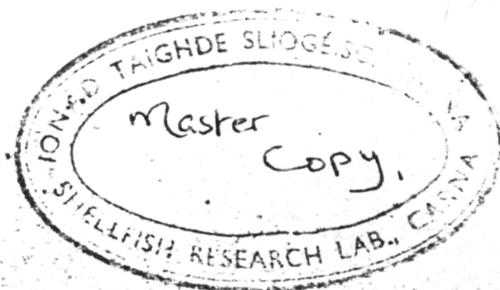

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IRISH FISHERIES INVESTIGATIONS

SERIES B (Marine)

No. 15 (1974)

AN ROINN TALMHAIOCHTA AGUS IASCAIGH
(Department of Agriculture and Fisheries)

FO-ROINN IASCAIGH (Fisheries Division)

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J. H. WILSON AND R. SEED.

REPRODUCTION IN *MYTILUS EDULIS* L. (MOLLUSCA: BIVALVIA) IN CARLINGFORD LOUGH, NORTHERN IRELAND.

IONAD TAIGHDE SLIOGÉISC, CÁRNA
SHELLFISH RESEARCH LAB., CARNA

Reproduction in *Mytilus edulis* L. (Mollusca: Bivalvia) in Carlingford Lough, Northern Ireland.

J. H. WILSON

AND

R. SEED

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Abstract

The reproductive cycles of several *Mytilus* populations in Carlingford Lough were investigated between November 1968 and May 1971.

The annual cycle varied slightly from population to population though spawning began simultaneously at all stations in the spring months when sea temperature was rising rapidly between 7.5° and 12°C.

A secondary phase of gametogenesis during the summer months was confirmed by oocyte counts and the onset of the secondary spawning period occurred from 4-8 weeks after the initial spring emission.

Although no significant differences were recorded in oocyte size in the different populations immediately before spawning oocyte densities were greatest at the seaward stations. Similarly, low shore populations had higher oocyte densities than those higher in the littoral zone where feeding time is severely curtailed.

Size did not seem to influence gametogenesis nor did the severely polluted conditions prevailing in Belfast Lough.

Seasonal changes in glycogen and lipid content of the mantle were studied in relation to the annual reproductive cycle.

Primary settlement of early plantigrades on algae occurred principally in summer and winter. Secondary settlement on artificial substrates coincided with the disappearance of early plantigrades from the algae.

Introduction

Whilst the literature relating to reproduction in *Mytilus edulis* L. is particularly extensive in view of its commercial importance, few of the older investigations go further than establishing the times of spawning or settlement and their conclusions are frequently conflicting and imprecise. Of the more recent accounts attention is drawn to those by Chipperfield (1953), Lubet (1957), Lubet and Le Gall (1967), Le Gall (1970) and Seed (1969, 1971, 1974).

Johnstone (1898) outlined a classification of the stages of gametogenesis which was subsequently developed by Chipperfield (1953) and Lubet (1957). More recently Seed (1969) adopted a system based on that used by Orton, Southward and Dodd (1956) for *Patella vulgata.* Such schemes provide simple yet relatively precise methods for describing the reproductive cycle more objectively than was hitherto possible from the more superficial assessment of gonad condition used by many early workers.

Many investigations of the spawning periods of *Mytilus* are based upon the appearance of larvae in the plankton or "spat" on the shore. Such observations may not, however, reflect the true spawning pattern for the area concerned since larvae and spat are not always homogeneous and may have been transported considerable distances by currents from localities with quite different hydrographic conditions. Extended periods of settlement can also be due to such incursions of "foreign" larvae. Furthermore the duration of planktonic life can be influenced by the availability of suitable substrates. Bayne (1965) observed that larvae of *M. edulis* can delay metamorphosis for up to seven weeks. Thus whilst three to four weeks normally elapse between fertilisation and settlement this period can be as long as eleven weeks during which time the parent mussel could have spawned a second or third time.

Despite numerous biochemical analyses of mussel tissue surprisingly few workers have attempted to relate changes in chemical composition to the state of the gonad. Daniel (1921, 1923) first suggested that marked seasonal fluctuations in the level of tissue glycogen could be related to gametogenesis. Chipperfield (1953) used Daniel's results in conjunction with his own analysis of gametogenesis to indicate the major role played by reproductive tissue in the metabolism of glycogen and lipid. Lubet (1957) directly correlated biochemical changes with the stages in the annual reproductive cycle.

This investigation examines the reproductive cycle of *Mytilus* in Carlingford Lough, Co. Down, using histological preparations of mantle tissue. Planometric methods are used to determine the density and volume of maturing oocytes whilst seasonal changes in the distribution and concentration of glycogen and lipid in the gonad have been followed histochemically and biochemically.

Materials and methods

Four low level populations on the northern shores of Carlingford Lough, Co. Down: Greencastle, Killowen Point, Rostrevor and Narrow Water (see Fig. 1) were sampled between November 1968 and May 1971. In addition, samples were collected for one year only from a midshore population at Rostrevor and from the mid and low shore populations at Holywood on Belfast Lough. Sampling was carried out monthly during the winter and every two-three weeks during the summer. Generally only mussels with a shell length of 4.5-5.5 cm were collected.

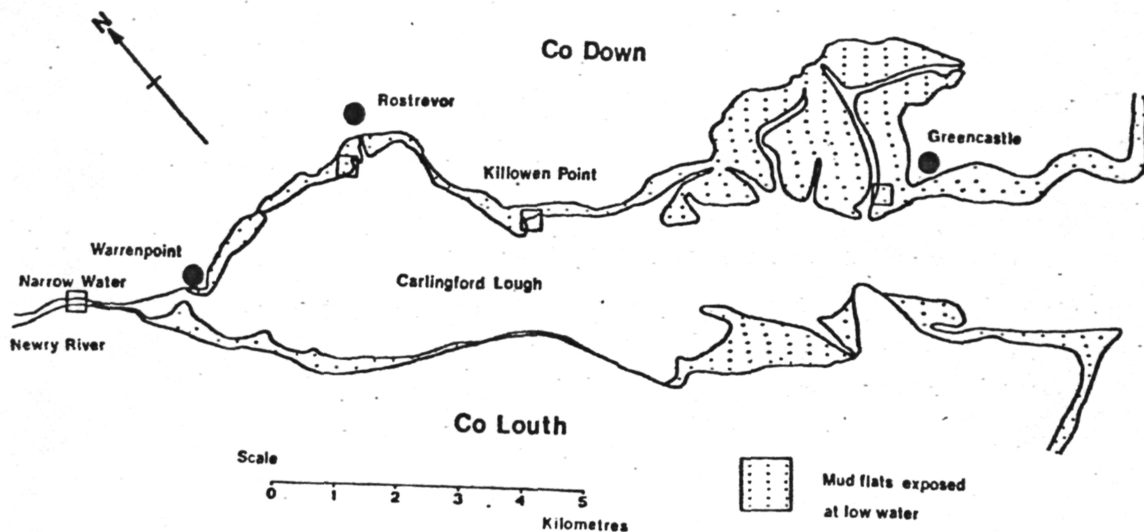


Fig. 1. Map showing sampling stations in Carlingford Lough.

Based on the Ordnance Survey by permission of the Government (Permit No. 1833).

Animals were either examined on the day of collection or kept overnight at 8°C in dry polythene containers. The central portion of one mantle lobe from each mussel was fixed in Gendre's or Bouin's fluid and stored in alcohol. Tissues embedded in paraffin wax (M.P. 56°C) and sectioned at 7.5-12 μ in thickness were stained in Mayer's haemalum. As many as 10-15 mantles could be embedded in the same wax block and sectioned simultaneously. The stained preparations were then classified using a slight modification to the system previously described by Lubet (1957).

The stages in this arbitrary scheme are as follows:—

Stage 0 (Plate IA). This is the resting phase in which there is no trace of sexuality. The genital canals have collapsed or degenerated and the connective tissue is packed with stores of lipid and glycogen.

Stage 1 (Plate IB). Here indications of the start of gametogenesis become apparent. Small clusters of germinal cells are scattered throughout the connective tissue. Oogonia and spermatogonia formed from the germinal epithelium line the walls of the follicles. Sex determination is still difficult especially in the early phases of this stage.

Stage 2 (Plate IC, D). The follicles in both males and females now occupy a large part of the mantle. In the male, masses of primary and secondary spermatocytes and spermatids fill the follicles while the small darkly staining nuclei of spermatozoa are scattered amongst the larger cells. In the female, oocytes have begun to accumulate yolk and have grown considerably. Some of the larger oocytes are still attached to the follicular epithelium by a slender stalk of cytoplasm which eventually ruptures to leave the oocyte free within the follicle.

Stage 3A (Plate IE, F). The gametes are now morphologically ripe. In the male the follicles are packed with spermatozoa arranged in lamellae converging towards the centre of the lumen. A few residual spermatocytes and spermatids may still be present. In the female the majority of the oocytes have reached their maximum size and lie packed tightly together in the follicles. The pressure within these follicles compresses the oocytes into polyhedral forms. The connective tissue which has now lost most of its reserves of glycogen and lipid may be almost completely obscured by the swollen follicles.

Lubet (1957) subdivided this stage into two further stages—$3A_1$ and $3A_2$. Mussels at stage $3A_2$ contain sperm which become motile and eggs which lose their germinal vesicles in seawater. It was found in the present investigation, however, that the proportion of sperm which was activated was extremely variable whilst a few active sperm were often encountered in mantles which had barely reached stage $3A_1$ in their morphological appearance. This created considerable doubt as to the value of sperm activity as a criterion of ripeness. It was decided, therefore, to avoid the use of stage $3A_2$ as it tended to contradict the morphological methods of classification.

Stage 3B (Plate IIA, B). Emission of gametes has now begun. However, large numbers of almost ripe oocytes are still present in the follicles. Residual oocytes tend to be spherical as the reduction in numbers greatly reduces compaction. Large numbers of spermatozoa line the follicles but their arrangement in lamellae has now disappeared.

Stage 3C (Plate IIC, D). In favourable conditions stage 3B is followed by a new phase of gametogensis. There is rapid proliferation and growth of oocytes and a densely staining band of spermatids gives rise to new lamellae of spermatozoa. Gametogenesis continues until a new stage 3A is reached prior to further spawning.

Stage 3D (Plate IIE, F). After the final spawning of the year the follicles begin to collapse and degenerate. The small number of unspawned gametes are rapidly broken down by amoebocytes and the animal again enters the neuter stage.

Although the diffuse nature of the reproductive system precluded any measure of absolute growth of the reproductive tissues during gametogenesis, comparisons were made between the mean densities of oocytes in the different populations. The number of eggs over 10 μ maximum diameter were counted in randon quadrats of 0.1 mm^2. Ten counts were made on each mantle using sections 10 μ in thickness. Furthermore, by projecting sections onto graph paper the cross sectional area of these irregularly shaped oocytes could be estimated. The mean oocyte area provided an index by means of which the growth and size of oocytes from the different populations could be compared.

During 1969 sections were also stained using the Periodic Acid-Schiff technique (PAS) with diastase as control for the detection of glycogen, and by the Sudan Black B method for neutral non-acidic lipids and phospholipids. The Feulgen method was also used to stain DNA when more detailed nuclear structure of the gametes was required.

