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SETTLING, GROWTH AND MORTALITY OF YOUNG BIVALVES IN THE ØRESUND

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ABSTRACT

The quantitative aspects of the settling of 11 bivalve species were registered in the Øresund, based on bottom samples from two localities. The time of spatfall and the numbers of settling specimens were related to existing data on occurrence of larvae in the plankton. The number per m^2 of settling specimens, the decrease of this number and the growth of the bivalves during the first months after spatfall were calculated. The growth rate in the Øresund seems to be smaller than in most other temperate areas. The possible reasons for this discrepancy are discussed and it is suggested that some of the results previously recorded in the literature on growth of newly settled bivalves are inaccurate on account of inadequate sampling-sieving techniques.

By comparing the number of settling specimens of the same species in the two localities it was confirmed that bivalve larvae are able to make a choice of settling place in nature.

Causes of the heavy decrease in number of spat during the first months after spatfall are discussed.

INTRODUCTION

In 1962 a quantitative investigation of the meiofauna was started in the Øresund. The meiofauna – animals with a body-length of 0.2-2.0 mm (Mare, 1942) – consists of two components, i.e. the permanent members such as harpacticoids, ostracods and nematodes and the temporary ones, i.e. young stages of macrofauna animals.

The main point of interest was the temporary members, as data on early life of macrofauna species were very scanty compared with our knowledge on the later part of their life-cycles.

The identity of a great many of the planktonic larvae in the area was already established, and data on their occurrence and abundance were also available (Thorson, 1946). The macro-fauna itself is well-known in Danish waters both qualitatively and quantitatively. The stages in between – the newly settled and young individuals – have been rather neglected qualitatively and almost totally neglected in the quantitative aspect. That means that we lack information on time of settling, the numbers of settling specimens, their rate of growth and their rate of mortality. Therefore, we started an investigation consisting of quantitative bottom-sampling, quantitative plankton-sampling and hydrographical measurements.

It was our hope that by sampling the larvae in the plankton simultaneously with the newly settled specimens in the bottom we could establish the relation between number of larvae and number of newly settled animals. It was proved, however, during the investigation that the Øresund is unsuited for this purpose on account of the hydrographical conditions.

The plankton investigation and the hydrographical measurements were carried out by Dr. A. Fosshagen and the results were used in a thesis at the University of Bergen (Fosshagen, 1965).

Material from the bottom-sampling has been used in two publications until now: M. Horikoshi: Reproduction, larval features and life-history of *Philine denticulata* (J. Adams) (Mollusca – Tectibranchia). Ophelia, 4: 43-89 (1967) and J. Van der Land: Systematics, zoogeography, and ecology of the Priapulida. Zool. Verh. Leiden. No. 112 (1970).

I am indebted to the late professor Gunnar Thorson, who started the investigation and placed a considerable amount of technical assistance at my disposal. My thanks are due to Dr. K. W. Ockelmann for the use of his unpublished identifications of newly settled bivalves, for information on the size at metamorphosis of the same bivalves, and for critical comments on the manuscript.

MATERIAL AND METHODS

The methods have been described earlier (K. Muus, 1966) but a short review will be given here. The two localities chosen for bottom sampling in the Øresund are rather close to each other, about 1 km in distance (Fig. 1), but different as to substrate and hydrography and, therefore, faunal composition. In the following they are called "18 m" and "27 m" according to depth.

From November 1962 to October 1965 bottom samples were taken every fortnight except during the period 7th January to 21st March 1963 when the boat was unable to leave the harbour because of ice. Every sampling day we took five quantitative bottom samples on each of the two localities. We tried to hit the same spot every time and according to the captain the maximum deviation was less than 100 m. This gave a total number of 300 18 m and 225 27 m samples (the smaller number of 27 m samples is due to a change of locality after the first year, in October 1963).

The instrument used was the mouse-trap constructed especially for quantitative meiofauna sampling (B. J. Muus, 1964). Each sample represented 189 cm² down to at least 2 cm's digging depth. The samples were brought up enclosed in a nylon bag with mesh-size 265 μ. Still in the bag they were gently washed with water from a hose. This proved less damaging to the animals than washing in a traditional sieve.

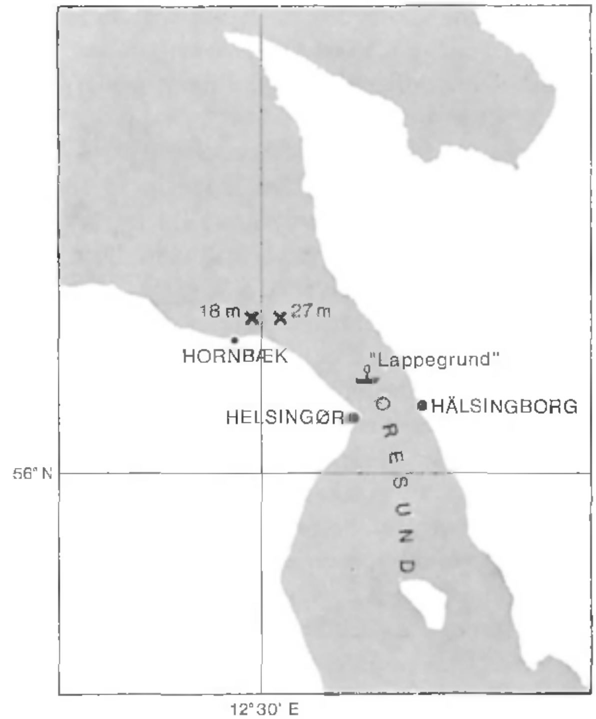

FIG. 1. Map of the area.

In the laboratory the samples were washed once more, this time in distilled water and then preserved in 70 % alcohol. The distilled water was used to remove the salt to preserve the tiny mollusc shells as well as possible. After sorting the molluscs were placed in 96 % alcohol.

The samples were sorted in small fractions under a microscope. All animals were picked out except the Foraminifera, which were sampled separately with the chandelier sampler (Hansen, 1965), and the nematodes.

If the nematodes should have been sorted out the sorting time would have been prolonged considerably and, furthermore, it was unlikely that great numbers of preserved nematodes would ever be identified.

To have a reserve of animals for size analyses etc. a non-quantitative detritus sample was taken with the Ockelmann dredge (Ockelmann, 1964) each sampling day.

