mortality rates act as a severe restraint to the establishment of extensive beds on many local shores.

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