Quantitative biochemical estimations of glycogen were made using the anthrone technique of Dreywood (1946). Although sensitive in the detection of glycogen, anthrone will also react with other carbohydrates. Alcohol precipitated carbohydrates which gave a positive reaction with anthrone will be referred to as "glycogen" in this account. Glycogen estimations were carried out on mantle tissues taken from individuals used previously in the histological classification of the gonads. Each sample was divided into sub-samples containing equal weights of mantle tissue from five individuals. The tissue was finely divided, placed in a Pyrex test tube and dried at 60°C to constant weight. Three ml of 30% A.R. potassium hydroxide were added to each tube and the tissue digested by boiling for half an hour in a water bath. The solution was cooled and 1.2 volumes of 90% alcohol added to precipitate glycogen. The precipitate was collected by centrifugation at 3,000 r.p.m. for 15 minutes. After allowing to drain for 10 minutes the precipitate was dissolved in 250 ml of distilled water. One ml of this solution was pipetted into a test tube and 5 ml of anthrone added with vigorous stirring.

The anthrone reagent was prepared by adding 1 litre of 72% A.R. sulphuric acid to 500 mg of anthrone and 10 g of A.R. thiourea. This was warmed to 80-90°C with occasional stirring. The reagent keeps for about 2 weeks at 4°C.

After adding the anthrone reagent the solution together with a blank and a standard glucose solution were heated for 15 minutes in a boiling water bath. On cooling, the optical density was read on an Eel colorimeter at 6200 Å. The glycogen content was then calculated from the formula:

$$\frac{D.U. \times C. \times V. \times 0.9}{D.S. \times T}$$

where D.U. and D.S. are the optical densities of the unknown and the standard respectively, C the concentration of the glucose standard, V the volume of the unknown solution, T the weight of the mantle tissue and 0.9 the conversion factor for glucose. Comparisons of glycogen levels in the anterior, median and posterior parts of the mantle lobes showed that glycogen was evenly distributed through the mantle. Furthermore, drying did not significantly reduce the glycogen content.

Mantle lipid was measured after a Folch extraction with chloroform-methanol (Folch, Lees and Sloane-Stanley, 1957). Subsamples each containing equal weights of mantle tissue from five animals were homogenised in a Waring blender with a 2:1 (v/v) chloroform:methanol mixture to a final dilution which was twenty times the volume of the tissue sample. The crude extract was mixed thoroughly in a separating funnel with 0.2 of its volume of 0.05 N potassium chloride and the mixture allowed to separate into two phases overnight. As much of the upper phase as possible was removed by siphoning and the interface rinsed several times with small amounts of upper phase solvent (chloroform:methanol:water in the proportions 3:48:47 by volume). The lipid extract was then drained into a crystallizing dish and the solvents evaporated *in vacuo*.

Settlement of young mussels was measured using both natural and artificial substrates. Samples of the alga *Polysiphonia lanosa* were collected from the midshore at monthly intervals during winter and every 2-3 weeks in summer. The alga was blotted dry and weighed and the attached plantigrades collected and measured. Two metre lengths of untreated coir rope 2 inches in circumference were suspended in cages on the mussel beds in the low shore. These were examined and replaced regularly and the late plantigrades removed and measured. The use of suspended rope collectors ensured that plantigrades were presented with a suitable substrate for attachment irrespective of the direction from which they approached the collector. The growth rate of early plantigrades on the algae was estimated using the technique described by Bayne (1964).

Results

The general pattern of gametogenesis and spawning was similar in all populations studied during the three years of the investigation. After completing spawning in the late summer months animals entered a resting phase in which there were no indications of gametogenesis. During this period the thin transparent mantle lobes gradually increased in thickness and became heavily pigmented. In autumn, gametogenesis recommenced and morphologically ripe gametes accumulated over winter. Spawning began in spring and continued sporadically into the summer. Renewed gametogenic activity was observed in the mantle between peaks of spawning. By mid to late summer, however, spawning had almost ceased and the animals returned to their resting condition.

Detailed analyses of gametogenesis in the low shore populations (Figs. 2 and 3) revealed significant variations in the basic pattern from year to year and from one population to another. The majority of animals were morphologically ripe by the beginning of April in 1969 and spawning began two weeks later. In 1970, however, there was a considerable delay between the attainment of ripeness and spawning. The majority of individuals in the population were at Stage 3A by the beginning of March 1970 but spawning did not begin until May—some two months later. In 1971 most populations were ripe by early March but the first spawning did not occur until mid April.

Spawning began more or less simultaneously at the four stations—mid April 1969, early May 1970 and mid April 1971. When this first spawning was completed rapid recovery of the gonad to the morphologically ripe condition was observed at all stations. However, the length of time required for recovery varied from station to station so that the onset of the period of secondary spawning occurred from 4-8 weeks after the initial spawning. Further minor spawnings were observed at some stations, the total spawning season lasting from 2-5 months.

The resting phase generally lasted from 2-4 months. Nevertheless, neuter individuals showing no obvious signs of gametogenic activity were frequently encountered at times of the year other than the periods following the total cessation of spawning. This was particularly noticeable at Rostrevor and Narrow Water (Fig. 3) during the winter of 1969-70.

Differences in the rate of gametogenesis were apparent between populations. The low shore population at Narrow Water had a significantly slower rate of gametogenesis and shorter spawning periods than at other stations. Comparisons between the annual cycle are facilitated by the use of a gonad index (Fig. 4) By giving the percentage in each stage an arbitary ranking each sample can be assigned a mean value indicative of the degree of gonad development. Stages 0-3A were ranked zero to three respectively, Stage 3B was ranked two, Stage 3C and 3D were respectively ranked three and one. The gonad index could thus vary from 0 (100% at Stage 0) to 300 (100% at Stage 3A or 3C).

Fig. 4 shows the gonad indices of the four low shore populations. Both the Greencastle and Killowen populations had somewhat longer spawning periods than those at Rostrevor and Narrow Water. Whilst the animals at the latter stations completed spawning earlier they had longer resting phases and slower rates of gametogenesis than the other two populations. Greencastle and Killowen were essentially similar but gametogenesis at Narrow Water was persistently slower than at Rostrevor.

Quantitative differences in the intensity of gametogenesis were found by comparing the densities of oocytes (Fig. 5). The increasing number of oocytes during the winter and early spring indicates that Stage 3A is a period of rapid proliferation and growth of gametes. The sharp decline during early May supports the conclusion that spawning occurred at that time whilst the increase in oocyte numbers at all stations except Narrow Water during late May indicates that a secondary spawning was preceded by a period of active gametogenesis. Oocyte densities were almost identical at Greencastle and Killowen whilst counts for the Rostrevor and more especially the Narrow Water populations were significantly lower especially as the spawning period approached. In May and June oocyte densities continued to decrease at Narrow Water as no major recovery between spawnings occurred at this station.

During the proliferation of gametes in the follicles oocytes increased considerably in size. The growth of oocytes in the low shore populations at Killowen and Narrow Water is illustrated in Fig. 6. Oocyte growth was significantly faster at Killowen though the oocytes tended towards the same final size immediately before spawning. Records were discontinued before the first spawning occurred as the contents of the follicles after a partial emission contained a mixture of developing and non-growing residual oocytes.

All animals used in these investigations were 4.5-5.5 cm in shell length. Size, however, did not appear to have any appreciable effect on gametogenic activity once maturity had been reached. During 1969 samples of mussels 3-7 cm in length were collected from Rostrevor and their gametogenic condition determined: no significant differences in their gonad indices were recorded.

The basic similarities in gametogenesis and spawning in the four low shore populations suggested that a regime of environmental conditions common to all stations might directly control reproduction. The annual cycle of mean sea temperature showed no significant variation from station to station. Sea temperature did, however, fluctuate quite markedly throughout the year, rising from 4°C in winter to 18-19°C in summer (Fig. 7).

Gametogenesis proceeded steadily throughout the winter despite low sea temperature. However, the development of gametes was more rapid in the warmer summer months. Redevelopment of ripe gametes after the initial spawning usually occurred within a month whereas gametogenesis in winter, although undoubtedly on a larger scale, took 4-5 months. The rapidity of gametogenesis during summer, however, may not be due entirely to elevated temperature but may also be influenced by improved feeding conditions.

Each station was characterised by a distinct salinity regime and although salinity exhibited some variation throughout the year a seasonal cycle was not evident. Salinities remained relatively constant over a tidal cycle at Killowen and Rostrevor. At Greencastle salinity dropped rapidly to 5‰ at low water due to a small freshwater stream which ran across the shore. Salinity readings were therefore made 30-60 minutes before low water at this station in order to avoid this anomaly. Salinity at Narrow Water dropped appreciably throughout the ebb tide from approximately 30‰ to 15‰. Gametogenesis was generally slower and oocyte numbers lower in stations of lower salinity though evidence that salinity was directly responsible for the differences between populations was inconclusive.

The variations in glycogen content of mantles throughout the year indicated that food reserves may play an important role in the maintenance of gametogenesis. Fig. 8 shows the seasonal variation of glycogen in the four low shore populations. The annual cycle shows little variation from station to station over most of the year. After spawning, the populations rapidly accumulated large reserves of glycogen representing as much as 33% of the total weight of the mantle and four times the level in the rest of the body tissue. As a new phase of gametogenesis proceeded, glycogen concentrations gradually dropped until a minimum was reached immediately before spawning the following year. Differences between the stations became apparent in May after the first spawning. Although all stations were essentially at the same stage of gametogenesis, i.e. Stage 3C, both Rostrevor and Narrow Water, unlike Greencastle and Killowen did not show any accumulation of glycogen reserves. After completing spawning glycogen levels rose to maxima except at Greencastle where some individuals were still spawning. There was no difference in the concentration of glycogen in male and female mantles at the same stage of gametogenesis.