Simultaneously with the bottom sampling and in the same area an investigation of the sediments and the distribution of the Foraminifera was carried out (Hansen, 1965). Hansen found three zones of sediment in the depth interval from 6 to 27 m. The bottom sampling localities are placed in zone II (18 m) and zone III (27 m). In zone II the sediments are well sorted and dominated by the two finest sand fractions (250-64 μ). The silt content is less than 1 %. The sediments in zone III are dominated by the finest sand fraction (125-64 μ) and contain about 5 % silt and clay.

Samples from the two localities differed conspicuously to the naked eye as regards both sediment and fauna. Characteristic species in 18 m samples were the anthozoan *Edwardsia longicornis*, the polychaete *Pectinaria koreni*, the bivalve *Venus striatula* and the brittlestar *Ophiura albida*, and in 27 m's it were the anthozoan *Virgularia mirabilis*, the bivalve *Nuculoma tenuis* and the brittlestar *Amphiura filiformis*. Although not dominating numerically these species were almost exclusively found in samples from only one of the two localities.

This paper deals only with the bivalves. The data for presence of bivalve larvae in the plankton have been combined from three investigations in the Øresund. The first by Jørgensen (in: Thorson, 1946), the second by Schram 1959-60 (Schram, 1962) and the third by Fosshagen 1.10.63-16.9.64 (Fosshagen, 1965) simultaneously with the first year of bottom sampling.

Fosshagen collected his plankton samples every fortnight by pumping 1000 l of water from the layer immediately above the bottom at the 18 m locality. The water was filtered through a plankton-net with mesh-size 180 μ, and the larvae were then identified and counted while the sample was still fresh.

The hydrography of the Øresund has been described earlier (e.g. Brattström, 1941). The Øresund has rather unstable hydrographical conditions, but the main characteristics are as follows: It is placed between the brackish Baltic Sea and the more marine Kattegat-North Sea area, and part of the water-exchange between these two areas takes place through the Øresund. Thus the salter water coming from the North follows the bottom and the outgoing brackish water from the Baltic runs in the surface. Normally the discontinuity layer is found at a depth of 10-15 m.

On the 18 m locality hydrographical data were collected in the period September 1963-August 1965 (Horikoshi, 1967). The collecting included measurements of temperature, salinity, oxygen content and current (velocity and direction) at 0, 5, 10, 15 and 18 m's depth. Fig. 2 shows the temperature and salinity values. Brattström (1941) has published the monthly mean values of temperature and salinity at the Lappegrund lightship (see Fig. 1) from the period 1923-1939. The temperature at 20 m's depth can be seen in Fig. 21.

The oxygen content of the water at 18 m's depth was 4-8 ml O_2/l.

Generally the current in all depths is either directed towards WNW or ESE, i.e. following the coast line. At a depth of 0.5 m there were equal numbers of days with ingoing and outgoing currents (24 observations during one year (Fosshagen, 1965)). In 18 m's depth the current was ingoing on 71 % of the observation days during a year. The current velocity measured in the surface varied between 10 and 122 cm/sec. and in 18 m's depth between 7 and 48 cm/sec.

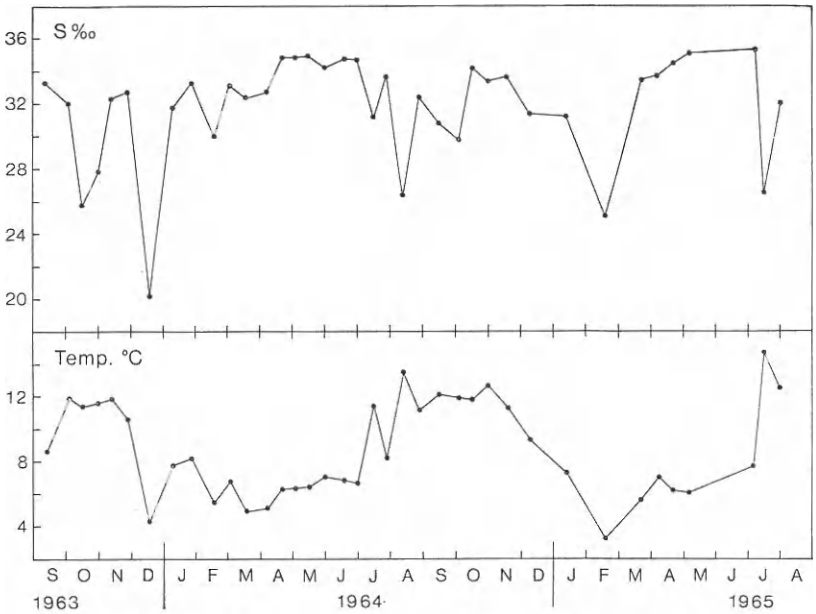

FIG. 2. Salinity and temperature, measured at the 18 m locality 1963-1965.

The bivalves were with a few exceptions identified to species. The complete list of the 47 bivalve species taken in the bottom samples is given in Table 1. Only 11 species occurred in such numbers that it was possible to calculate their growth and mortality. Of these, four species were studied in both localities.

The mesh-size of the bag in which the bottom samples were taken (265 μ) ensured that few if any newly settled bivalves escaped. Thus it was possible to fix the beginning of the spatfall within 14 days (between the last sample without and the first containing newly settled specimens). Dr. K. W. Ockelmann (pers. comm.) has found lately that some of the bivalves in question have a smaller size at metamorphosis than believed when the mesh-size was chosen. This means that the date for start of spatfall for some of the species (four) will not be correct. The size at metamorphosis, according to Dr. Ockelmann's results, is given for each species.

For most species the spatfall will go on continuously for some time with decreasing numbers of new spat appearing on the bottom. It was not possible to single out size groups within the spatfall of a season and it was, therefore, treated as one group in further calculations. The age of the 0-group was recorded counting from the start of the spatfall, as this was the only date possible to estimate.

The length of the bivalves was measured by means of an ocularmicrometer; for specimens smaller than 2.0 mm to the nearest 0.025 mm, for those bigger

TABLE 1. List of bivalve species found as spat in the bottom samples. Encircled cross indicates that only one specimen was taken. *Thyasira* found at 18 m were not identified to species.