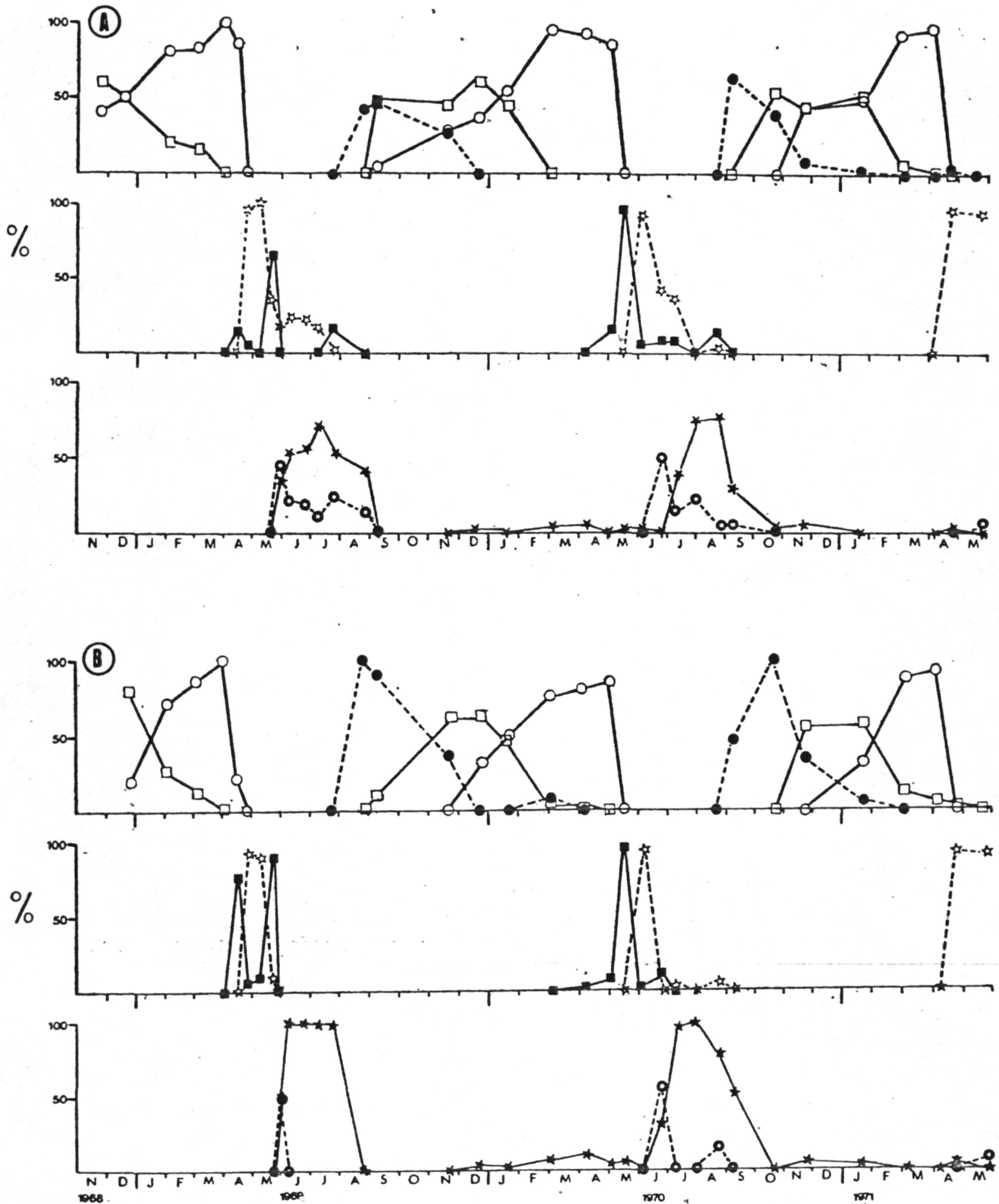


Fig. 2. Reproductive cycles of low shore populations from:—
(A) Greencastle; (B) Killowen Point.
Key: stage 1 —•— stage 2 —□— stage 3A —O—
stage 3B —■— stage 3C —☆— stage 0 —★—
stage 3D —✪—

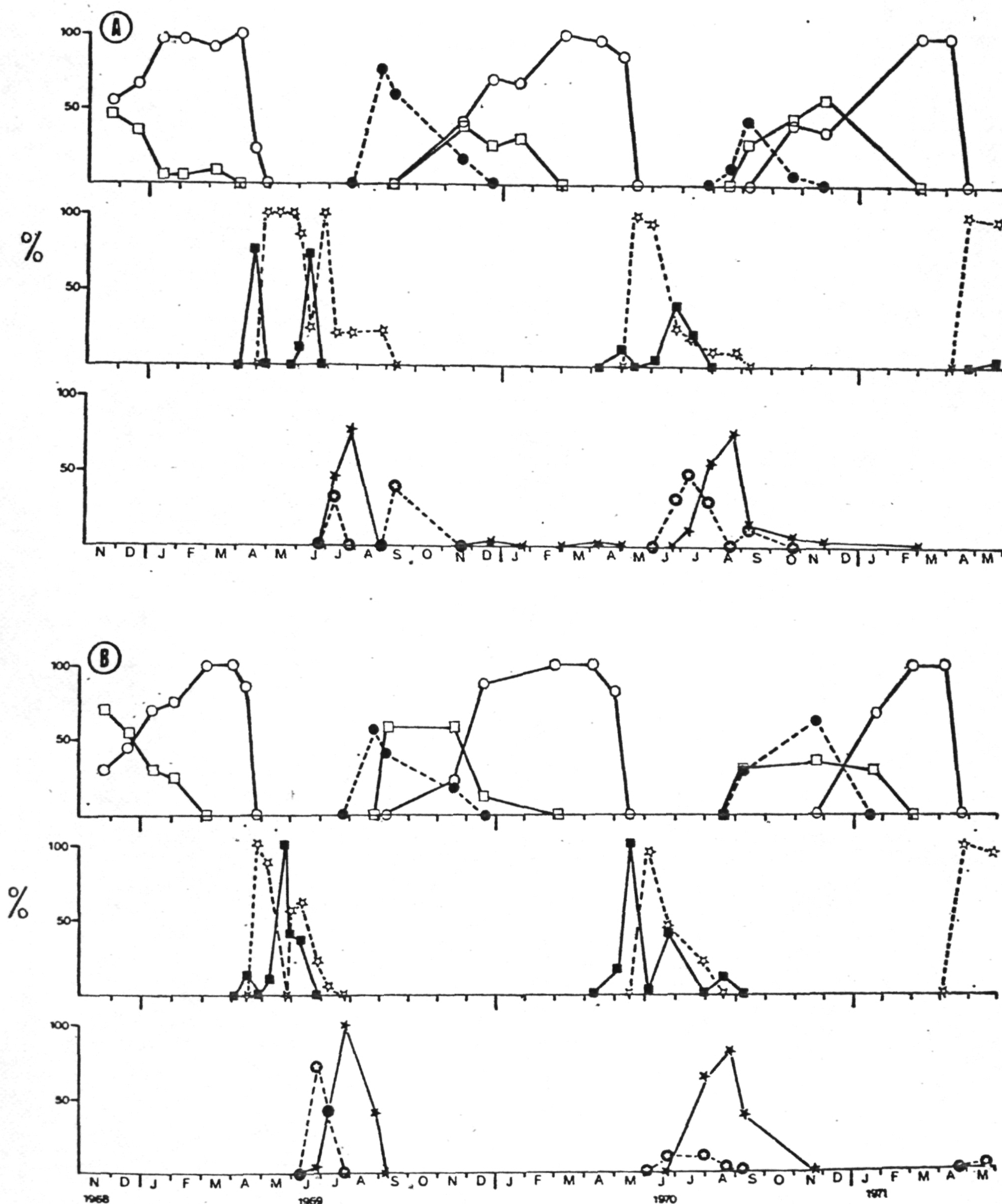


Fig. 3. Reproductive cycles of low shore populations from (A) Rostrevor, (B) Narrow Water. Key: as Fig. 2.

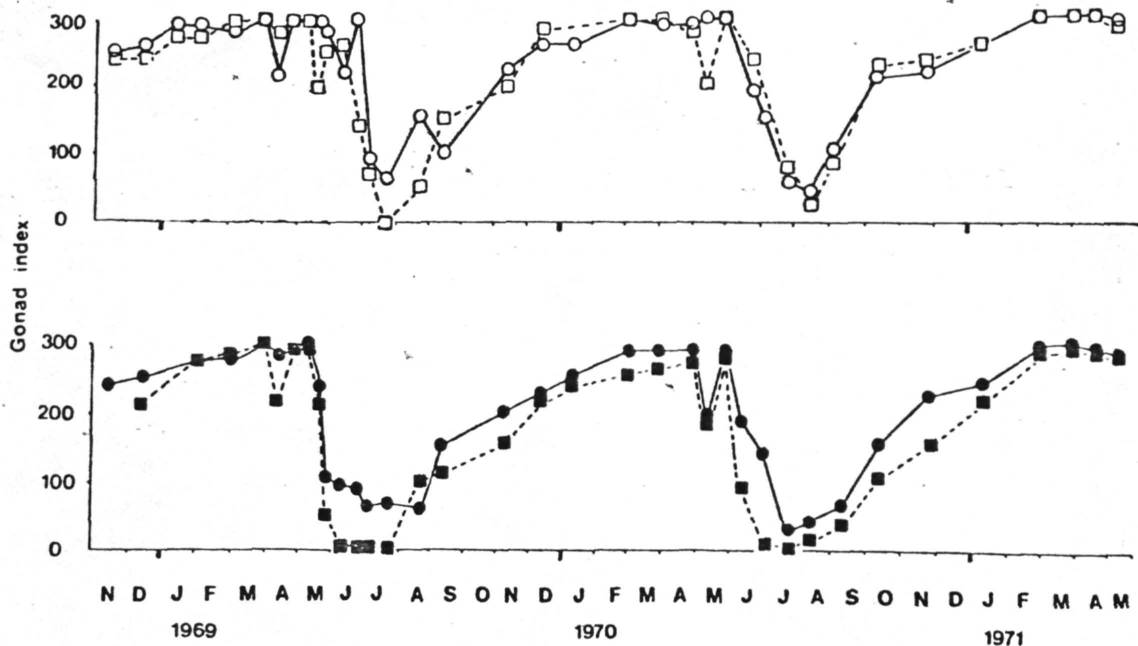


Fig. 4. Gonad indices for the four low shore populations in Carlingford L.

——O—— Greencastle; —— • —— Rostrevor;

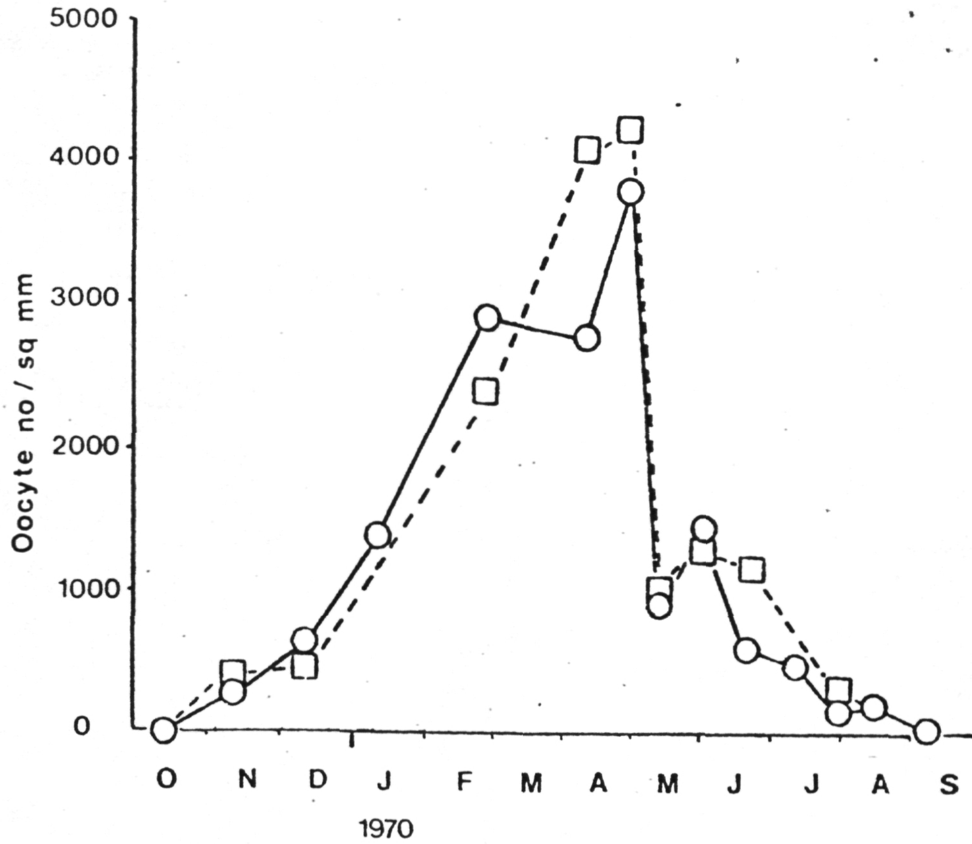
——□—— Killowen Pt.; ——■—— Narrow Water.