	18 m	27 m
Nucula nitidosa Winckworth (*N. nitida* Sowerby)	+	+
Nuculoma tenuis (Montagu)	+	+
Nuculana pernula (Müller)	+	+
Nuculana minuta (Müller)	+	+
Mytilus edulis L.	+	+
Modiolus modiolus (L.)	+	+
Modiolus phaseolinus (Philippi)	+	
Modiolus adriaticus (Lamarck)	+	
Musculus discors (L.)	⊗	
Musculus niger (Gray)	+	+
Musculus tumidus (Hanley) (*Modiolaria marmorata* (Forbes))	+	+
Aequipecten opercularis (L.)		⊗
Palliolum furtivum (Lovén)		⊗
Lima (Limaria) loscombi G. B. Sowerby		+
Thyasira sarsi (Philippi)	?	+
Thyasira flexuosa (Montagu)	?	+
Thyasira (Parathyasira) equalis (Verrill & Bush)	?	+
Lucina (Lucinoma) borealis (L.)		⊗
Kellia suborbicularis (Montagu)	⊗	
Montacuta ferruginosa (Montagu)	+	+
Mysella bidentata (Montagu)	+	+
Cardium (Cerastoderma) sp.	+	+
Arctica islandica (L.)	+	+
Dosinia lincta (Pulteney)	⊗	
Venus (Chamelea) striatula (da Costa)	+	+
Macoma calcarea (Gmelin)	+	+
Tellina tenuis da Costa	+	
Tellina (Fabulina) fabula Gmelin	+	+
Abra alba (W. Wood)	+	+
Abra nitida (Müller)	+	+
Psammobia fervensis (Gmelin)	+	+
Ensis sp. (probably *E. arcuatus* (Jeffreys))	+	
Cultellus pellucidus (Pennant)	+	+
Mactra corallina (L.)	+	+
Spisula elliptica (Brown)	+	+
Spisula subtruncata (da Costa)	+	+
Mya truncata L.	+	+
Mya arenaria L.	⊗	
Corbula gibba (Olivi)	+	+
Hiatella arctica (L.)	+	+
Hiatella striata (Fleuriau)	+	+
Panomya arctica (Lamarck)		+
Saxicavella jeffreysi Winckworth	+	+
Barnea candida (L.)		+
Zirfaea crispata (L.)	+	+
Thracia phaseolina (Lamarck)	+	+
Cuspidaria cuspidata (Olivi)	⊗	

than 2.0 mm to the nearest 0.100 mm. The greatest length was chosen as parameter as it is the easiest measure to obtain and, therefore, the most commonly used in other bivalve growth studies. Thus it will be possible to compare the results with those from other investigations. The bivalves contained in the five samples from the same day and same locality were treated together. The measurements from one date were placed in length-frequency diagrams. A typical example can be seen in Fig. 16.

Based on the length-frequency diagrams the mean length of a certain group was calculated for each date. The mean lengths together with the length of the smallest and biggest specimen in the group can be seen in Figs 3, 5-15, and 17-19.

In a few cases material from the detritus-dredge samples mentioned above has been used to fill out gaps in the quantitative material. These cases are marked differently in the figures.

In some cases members of more than one year-class were found in the samples. The mean lengths were then calculated for each group and the number of specimens in each group is given, converted to number per m^2.

The maximum lengths of the species, obtained in Danish waters, are given in the text. These measures were taken from "Danmarks Fauna" (Jensen & Spärck, 1934).

RESULTS

Montacuta ferruginosa (Figs 3 & 4)

Jørgensen found the larvae of this species in the plankton during July-October and Schram during July-February. Fosshagen found them in July-October with the maximum, 20 specimens per m^3, in August 1964.

The first spat of the season settled on the bottom in August for three years consecutively in both localities, and until the end of January there were still a few newly settled specimens in the samples. Thus for this species there is good agreement between plankton finds and presence of spat in the bottom.

At 27 m the distribution of both spat and older individuals was uneven and the length-frequency diagrams are complex and totally unfit as base for further calculations. An explanation could be found in the association with *Echinocardium* mentioned below.

At 18 m the 1964 spat were abundant and it was possible to estimate the growth and abundance for the first year after settlement. In the beginning of the season, at the end of August, there were 250 spat per m^2 which number increased to $1000/m^2$ at the end of November (Fig. 3). By July 1965 the number had decreased to about $100/m^2$ (based on five 189 cm^2 samples). The growth was therefore calculated for the first year only. The length at metamorphosis is 0.35-0.41 mm; at first appearance in the samples it was 0.4-0.7 mm (mean 0.5),

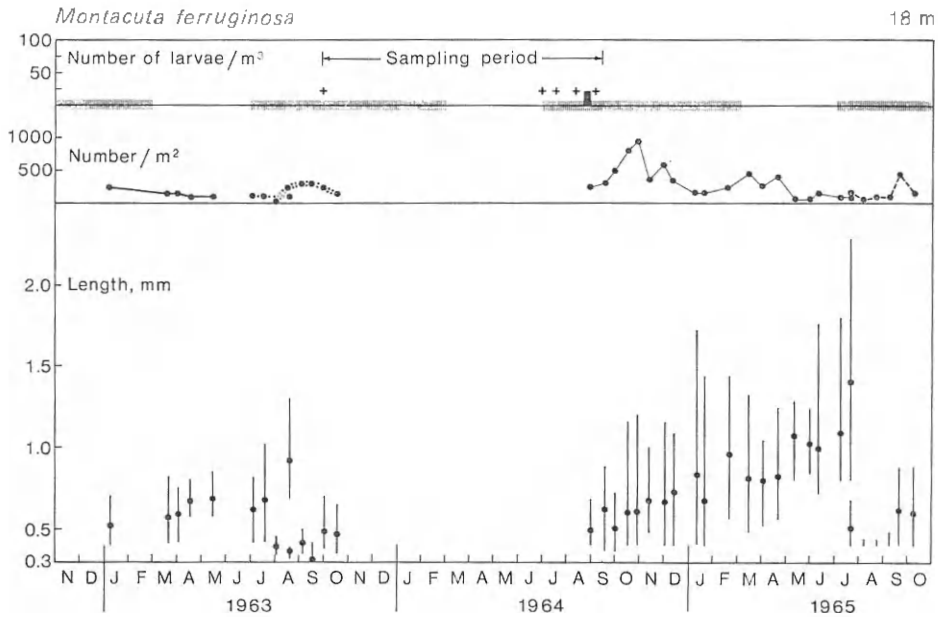

FIG. 3. *Montacuta ferruginosa,* 18 m. Upper part: Number of larvae found in bimonthly plankton samples in October 1963-September 1964 (no samples in Dec. 1963) by Fosshagen (1965). A cross indicates less than 10 larvae per m³. Hacked bars show periods of the year in which larvae have been found by earlier investigators. Middle part: Number of specimens per m² in bottom for each year-class. Lower part: Mean length and size variation for each year-class.

and after 11 months in the bottom it was 0.8-2.3 mm (mean 1.4). The maximum length is 8 mm.