Lipid concentrations in the gonad tended to vary in much the same way as glycogen as seen in Fig. 9. However, some populations had consistently higher lipid concentrations than others and those with the highest levels such as Greencastle and Killowen also had the highest oocyte densities. This may be due to the large quantities of lipid present in oocytes: females contained 1.5 times the amount of lipid as males at the same stage of gametogenesis. Perhaps surprisingly, however, spawning did not cause a drastic decline in lipid, a large part of which is contained in the connective tissue and residual gametes.

The effects of reduced food intake on gametogensis was examined by comparing samples from populations in the mid and low shore at Holywood and Rostrevor—animals in the mid-shore having considerably reduced feeding periods. In neither case were any significant differences in gametogenesis recorded though populations in the low shore had higher oocyte densities than animals of similar size from the mid shore (Fig. 10).

The Holywood populations on Belfast Lough live under conditions of severe industrial and domestic pollution. In spite of this, oocyte densities were higher than those in Carlingford Lough populations. In addition they spawned frequently, with rapid redevelopment between each emission. It appears, therefore, that pollution in this locality does not have any adverse effects on gametogenesis or spawning.

Spawning commenced simultaneously at all stations in Carlingford Lough at approximately the same temperature each year. At that time temperatures were rising rapidly from 7 to 10°C in 1969, from 7.5 to 12°C in 1970 and from 9 to 11°C in 1971. Furthermore, spawning in the Holywood population commenced when the temperature was rising between 8.5 and 11°C—two weeks after the Carlingford populations. These data strongly suggest that sea temperature may be an important factor in initiating spawning.



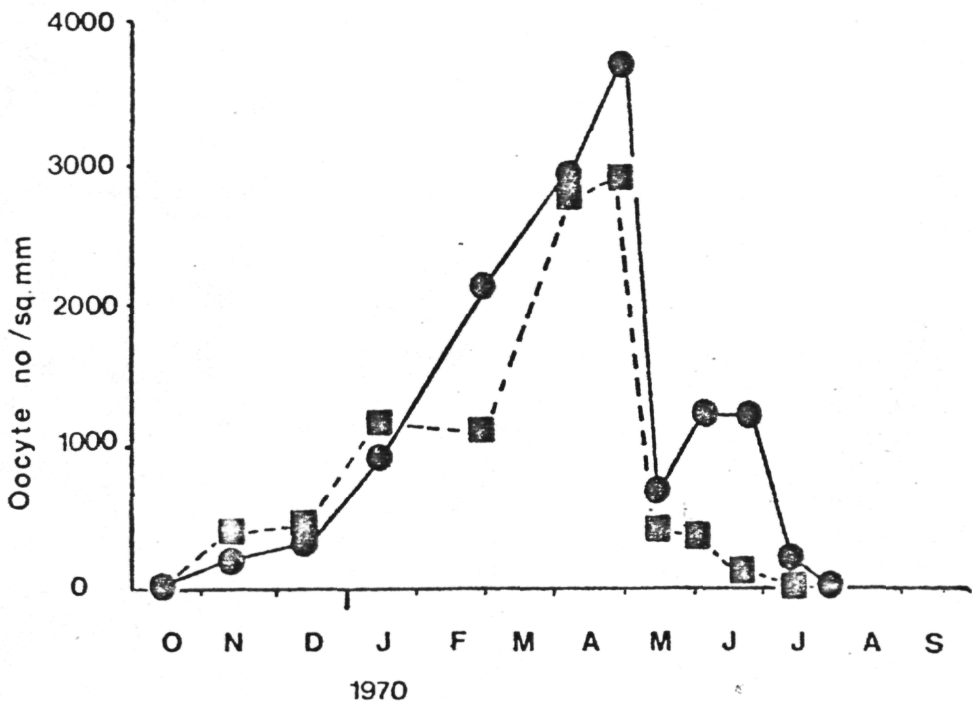


Fig. 5. Density of oocytes (over 10 μ diameter) in the four low shore populations in Carlingford L.
—O— Greencastle; —•— Rostrevor;
—□— Killowen Pt.; —■— Narrow Water.

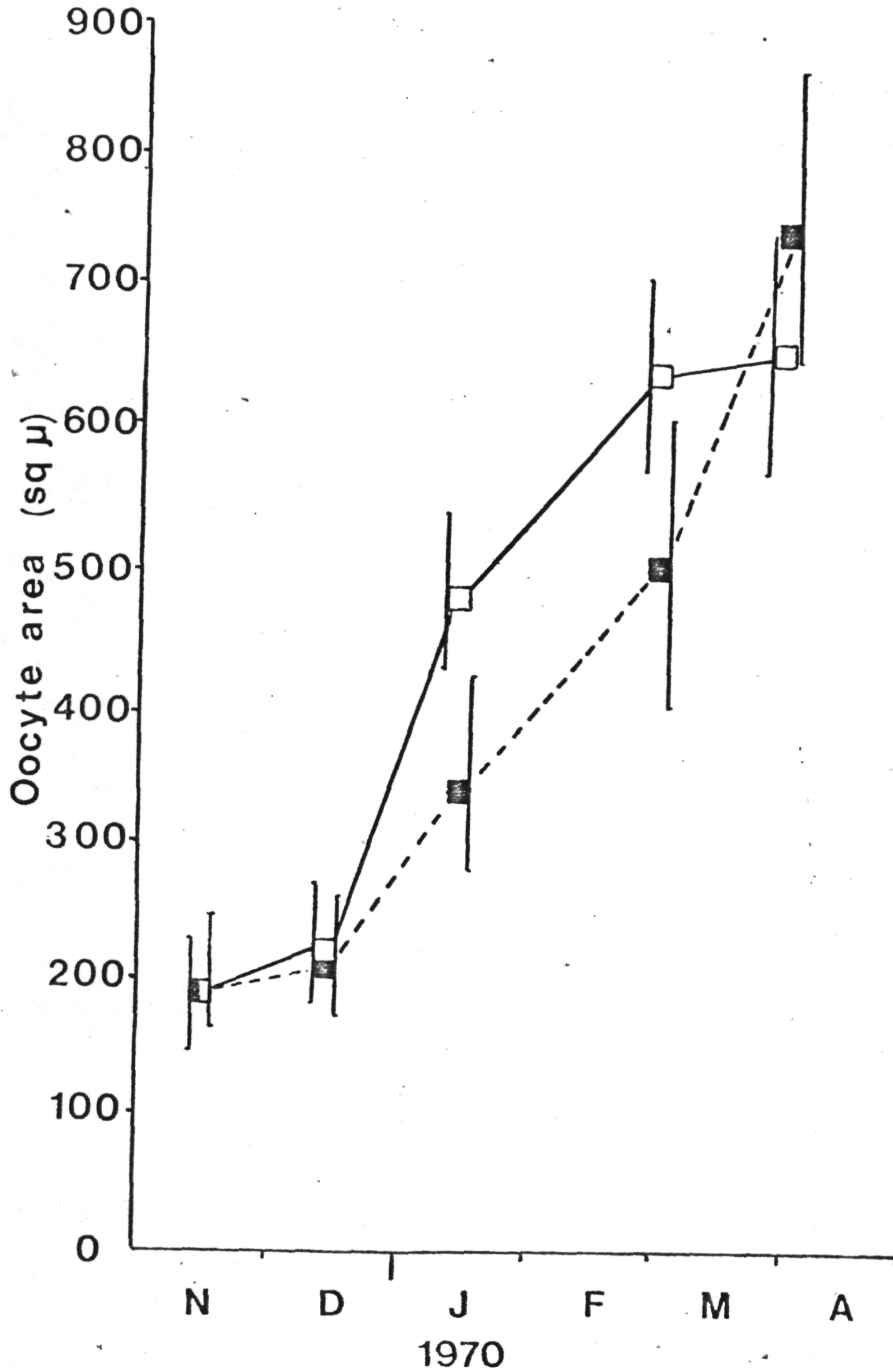


Fig. 6. Oocyte growth at Killowen Pt. —☐— and Narrow Water —■—

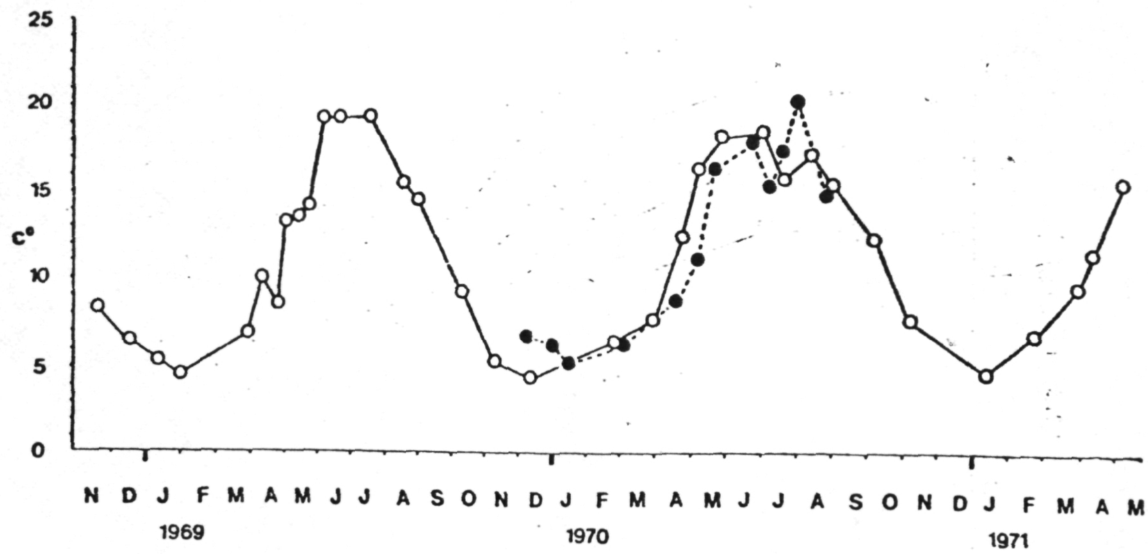


Fig. 7. Sea temperature in Carlingford ——O—— and Belfast Loughs. —— • ——

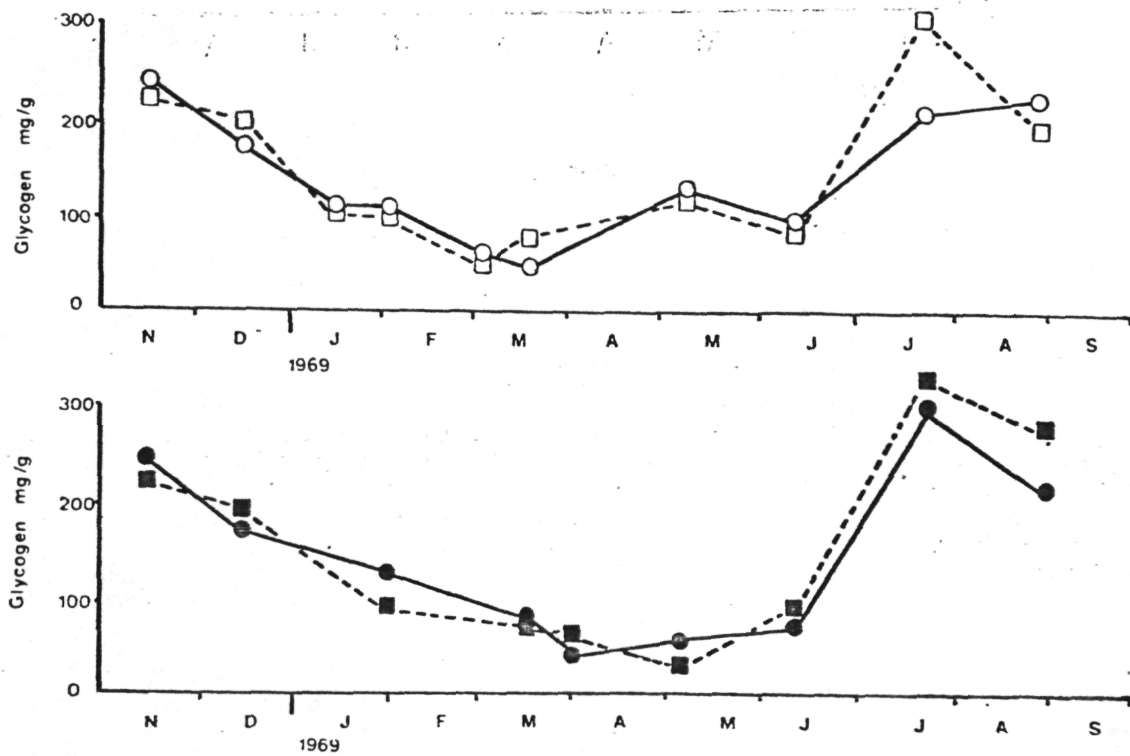


Fig. 8. Seasonal variation in glycogen content of mantle tissue at:

——O—— Greencastle; ——□—— Killowen Pt.;

—— • —— Rostrevor; ——■—— Narrow Water.

150
100
Lipid (mg/g)
50
0
J F M A M J J A S
1969

Fig. 9. Seasonal variation in lipid content of mantle tissue at:

—O— Greencastle; —□— Killowen Pt.;

—•— Rostrevor; —■— Narrow Water.

Despite heavy spawnings relatively few young mussels (plantigrades) were found on either the algae or the rope substrates (Fig. 11). Primary settlement on the algae occurred mainly over the summer and winter months even though a low background level persisted more or less throughout the year. Those settling in summer generally appeared 2-4 weeks after spawning and consisted chiefly of small individuals 250-300 μ in length. Settlements in the winter, however, consisted of larger mussels, mostly over 500 μ and could not be related to any particular spawning period for this locality. It seems likely that these settlements are due to movement of plantigrades from other sites of primary attachment. Experiments during 1969 showed that the average growth of early plantigrades (500-1000 μ) was 27.0 $\pm$ 3.8 μ/day. Assuming mussels settle on the algae when they are about 250 μ and leave at 1500 μ their period of attachment would be about 5-6 weeks. The gradual reduction in numbers of plantigrades on the algae in late summer corresponds to the settlement of later plantigrades on the rope.

Although these data concerning mussel settlement in Carlingford Lough are rather inconclusive they by no means contradict the concept of a primary and secondary phase of settlement previously described and discussed in some detail by Bayne (1964) and Seed (1969)

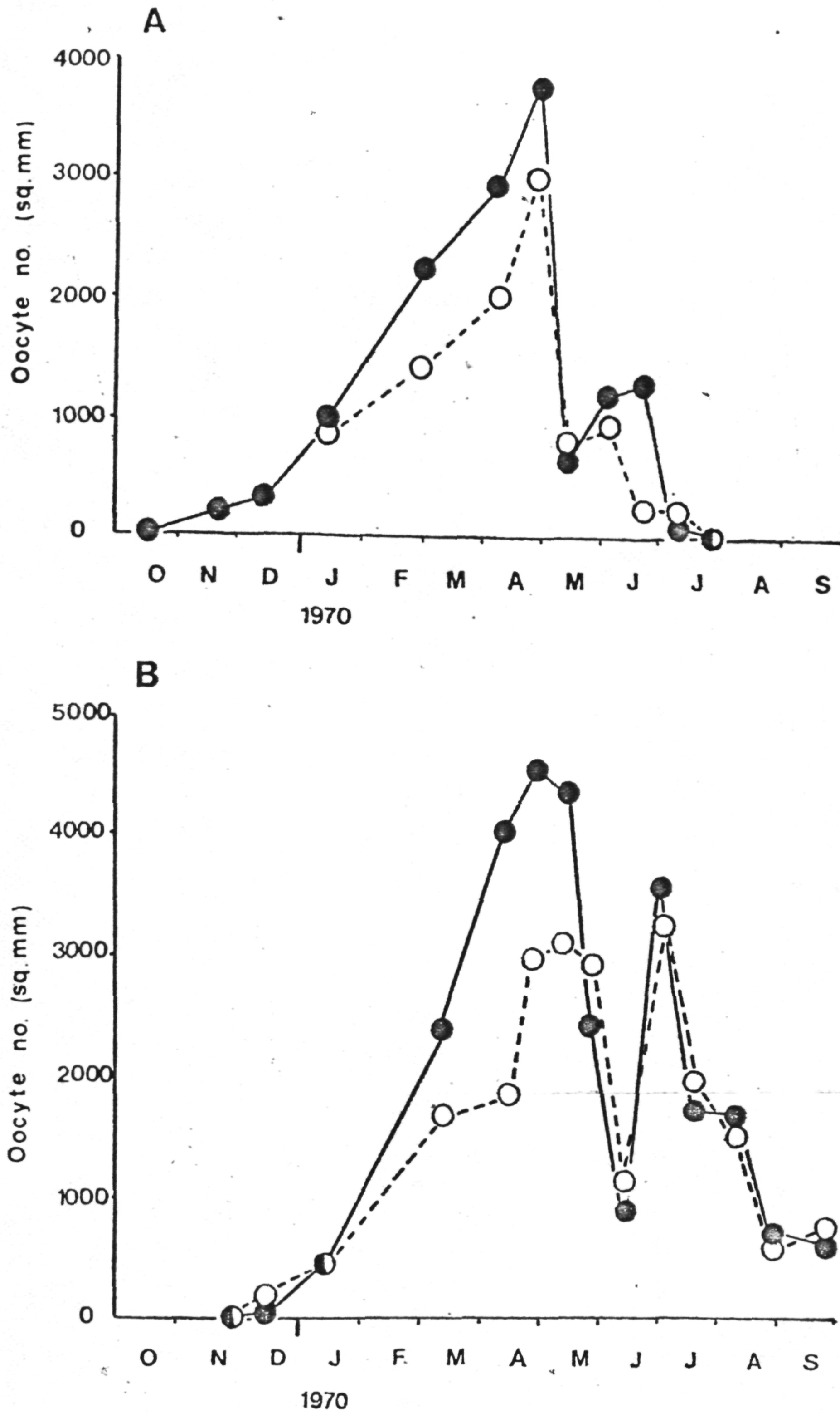


Fig. 10. Density of oocytes in (A) the Rostrevor and (B) the Holywood populations.

—•— Low Shore; —O— Mid shore.

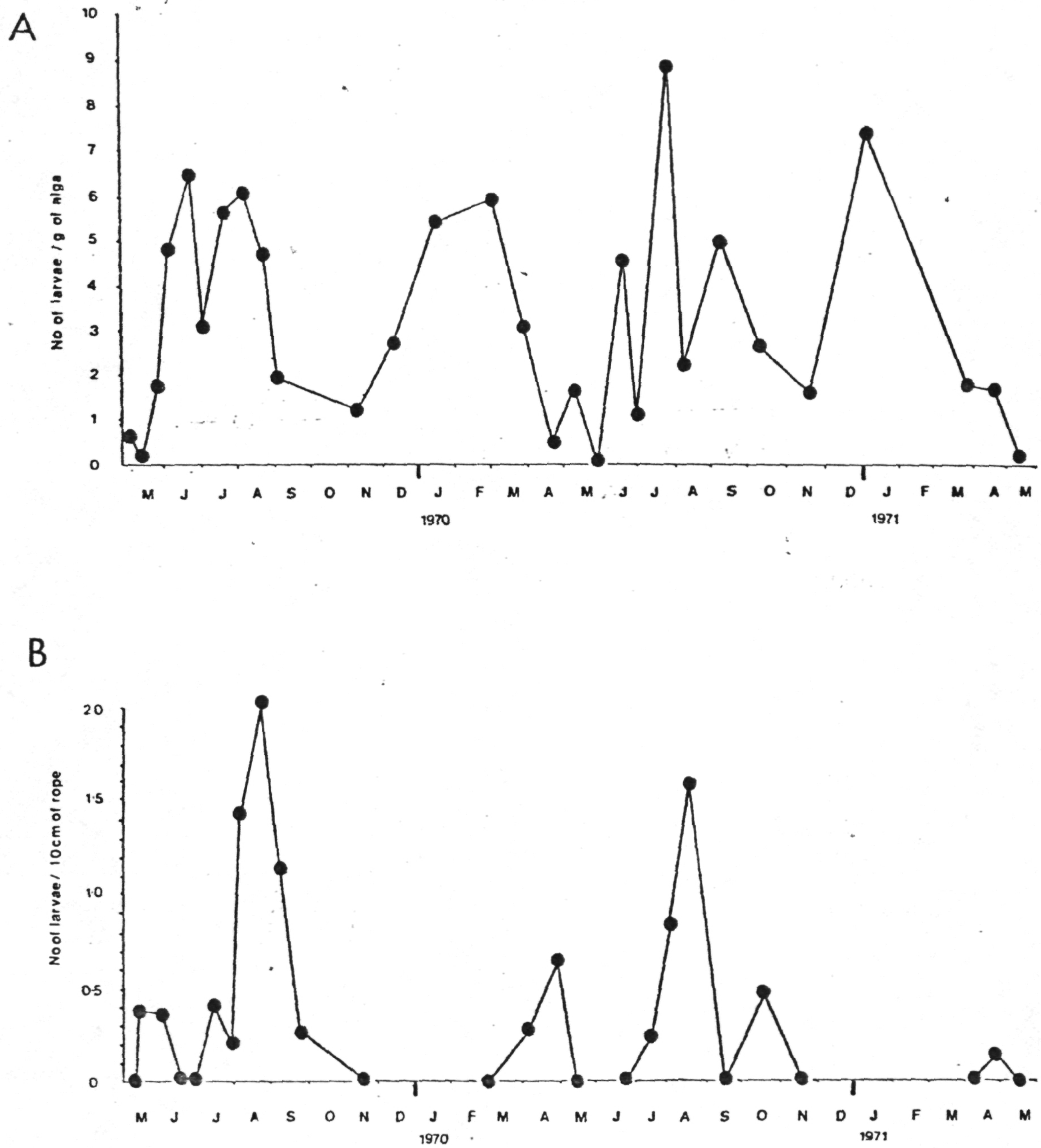


Fig. 11. Average density of (A) early plantigrades on *Polysiphonia* in the midshore and (B) late plantigrades on artificial rope substrates in the low shore at the four Carlingford stations.

Discussion

It is apparent from observations of the breeding cycle of *Mytilus* in Carlingford Lough that three basic processes in the gonad lead successively to the production of ripe gametes. Prior to the initiation of gametogenesis the animal accumulates food reserves in the gonad. This is followed by development of the gametes which are eventually released during spawning. Each of these processes is closely linked with the others; changes in the rate or duration of one ultimately affecting the entire cycle.