M. ferruginosa is generally considered as commensal with the spatangoids *Spatangus purpureus* and *Echinocardium cordatum,* mainly the last one. *Spatangus* is quite rare in the Øresund, but *Echinocardium* was common in the samples. This association probably affects the distribution of *Montacuta.* Gage (1966, a, b, c) has described the relation between *M. ferruginosa* and *E. cordatum* very thoroughly.

I have never found *Montacuta* attached to *Echinocardium,* nor have I seen aggregations of it from the burrows of the urchin. Most of the *Montacuta*'s found were quite small (1 mm or less), but Gage (1966c) found that the bivalve may attach to an urchin very early in life at a size of only 0.33 mm. Possibly the washing of the samples in distilled water and alcohol had an effect similar to the anaesthetization which Gage used to remove the bivalves from the urchins (1966c, p. 500).

Since the samples yielded no direct evidence of the mentioned association I looked for some indirect evidence. Hence I tried to relate number of *Montacuta*

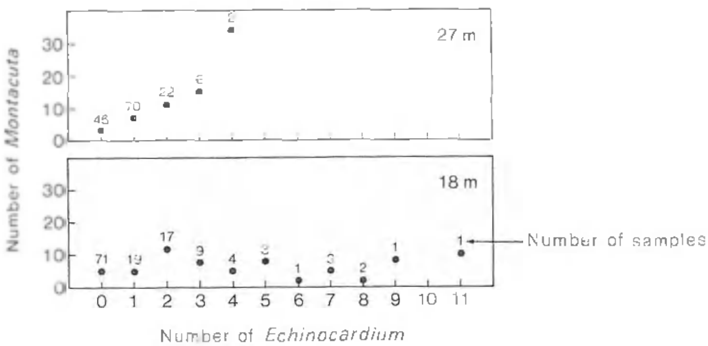

FIG. 4. Average number per sample of *Montacuta ferruginosa* related to number of *Echinocardium cordatum* (length ≧ 10 mm) per sample.

per sample to number of *Echinocardium* of a suitable size, i.e. 10 mm or more in length. From each locality 225 samples were examined. 94 out of the 18 m and 80 of the 27 m samples held neither of the species. The figures for the remaining samples can be seen in Fig. 4.

The distribution of *Montacuta ferruginosa* in relation to number of *Echinocardium* was different for the two localities. In the 18 m samples there was obviously no relation, whereas the 27 m samples clearly showed higher numbers of *Montacuta* with increasing numbers of *Echinocardium*. I will not venture to explain this difference between the samples from the two kinds of bottom. Gage (1966a) has ascertained that *M. ferruginosa* can remain free-living in the substrate for long periods.

Mysella bidentata (Figs 5 & 6)

This species was the most numerous and constantly occurring bivalve species in both localities. The larvae have been found in the plankton during all months except March, April and December. Jørgensen found them from July to November and also in January, Schram from June to November and also in February. Fosshagen found them from July to November and one specimen in May. The maximum occurrence, $70/m^3$, was found in July 1964, and shortly after (also in July) a maximum spat number/m^2 occurred in both localities. The main spatfall in both localities always started in July, a fact which agrees well with the above plankton data. Small numbers of newly settled specimens were present until about December.

At 18 m four year classes could be followed for some time (Fig. 5). The "best" class, i.e. the most numerous, was the 1964 – the "worst" the 1965 class which was few in number and disappeared already in October 1965.

The length at metamorphosis is 0.40-0.55 mm; at first appearance in the

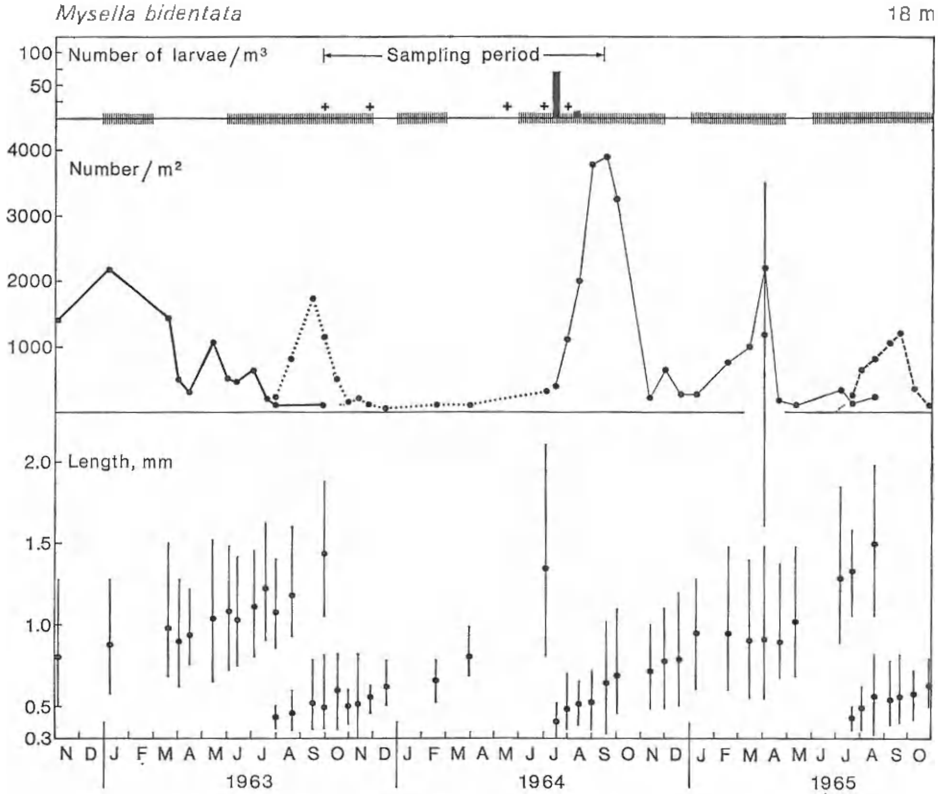

FIG. 5. *Mysella bidentata*, 18 m. For explanation of symbols see Fig. 3.

samples it was 0.3-0.5 mm (mean 0.4) and after about one year in the bottom (August 1965) 1.0-2.0 mm (mean 1.5).

Apparently there was a winter stagnation of growth in 1963 and – more clearly seen – in 1965. However, the number per m² rose in the early summer of 1963 and in the late winter of 1965. Thus it might be implied that this "stagnation" was caused by a new spatfall. The length-frequency diagrams, however, show the same distribution through the period and it must, therefore, have been a true stagnation.