Accumulation of glycogen and lipid is maximal during stage 0 when the gonad is little more than a matrix of connective tissue containing small islands of rudimentary reproductive tissue. Increases are also observed during stage 3C when gametogenesis is renewed between periods of spawning. The concentration of glycogen accumulated at stage 0 varied little from one population to another. Renzoni (1960) observed that the amount of glycogen stored in the mantle of *Mytilus galloprovincialis* is proportional to the number of vesicular cells in the interstitial tissue, while Ansell, Loosmore and Lander (1964) stated that in *Venus mercenaria* change in the relative proportions of gonad and other body tissues results in change in the carbohydrate: protein ratio of the whole animal. Thus, it seems probable that in favourable feeding conditions accumulation of glycogen leads to a proliferation of cells rather than elevated levels in individual cells. Conversely, Ingle (1949) found a poor correlation between glycogen content and the dry weight condition index in oysters of low vigour.

As gametogenesis proceeds, glycogen and lipid levels drop. The maintenance of gametogenesis during winter must be attributed in the most part to the utilisation of reserves. During this period the number and volume of gametes in the mantle increases steadily while the body weight of the animal decreases. The relatively small decreases in total lipid concentration in mantles developing large numbers of gametes suggests that lipid is incorporated directly into the gametes. This is most evident in the females where large quantities of lipid are deposited in the maturing oocytes (see Timon-David and Ceresola, 1935; Giese, 1966).

The quantity of glycogen and lipid stored before gametogenesis must ultimately determine the number of gametes produced. Animals living on the mid-shore, although capable of normal gametogenesis and spawning, do not produce as many gametes as those on the low-shore. Similarly, reduced feeding periods due to salinity variations at Narrow Water may be responsible for low oocyte densities at this station. Ingle and Dawson (1930) showed that fluctuations in salinity hinder the accumulation of glycogen in *Crassostrea virginica*, while Bourcart and Lubet (1965) found that the period during which reserves are built up in *Mytilus galloprovincialis* is prolonged by unfavourable feeding conditions in general. Moreover, Walne (1964) states that oysters in "good condition" have an egg production up to 50% higher than those of equivalent size in "poor condition".

The second process to be considered is that of gametogenesis. While the number of gametes is dependent on the quantity of reserves stored during the recovery period, the rate of gametogenesis is controlled mainly by prevailing environmental conditions. Ansell, Lander, Coughlin and Loosmore (1964) found that exposure to warm water from the cooling outfalls of electricity generating stations produced an earlier build up of "spawning potential" than in populations living at normal temperatures. While Loosanoff (1945) induced precocious gonad development in oysters in winter by exposure to high temperatures, Loosanoff and Davis (1952) found that gametogenesis in *Crassostrea virginica* and *Venus mercenaria* was slowed down by transplanting animals from Long Island Sound to the colder waters of Maine. Bayne (1965) halted gametogenesis in *Mytilus edulis* by lowering the temperature to 5°C. No resorption of the gametes occurred within 12 months.

Loosanoff (1950, 1952) found that normal gonad development in *Crassostrea virginica* was halted when the salinity of the medium was depressed below 7.5‰. Oysters kept at 10-12‰ ripened but were less advanced than control animals kept at 27‰. A similar reduction in the rate of gametogenesis occurs in the Narrow Water population where salinities show considerable variation. It is not clear, however, whether this reduction is brought about by osmotic stress or a reduction in food levels. Although egg numbers are lower at Narrow Water the size of the eggs is not significantly greater than at stations with higher salinities. Eggs produced by the gastropod *Neritina fluviatilis* in a brackish water habitat, while being fewer, are larger than in marine populations (Bondesen, 1940).

No differences were found between the rates of gametogenesis in mature animals of different sizes. Seed (1969) showed that the gonad index in samples including very small mussels is usually somewhat lower at any particular time due to the presence of virgin animals or those with a rudimentary genital system. Chipperfield (1953) found no difference in the time of maturation in mussels of different sizes. On the other hand, Jensen and Sparck (1934) observed that the gonads of smaller, younger individuals mature later than those of larger animals. Walne (1964) points out that older oysters may possibly exhibit a decreasing fertility which is not attributable to condition.

There is no evidence that parasitic castration occurred in the Carlingford populations. Seed (1969) observed some cases of inhibition of gametogenesis in *Mytilus edulis* due to infestation by sporocysts of *Bucephalus* spp. According to Meyer-Waarden and Mann (1954) and Mann (1956) gonad weights of individuals infested with the copepod *Mytilicola intestinalis* were 10 to 30% less than those of non-parasitised mussels. Field (1922) and Sprague (1965) found *Mytilus* eggs infected by the haplosporidian, *Chytridiopsis mytilovum*. The parasite was highly prevalent in some of Sprague's samples although the proportion of infected eggs to normal eggs in any individual was low. Inhibition of normal gonad development in oysters due to infestation by the fungus *Dermocystidium marinum* has been described by Ray, Mackin and Boswell (1953).

The synchronisation and magnitude of the initial spawning of mussels in neighbouring populations suggests that spawning is induced by an external stimulus common to all stations. Physiological ripeness is not in itself the direct cause of spawning. Loosanoff and Davis (1950) found that strong thermal stimulation in *Venus mercenaria* compelled some individuals to abort eggs which were not fully ripe. Such eggs usually developed into feeble larvae which soon died. Lubet (1956) believed that spawning was due to the interaction of external and internal factors. Ablation of the cerebral ganglia made the animal receptive to spawning stimuli. He concluded that neurosecretion present in the ganglia inhibited spawning irrespective of external stimulation. This may explain why stimuli do not always act with equal effect on all animals.

Various exogenous factors have been reported to induce spawning in *Mytilus edulis*. Field (1922) found that mechanical disturbance was an effective stimulus, while Young (1945) observed that exposure to air as well as shaking induced spawning in *M. californianus*. Direct stimulation of the adductor muscles by wedging open the valves or pricking the muscle tissue was found to be effective by Loosanoff and Davis (1963) Iwata (1951c) concluded that a rapid rise in temperature stimulates spawning while Bayne (1965) used a combination of elevated temperature and chemical stimulation with potassium ions. Chemical stimulation alone was found to be effective by Iwata (1951a, 1951b). Stimulation of spawning by the addition of gametes to the medium has been reported by Young (1945) in *M. californianus* but there is no evidence that this method is effective in the case of *M. edulis*.

The complexity of the environmental regime prevents a precise definition of the factors which stimulate spawning in the natural habitat. Nevertheless, consideration of the conditions prevailing during spawning gives some insight of the roles played by factors which have been shown to induce spawning in the laboratory.

Mussels are capable of detecting very slight mechanical disturbances. Indeed, in its natural habitat the animal is probably frequently disturbed by wave action. It is difficult, therefore, to assess the importance of such disturbances as a stimulus for spawning. Normal spawning in the population living in the extremely sheltered conditions at Narrow Water suggests that mechanical disturbances if indeed important need not be very great. Furthermore, no marked differences were recorded in the mid and low shore populations at Rostrevor and Holywood suggesting that exposure to air is of little importance. Temperature changes, however, seem to affect all populations and spawning began at all stations when temperatures were rising rapidly. The observations of Berner (1935), Chipperfield (1953), Bouxin (1956) and Heinonen (1962) indicate that rising temperature can be correlated with the onset of spawning. Coe and Fox (1942) and Young (1942), on the other hand, found no definite evidence that spawning in *M. californianus* is induced by temperature or temperature changes. Moreover, it is not clear whether a rise in temperature induces spawning or merely sensitises the animal to other stimuli. Young (1942) and Berner (1935) also recorded marked changes in salinity directly before spawning. In the present investigation, however, no correlation between spawning and salinity variations were noted. The presence of a lunar rhythm in spawning as suggested by Korringa (1947) and Lubet (1956) was not observed in the present investigation.

Following fertilisation, the larvae enter a planktonic phase. Rees (1954) records large numbers of *Mytilus* larvae more than 200 miles from land, while Mass Geesteranus (1942) considered larvae to be extant in most areas. Dispersion of larvae is so effective that it is frequently impossible to correlate their presence with the spawning periods of populations in the same locality. However, most spawnings in Carlingford Lough are followed 3 to 4 weeks later by peaks in the primary settlement of plantigrades. Bayne (1964, 1965) observed that a mobile foot becomes functional in larvae 260 to 265 μ in length, and it is during this pediveliger stage that larvae are capable of primary settlement. Bayne has stressed that size rather than age is the criterion for settlement which can be delayed in the absence of suitable substrates for as long as 70 days depending on environmental conditions. The maximum shell length reached by such larvae was 332 μ. Settlements during the summer contain large numbers of plantigrades measuring 250 to 300 μ. In the winter, on the other hand, large numbers of larvae over 500 μ settle on the alga. Their size clearly rules out any possibility that they may have delayed settlement since the summer and it is probable that such settlements are due to migrations from

other primary sites of attachment. Seed (1969) suggests that sites of temporary attachment could provide reservoirs of plantigrades from which varying numbers might migrate at any time of year. As their original settlement site is unknown, no explanation can be offered as to why the early plantigrade phase is prolonged. However, Bayne (1965) has shown that growth can be reduced or temporarily halted without any permanent damage to the larvae by low temperatures, food type and concentration and low salinities. Such factors might prolong the time of attachment to the alga, while liberation of plantigrades in winter might be due to certain species of algae dying back at that time of year (Seed, 1969).

The gradual reduction in the number of plantigrades on the algae during late summer and winter corresponds to the settlement of plantigrades over 500 μ on rope substrates. Early plantigrades are generally found attached to branches of the alga with larger individuals tending to aggregate on the thicker filaments whilst late plantigrades are invariably found in the crevices between the strands of the rope. Thus, a change appears to occur in the preferences of growing plantigrades from filamentous substrates to grooves and crevices. Although there is no direct proof that plantigrades move from algae to secondary settlement sites on the adult beds, these observations in no way contradict this hypothesis.

The absence of plantigrades at Narrow Water during the period that records were kept for this station may be due to the heavy accumulation of silt on the alga and ropes. Both Verwey (1954) and Galtsoff (1959) found that a layer of silt on the substrate prevents larval attachment. Furthermore, Loosanoff (1961) observed that high concentrations of silt in suspension cause high mortality among oyster and clam larvae. The salinity regime of this station may also interfere with the normal settlement and survival. Chanley (1958), Davis and Ansell (1962) and Davis and Calabrese (1964) have shown that in several bivalve species including *M. edulis* low salinities inhibit normal growth. Moreover, the combination of silt and low salinities may place the larvae at a considerable disadvantage in competing with the adult population at this station.

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APPENDIX.

TABLE 1 : Distribution of gonad stages in samples of *M. edulis* from the low shore at Greencastle.

Date	No.	Percentage of sample at stage: 0	1	2	3A	3B	3C	3D	Index
1968									
25 Nov.	20	—	—	45.0	55.0	—	—	—	255
17 Dec.	20	—	—	35.0	65.0	—	—	—	265
1969									
13 Jan.	20	—	—	5.0	95.0	—	—	—	295
3 Feb.	20	—	—	5.0	95.0	—	—	—	295
5 Mar.	42	—	—	9.5	90.5	—	—	—	290
1 Apr.	31	—	—	—	100.0	—	—	—	300
14 Apr.	50	—	—	—	24.0	76.0	—	—	224
25 Apr.	35	—	—	—	—	—	100.0	—	300
8 May	41	—	—	—	—	—	100.0	—	300
19 May	37	—	—	—	—	—	100.0	—	300
30 May	39	—	—	—	—	12.8	87.2	—	287
11 June	51	—	—	—	—	74.5	25.5	—	226
24 June	45	—	—	—	—	—	100.0	—	300
7 July	44	47.7	—	—	—	—	20.4	31.9	93
24 July	45	77.9	—	—	—	—	22.1	—	66
28 Aug.	45	—	75.6	—	—	—	24.4	—	149
8 Sept.	50	—	60.0	—	—	—	—	40.0	100
17 Nov.	33	—	18.2	39.4	42.4	—	—	—	224
18 Dec.	38	2.6	—	26.3	71.1	—	—	—	266
1970									
17 Jan.	38	—	—	31.6	68.4	—	—	—	268
2 Mar.	37	—	—	—	100.0	—	—	—	300
7 Apr.	35	2.9	—	—	97.1	—	—	—	291
1 May	40	—	—	—	87.5	12.5	—	—	288
15 May	36	—	—	—	—	—	100.0	—	300
3 June	40	—	—	—	—	5.0	95.0	—	295
24 June	34	—	—	—	—	41.2	26.4	32.4	194
10 July	27	11.1	—	—	—	22.2	18.5	48.2	148
30 July	29	58.8	—	—	—	—	10.3	30.9	62
18 Aug.	38	76.4	13.1	—	—	—	10.5	—	45
7 Sept.	45	13.3	44.5	28.9	—	—	—	13.3	116
22 Oct.	34	6.0	6.0	45.4	42.6	—	—	—	225
23 Nov.	46	4.4	—	58.6	37.0	—	—	—	228
1971									
2 Mar.	36	—	—	—	100.0	—	—	—	300
4 Apr.	41	—	—	—	100.0	—	—	—	300
21 Apr.	45	—	—	—	—	—	100.0	—	300
19 May	38	—	—	—	—	2.6	97.4	—	297

TABLE 2: Distribution of gonad stages in samples of *M. edulis* from the low shore Killowen Point.

Date	No.	Percentage of sample at stage: 0	1	2	3A	3B	3C	3D	Index
1968									
25 Nov.	20	—	—	70.0	30.0	—	—	—	230
17 Dec.	20	—	—	55.0	45.0	—	—	—	245
1969									
13 Jan.	20	—	—	30.0	70.0	—	—	—	270
3 Feb.	20.	—	—	25.0	75.0	—	—	—	275
5 Mar.	39	—	—	—	100.0	—	—	—	300
1 Apr.	34	—	—	—	100.0	—	—	—	300
14 Apr.	37	—	—	—	86.5	13.5	—	—	287
25 Apr.	33	—	—	—	—	—	100.0	—	300
8 May	27	—	—	—	—	11.1	88.9	—	289
19 May	22	—	—	—	—	100.0	—	—	200
30 May	40	—	—	—	—	42.5	57.5	—	258
11 June	32	—	—	—	—	37.5	62.5	—	263
24 June	39	2.6	—	—	—	—	23.1	74.3	144
7 July	27	44.5	—	—	—	—	11.0	44.5	78
24 July	39	100.0	—	—	—	—	—	—	0
28 Aug.	21	42.8	57.2	—	—	—	—	—	57
8 Sept.	36	—	41.7	58.3	—	—	—	—	158
17 Nov.	38	—	18.3	58.0	23.7	—	—	—	205
18 Dec.	42	—	—	11.9	88.1	—	—	—	288
1970									
2 Mar.	57	—	—	—	100.0	—	—	—	300
7 Apr.	42	—	—	—	100.0	—	—	—	300
1 May	40	—	—	—	82.5	17.5	—	—	283
15 May	50	—	—	—	—	100.0	—	—	200
3 June	31	—	—	—	—	3.2	96.8	—	297
24 June	36	—	—	—	—	41.6	47.2	11.2	236
[illegible] July	24	66.7	—	—	—	—	20.8	12.5	75
[illegible] Aug.	25	84.0	—	—	—	12.0	—	4.0	28
7 Sept.	49	40.0	28.0	30.0	—	—	—	2.0	90
[illegible] Nov.	35	—	62.9	37.1	—	—	—	—	237
1971									
[illegible] Jan.	49	—	—	30.5	69.5	—	—	—	270
2 Mar.	35	—	—	—	100.0	—	—	—	300
4 Apr.	37	—	—	—	100.0	—	—	—	300
21 Apr.	44	—	—	—	—	—	100.0	—	300
[illegible] May	32	—	—	—	—	—	96.4	3.1	293

TABLE 3 : Distribution of gonad stages in samples of *M. edulis* from the low shore Rostrevor.

Date	No.	Percentage of sample at stage:							Index
		0	1	2	3A	3B	3C	3D	
1968									
25 Nov.	20	—	—	60.0	40.0	—	—	—	240
17 Dec.	20	—	—	50.0	50.0	—	—	—	250
1969									
3 Feb.	20	—	—	20.0	80.0	—	—	—	280
5 Mar.	28	—	—	17.9	82.1	—	—	—	282
1 Apr.	33	—	—	—	100.0	—	—	—	300
14 Apr.	27	—	—	—	85.3	14.7	—	—	285
25 Apr.	40	—	—	—	—	5.0	95.0	—	295
8 May	32	—	—	—	—	—	100.0	—	300
19 May	40	—	—	—	—	65.0	35.0	—	235
30 May.	37	35.2	—	—	—	—	18.8	46.0	102
11 June	33	54.5	—	—	—	—	24.2	21.3	94
24 June	35	57.2	—	—	—	—	22.8	20.0	88
7 July	35	71.5	—	—	—	—	17.1	11.4	63
24 July	35	54.3	—	—	—	17.1	2.9	25.7	69
28 Aug.	35	42.8	42.8	—	—	—	—	14.4	57
8 Sept.	42	—	47.6	47.6	4.8	—	—	—	157
17 Nov.	33	—	27.1	45.8	27.1	—	—	—	200
18 Dec.	30	3.3	—	60.0	36.7	—	—	—	230
1970									
17 Jan.	44	—	—	45.5	54.5	—	—	—	255
2 Mar.	48	4.2	—	—	95.8	—	—	—	287
7 Apr.	32	6.3	—	—	93.7	—	—	—	281
1 May	40	—	—	—	85.0	15.0	—	—	285
15 May	41	2.4	—	—	—	97.6	—	—	195
3 June	34	2.9	—	—	—	5.9	91.2	—	285
24 June	24	—	—	—	—	8.3	41.7	50.0	192
10 July	25	40.0	—	—	—	8.0	36.0	16.0	140
30 July	29	76.0	—	—	—	—	—	24.0	24
18 Aug.	37	78.4	—	—	—	13.5	2.7	5.4	40
7 Sept.	35	29.3	64.8	—	—	—	—	5.9	71
22 Oct.	44	4.6	40.9	54.5	—	—	—	—	150
23 Nov.	31	6.5	9.7	48.4	45.5	—	—	—	233
1971									
18 Jan.	37	—	2.5	51.5	46.0	—	—	—	243
2 Mar.	62	—	—	6.3	93.8	—	—	—	294
4 Apr.	40	—	—	2.5	97.5	—	—	—	298
21 Apr.	45	2.2	2.2	—	—	—	95.6	—	289
19 May	33	—	—	—	—	—	93.9	6.1	288

TABLE 4: Distribution of gonad stages in samples of *M. edulis* from the low shore Narrow Water.

Date	No.	Percentage of sample at stage: 0	1	2	3A	3B	3C	3D	Index
1968									
17 Dec.	20	—	—	80.0	20.0	—	—	—	220
1969									
3 Feb.	29	—	—	27.5	72.5	—	—	—	273
5 Mar.	30	—	—	13.3	86.7	—	—	—	287
1 Apr.	31	—	—	—	100.0	—	—	—	300
14 Apr.	36	—	—	—	22.2	77.8	—	—	222
25 Apr.	40	—	—	—	—	7.5	92.5	—	293
8 May	20	—	—	—	—	10.0	90.0	—	290
19 May	30	—	—	—	—	90.0	10.0	—	210
30 May	30	50.0	—	—	—	—	—	50.0	50
11 June	46	100.0	—	—	—	—	—	—	0
24 June	25	100.0	—	—	—	—	—	—	0
7 July	28	100.0	—	—	—	—	—	—	0
24 July	30	100.0	—	—	—	—	—	—	0
28 Aug.	34	—	100.0	—	—	—	—	—	100
8 Sept.	40	—	90.0	10.0	—	—	—	—	110
17 Nov.	34	—	38.2	61.8	—	—	—	—	162
18 Dec.	31	3.2	—	64.5	32.3	—	—	—	226
1970									
17 Jan.	34	2.9	—	47.1	50.0	—	—	—	244
2 Mar.	22	9.1	9.1	4.6	77.2	—	—	—	250
7 Apr.	27	11.1	—	3.7	81.5	3.7	—	—	259
1 May	41	4.9	—	—	85.3	9.8	—	—	276
15 May	39	5.1	—	—	—	94.5	—	—	190
3 June	39	2.6	—	—	—	2.6	94.8	—	290
24 June	35	31.4	—	—	—	11.4	—	57.2	80
10 July	32	96.9	—	—	—	—	3.1	—	9
30 July	33	100.0	—	—	—	—	—	—	0
18 Aug.	52	78.8	—	—	—	—	5.8	15.4	33
7 Sept.	38	52.7	47.3	—	—	—	—	—	47
22 Oct.	37	—	100.0	—	—	—	—	—	100
23 Nov.	28	7.1	35.7	57.2	—	—	—	—	150
1971									
18 Jan.	31	3.2	6.5	58.1	32.2	—	—	—	219
2 Mar.	30	—	—	12.5	87.5	—	—	—	288
4 Apr.	36	—	—	7.7	92.3	—	—	—	292
21 Apr.	39	2.6	—	5.1	—	—	92.3	—	287
19 May	37	—	—	—	—	—	91.9	8.1	284

TABLE 5 : Distribution of gonad stages in samples of *M. edulis* from the middle shore Rostrevor.

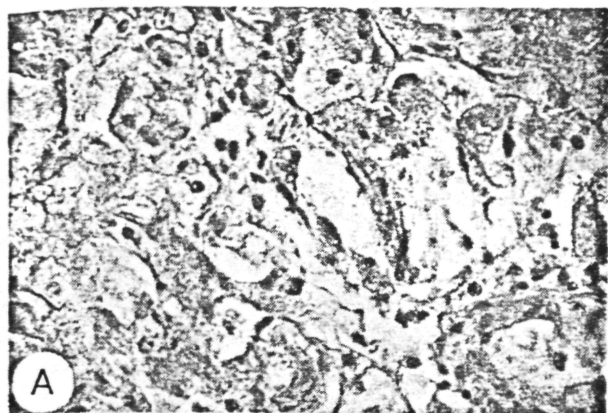
Date	No.	Percentage of sample at stage: 0	1	2	3A	3B	3C	3D	Index
1970									
17 Jan.	26	3.9	11.5	65.4	19.2	—	—	—	200
2 Mar.	47	4.3	—	—	95.7	—	—	—	287
7 Apr.	33	9.1	—	15.4	75.5	—	—	—	257
1 May	41	—	—	—	90.2	9.8	—	—	290
15 May	39	—	—	—	—	100.0	—	—	200
3 June	31	—	—	—	—	3.2	96.8	—	297
24 June	39	—	—	—	—	28.2	35.9	35.9	200
10 July	26	46.2	—	—	—	15.4	19.2	19.2	108
30 July	20	75.0	—	—	—	—	5.0	20.0	35
17 Aug.	79	62.0	—	—	—	19.0	—	19.0	57
7 Sept.	32	43.8	43.8	—	—	—	—	12.4	56

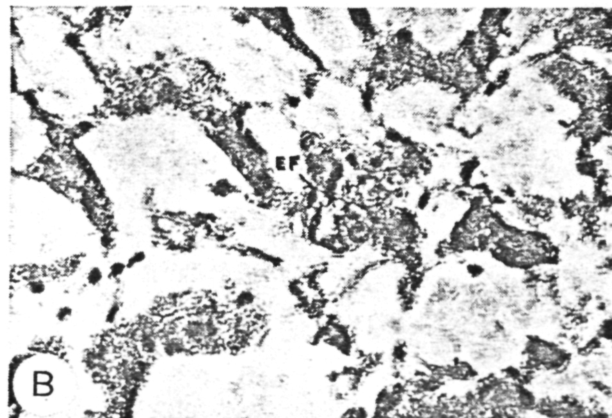
TABLE 6 : Distribution of gonad stages in samples of *M. edulis* from the low shore Holywood.