There was a single find in April 1965 of 63 specimens showing that the length after 20 months was 1.6-3.7 mm (mean 2.8). It is possible, however, that this group comprised two inseparable classes (cf. Fig. 6, 27 m).

At 27 m (Fig. 6) it was possible to calculate the growth until *Mysella* was three years old (July 1964). As at 18 m the 1964 year class was very numerous whereas the next was few in number.

The length at spatfall, the time of the main spatfall, and the growth during the first year in the bottom were very much the same as at 18 m.

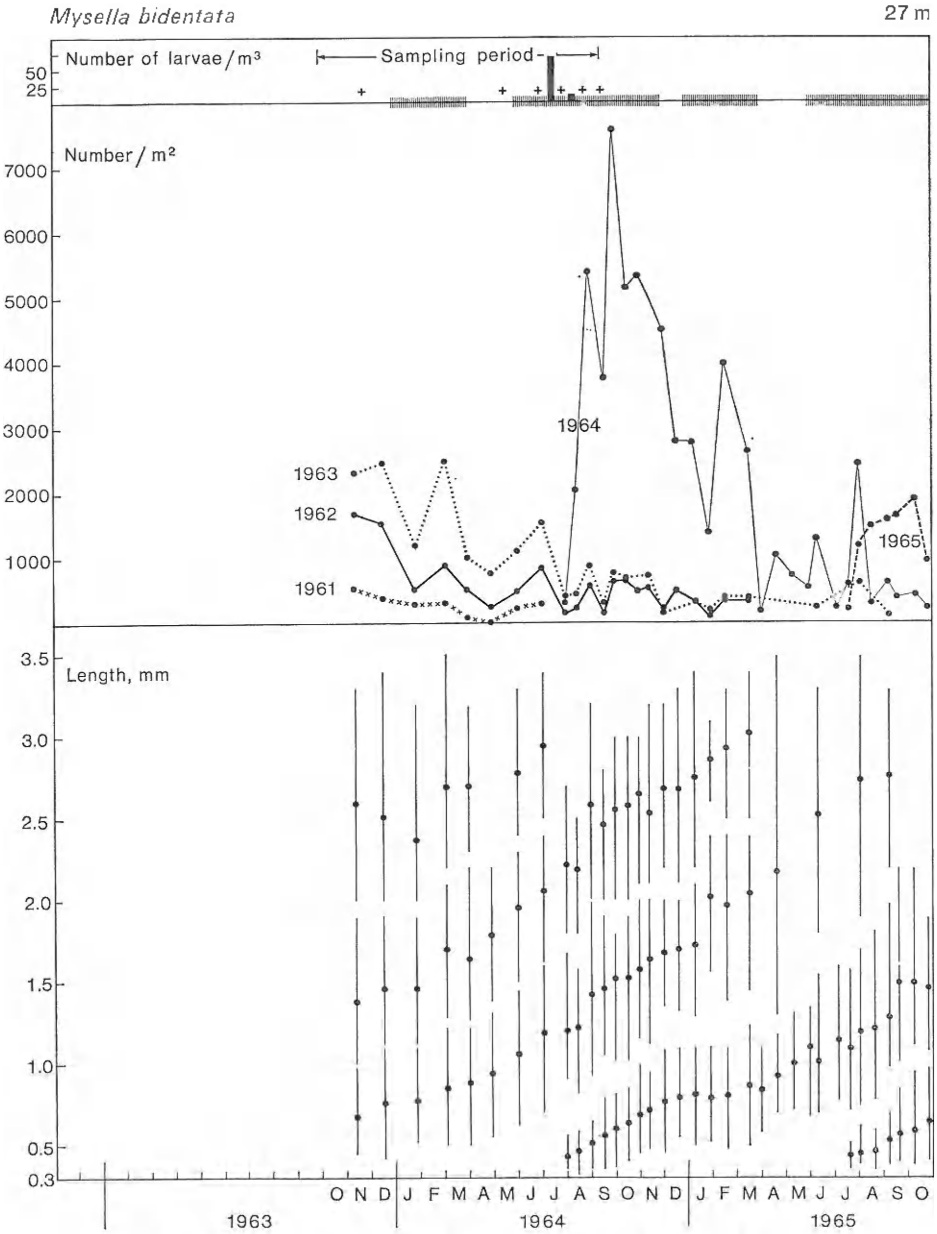

FIG. 6. *Mysella bidentata*, 27 m. For explanation of symbols see Fig. 3.

Two years after spatfall (September 1964) the length was 2.0-2.8 mm (mean 2.5). The length after three years, based on the 1961 year class in the samples from July 1964, can with some hesitation be estimated to be 2.5-3.4 mm (mean 2.95). I hesitate because the specimens got fewer and year class separation more difficult as time passed. In the period April-September 1965 it is thus likely that the oldest group in the figure consists of both the 1962 and 1963 year classes.

If this rate of growth continues the animals will be at least four years old when they reach their maximum length – about 5 mm.

Also at 27 m there was a winter stagnation in 1965.

Arctica islandica (Figs 7 & 8)

The larvae of this species have been found in the Øresund plankton during all months of the year. Jørgensen had the greatest numbers in October and November, but found none in March-July. (His *Venus gallina* was in fact *A. islandica*, Ockelmann, personal communication). Schram found the same period of maximum occurrence and he found larvae in June-July also. Fosshagen found maximum numbers in October ($100/m^3$) and February ($80/m^3$), and he found them in March-May also.

It is remarkable that the larvae found in the plankton from the beginning of October to the end of November 1963 did not cause a spatfall in any of the localities.

At 18 m the first spatfall of the year took place in February and until August there were still a few spat in the samples. In July 1963 a new smaller spatfall took place and this was probably also the case in 1964 but not in 1965.