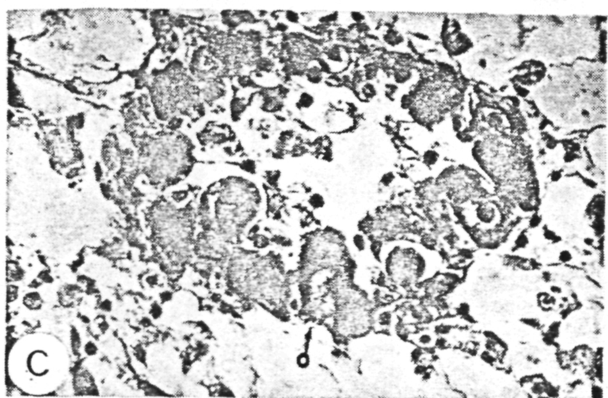
Date	No.	Percentage of sample at stage: 0	1	2	3A	3B	3C	3D	Index
1969									
7 Nov.	33	3.0	27.3	48.5	21.2	—	—	—	188
15 Dec.	30	3.3	26.7	30.0	40.0	—	—	—	207
1970									
12 Jan.	46	21.6	4.4	39.2	34.8	—	—	—	187
12 Feb.	50	4.0	4.0	36.0	56.0	—	—	—	244
12 Mar.	31	6.5	—	3.2	90.3	—	—	—	277
14 Apr.	37	5.4	—	—	94.6	—	—	—	284
27 Apr.	29	3.5	—	—	96.5	—	—	—	290
11 May	37	—	—	—	89.2	10.8	—	—	289
28 May	31	3.2	—	—	—	96.8	—	—	194
16 June	30	—	—	—	—	6.7	90.0	3.3	287
3 July	42	—	—	—	—	—	88.1	11.9	276
23 July	33	—	—	—	—	—	100.0	—	300
10 Aug.	23	13.0	—	—	—	4.4	82.6	—	257
4 Sept.	52	38.5	—	—	—	21.2	26.9	13.4	137

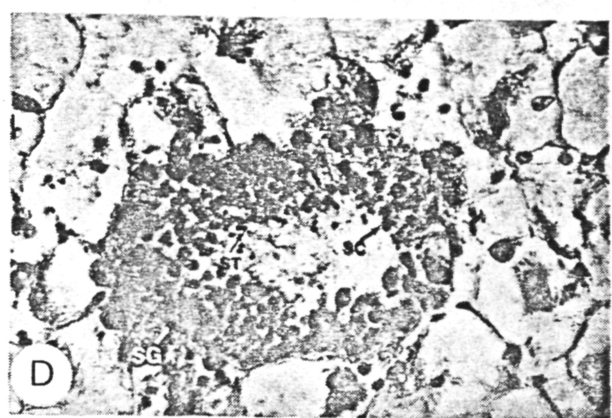
TABLE 7: Distribution of gonad stages in samples of *M. edulis* from the middle shore Holywood.

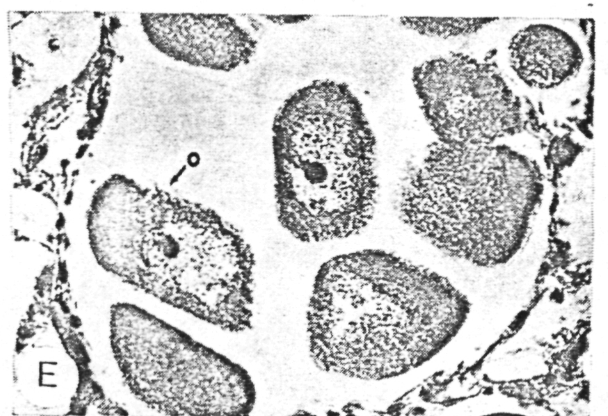
Date	No.	Percentage of sample at stage: 0	1	2	3A	3B	3C	3D	Index
1969									
28 Nov.	46	21.7	26.1	28.3	23.9	—	—	—	151
15 Dec.	30	3.3	13.3	53.3	30.1	—	—	—	210
1970									
12 Jan.	38	13.2	13.2	50.0	58.3	—	—	—	184
13 Feb.	24	—	12.5	29.2	23.6	—	—	—	246
12 Mar.	27	—	—	18.5	81.5	—	—	—	282
14 Apr.	57	—	—	3.5	96.5	—	—	—	297
27 Apr.	52	1.9	—	—	98.1	—	—	—	294
11 May	37	—	—	—	94.6	5.4	—	—	295
28 May	41	—	—	—	—	100.0	—	—	200
16 June	29	—	—	—	—	3.5	96.5	—	297
3 July	34	—	—	—	—	—	100.0	—	300
23 Aug.	21	4.8	—	—	—	4.8	85.6	4.8	271
13 Sept.	31	12.9	—	—	—	12.9	74.2	—	248
4 Oct.	49	8.2	—	—	—	34.7	28.5	28.5	184

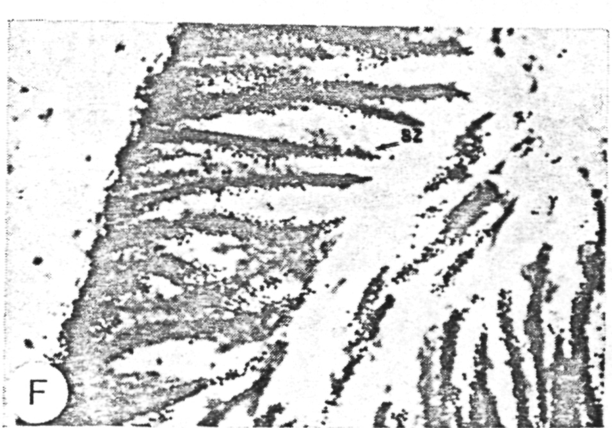












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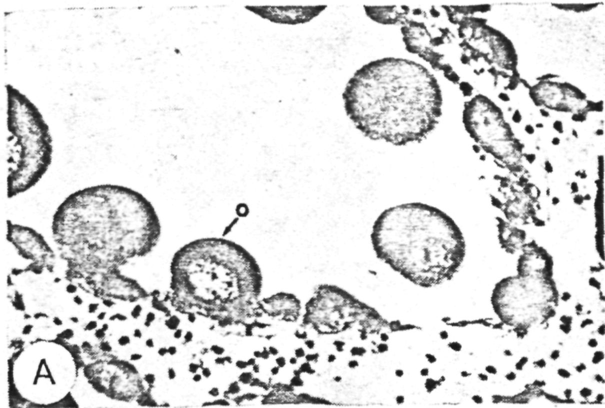

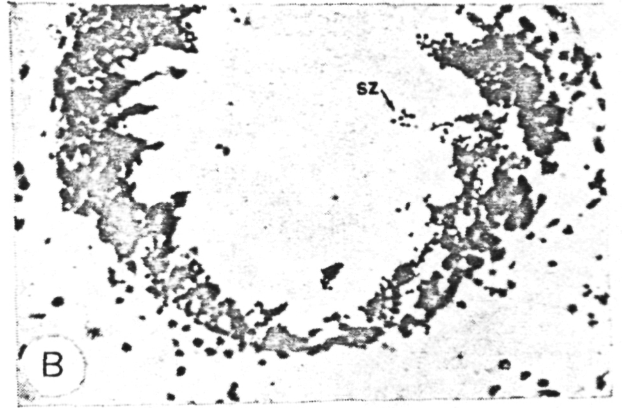

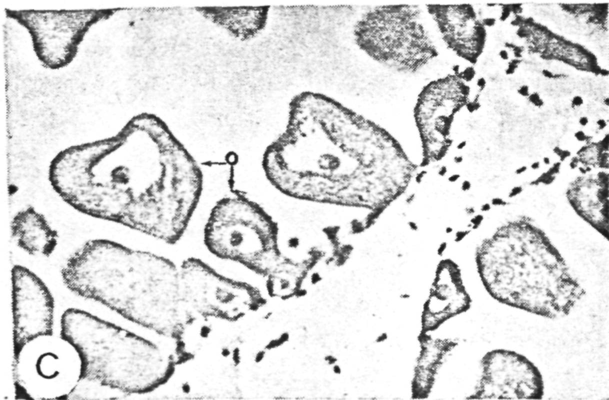

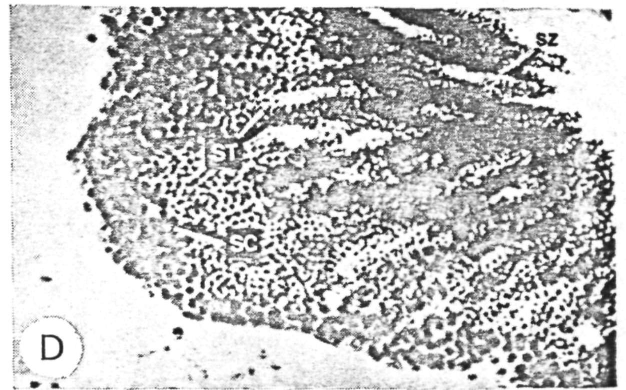

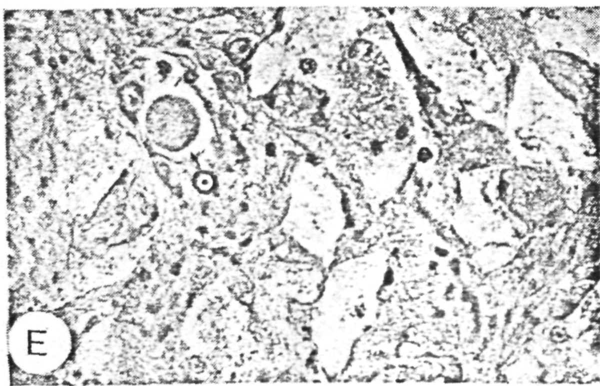

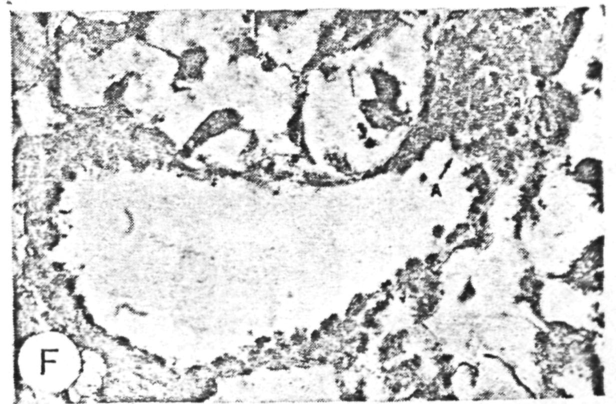

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