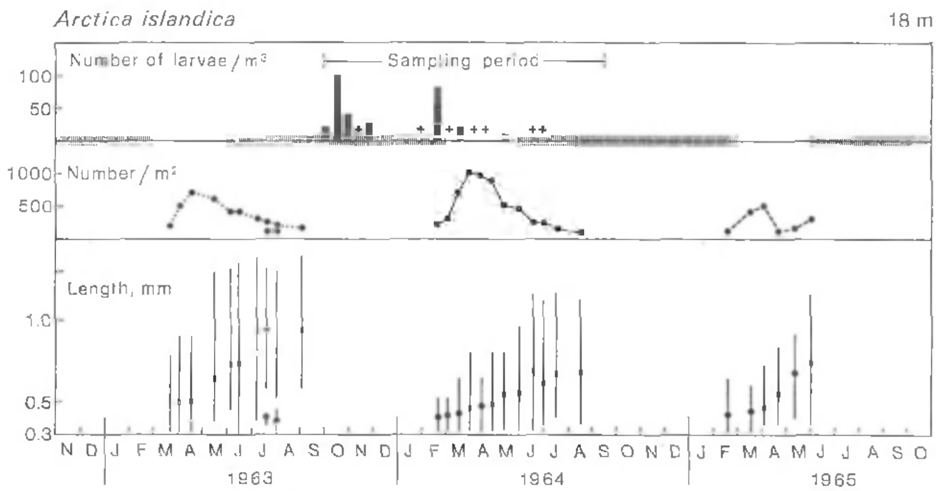

FIG. 7. *Arctica islandica*, 18 m. For explanation of symbols see Fig. 3.

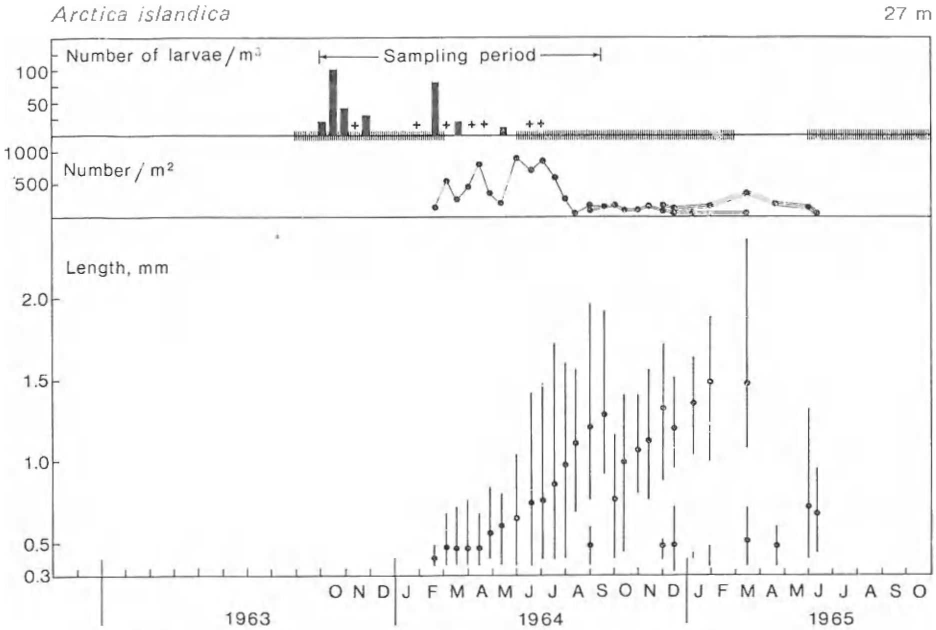

FIG. 8. *Arctica islandica*, 27 m. For explanation of symbols see Fig. 3.

The species was never very numerous in the bottom, only once did it reach 1000/m² (March 1964). The number also diminished rather fast, so it was only possible to calculate growth for about six months. The length at metamorphosis is 0.23-0.30 mm; at first appearance in the samples it was 0.3-0.6 mm (mean 0.4) and after about six months (October 1963) 0.6-1.4 mm (mean 0.9).

The data from 27 m are a bit different. The spatfall of February 1964 was successful and during about seven months the spat grew from 0.4-0.5 mm (mean 0.4) to 0.9-1.9 mm (mean 1.3) which is a somewhat faster growth than at 18 m. In early September there was a new successful and clearly discernible spatfall. The specimens of this group grew even faster, reaching a size of 1.0-1.9 mm (mean 1.5) in five months. It is possible though that this group included a few specimens which started to settle in February. The maximum length of the species is 120 mm.

Venus striatula (Fig. 9)

Quantitative records of *Venus* larvae in the Øresund are almost non-existent. Both Jørgensen and Schram record it, but their specimens belong in reality to *Arctica* (see p. 90). It is probable, however, that some *Venus* were hidden among the *Arctica*'s. When Fosshagen took his samples the identification problem had been solved, and yet he found only one larva in June during one year of sampling.

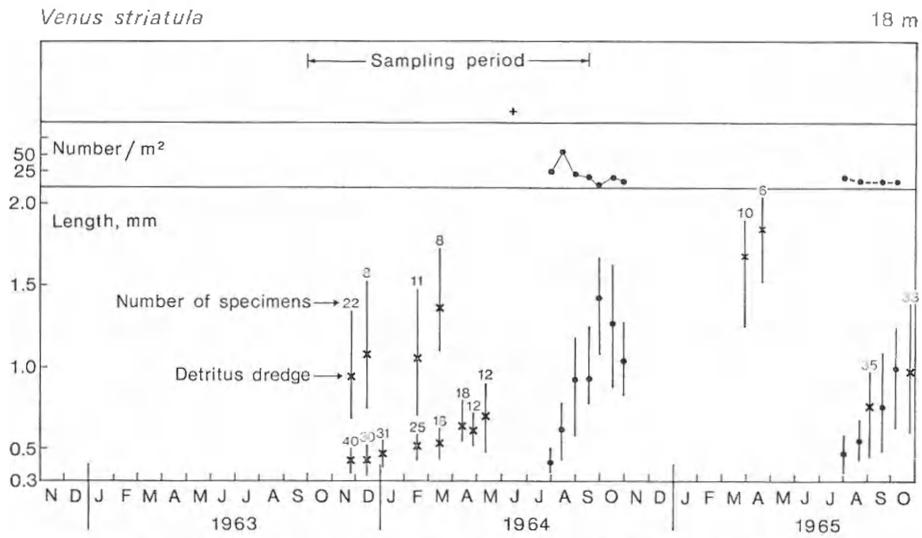

FIG. 9. *Venus striatula*, 18 m. For explanation of symbols see Fig. 3.

The spat also occurred sparingly at all times in the bottom. At 27 m only a few spat were found and even at the 18 m locality, which generally is considered as inhabited by a *Venus* community, 500/m² was the absolute maximum (August 1964) and this number diminished rapidly.

In the detritus dredge samples *Venus* was quite numerous, and the data from these were used as a supplement in the growth calculations. Even with this supplement the growth data are somewhat scanty.

The appearance in the samples at 18 m started in August, both in 1964 and 1965. Seemingly settling was delayed in 1963, probably due to the preceding severe winter. In 1964 and 1965 the spatfall was more concentrated in time than for other bivalve species i.e. no new spat occurred in the samples after August-September.

The length at metamorphosis is 0.23-0.33 mm. If one considers the growth of the spat from August 1964 one finds that the length at first appearance in the samples was 0.35-0.5 mm (mean 0.4) and after about two months (middle of October) it was 0.9-1.6 mm (mean 1.3) i.e. a mean growth of 0.9 mm. The two values from detritus samples taken in April 1965 are based on ten and six individuals only. They indicate that the length was 1.5-2.5 mm (mean 1.85) after about eight months in the bottom.

Compared with other bivalves in the Øresund *Venus* seems to grow rather fast. The more restricted settling period of *Venus* may, however, partly explain this phenomenon.

The maximum length is 34 mm.

Macoma calcarea (Figs 10 & 11)

Larvae of *M. calcarea* were formerly considered non-pelagic (Thorson, 1936), but Ockelmann (1958) found that they are pelagic after all. Consequently, there are no larvae identified to this species in Jørgensen's paper. Schram did not find the larva, but Fosshagen found it in small numbers in May-August.

The main spatfall accordingly took place in June, and until September there were still some new spat in the samples. The number of spat was great in 1963 (max. 4000/m² in July, 18 m,) and in 1964 there was a maximum in both localities of about 1500/m². Yet the spat disappeared very rapidly. At 18 m the maximum duration in the bottom was 4½ months – at 27 m six months.

During student courses in the last few years core samples have been taken where the present investigation was carried out. Adult *M. calcarea* were found frequently in a depth of about 20 cm, i.e. much deeper than hitherto believed. Thus it is possible that even the 0-group is situated below the two cm's digging depth of the mouse-trap, and this may explain the rapid disappearance from the samples.

The length at metamorphosis is 0.29-0.37 mm; at first appearance in the samples it was 0.3-0.5 mm (mean 0.4), and after about five months in the bottom (27 m, November 1964) 0.5-1.0 mm (mean 0.75).

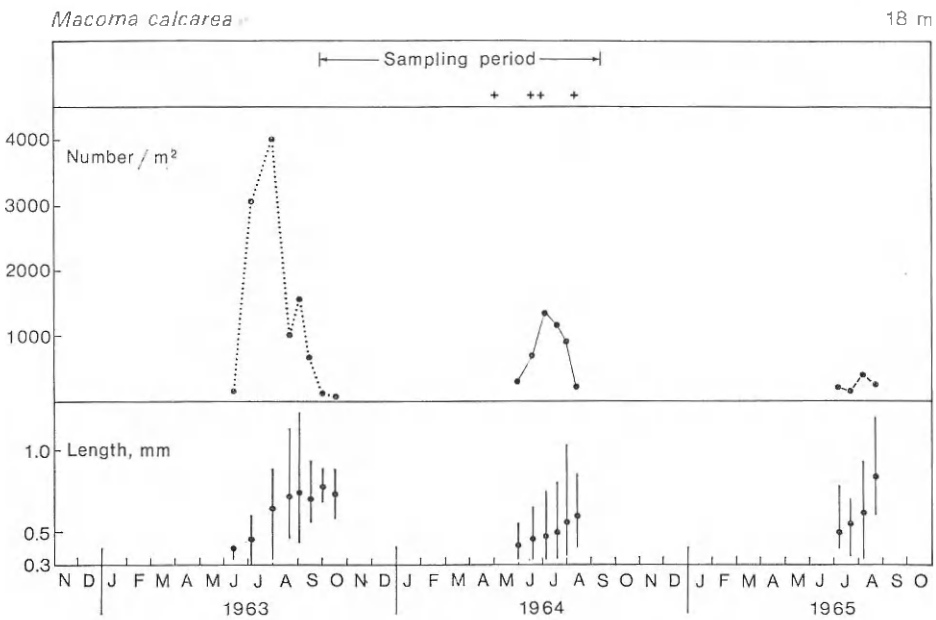

FIG. 10. *Macoma calcarea*, 18 m. For explanation of symbols see Fig. 3.

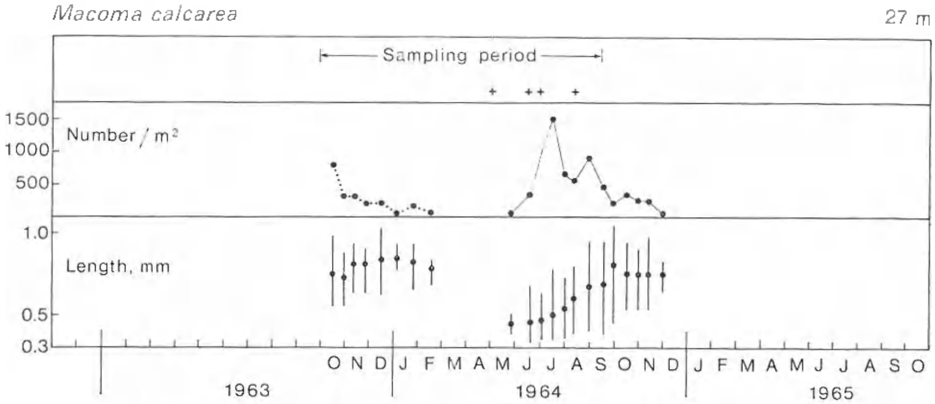

FIG. 11. *Macoma calcarea*, 27 m. For explanation of symbols see Fig. 3.

A winter growth stagnation is indicated for 1963-64 and 1964, but since the material was scanty this may not be true.

The maximum length is about 50 mm.

Tellina fabula (Fig. 12)

Jørgensen did not find the larva at all and Schram found it only in July. Fosshagen found one specimen in January, but several to many in July-October, with a maximum of 140/m³ in July.

The main spatfall took place in August and until February there could still be a few newly settled specimens in the samples.

The number of spat was never very great. The maximum occurred in August 1965 (1250/m²). The plankton maximum in July 1964 only resulted in 250 spat per m² (August 1964). Only at the 18 m locality was the spat sufficiently numerous for growth calculations.

The length at metamorphosis is 0.29-0.40 mm; at first appearance in the samples it was 0.3-0.6 mm (mean 0.4) and after one year the mean length was approximately 1.5 mm. The length after about 17 months (January 1964) was 2.0-3.6 mm (mean 2.9) and after about 21 months (June 1963) it was 3.0-4.5 mm (mean 3.7).

The maximum length of the species is about 20 mm.

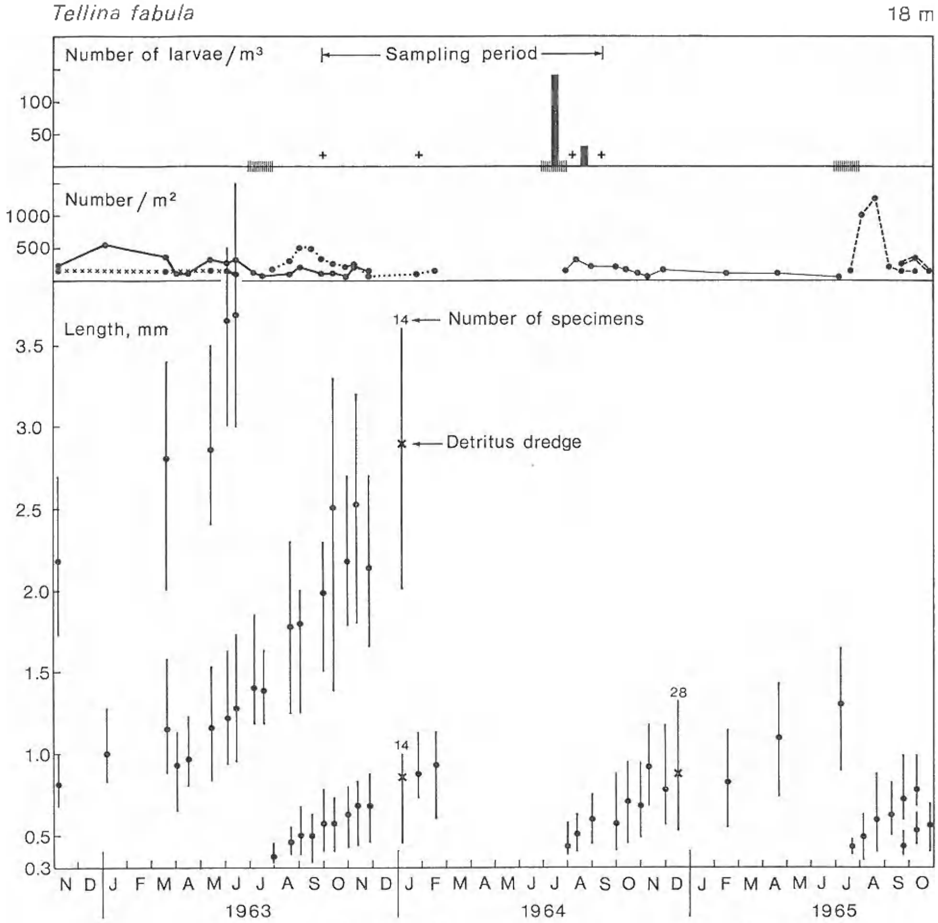

FIG. 12. *Tellina fabula*, 18 m. For explanation of symbols see Fig. 3.

Abra alba (Figs 13 & 14)

When Jørgensen and Schram took their plankton samples it was not possible to distinguish the larvae of *A. alba* from those of *A. nitida*, so these records cannot be used. Fosshagen found *A. alba* larvae in February-March, in May and in August-November. Maximum in the plankton (294/m³) occurred in August 1964.

The main spatfall of the year began at varying dates from the middle of August to the middle of October, and new spat were seen in small numbers until April.

At 18 m the number per m² never exceeded 1000. It is somewhat surprising that the plankton maximum in August 1964 (294/m³) – by far the biggest recorded

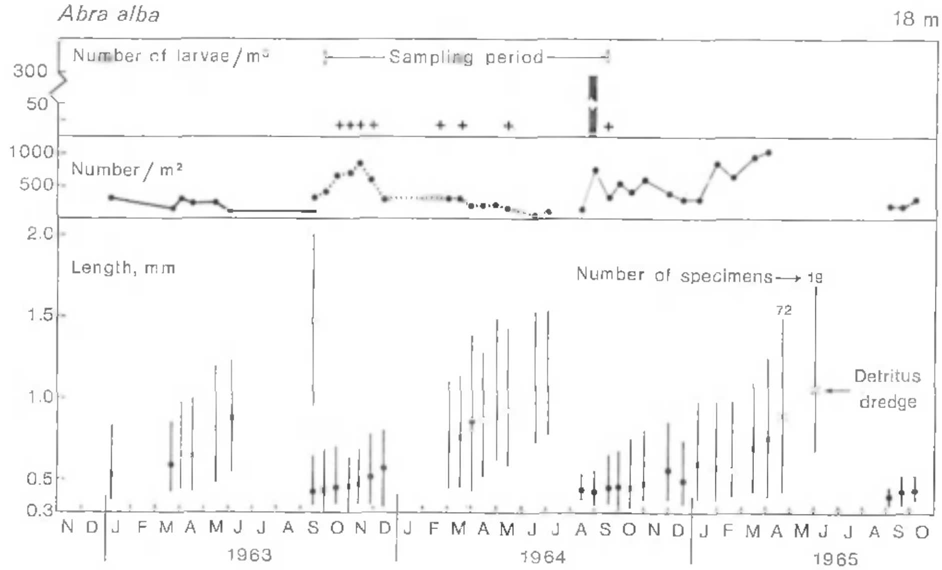

FIG. 13. *Abra alba*, 18 m. For explanation of symbols see Fig. 3.

during the plankton investigation – only resulted in 750 spat per m² at 18 m. At 27 m a maximum of 3000/m² occurred shortly after the plankton maximum.

At both localities the number normally decreased gradually towards 100/m². This was not so for the 1964 year class at 18 m. Here, in January 1965, there was a rise in number which continued until April when the species disappeared abruptly. The length-frequency distribution shows that both in January and in April some new spat were added. During the same period the picture was different at 27 m. There was a slight rise in January 1965, but otherwise the number decreased gradually until July.

Few larvae settled in September 1965 and the spat disappeared within two months in both localities.

The length at metamorphosis is 0.30-0.40 mm; at first appearance in the samples it was 0.3-0.6 mm (mean 0.4). Only twice was the length recorded about one year after spatfall began, viz. in September 1963, 18 m: 1.0-2.0 mm (mean 1.5) and October 1963, 27 m: 1.2-1.9 mm (mean 1.4). At 27 m the growth accelerated considerably after the first year. The length increased from the middle of October to the middle of November from 1.2-1.9 mm (mean 1.4) to 1.9-2.6 mm (mean 2.3). In August 1964, 27 m, there was likewise an indication of accelerated growth.

The maximum length is 25 mm.

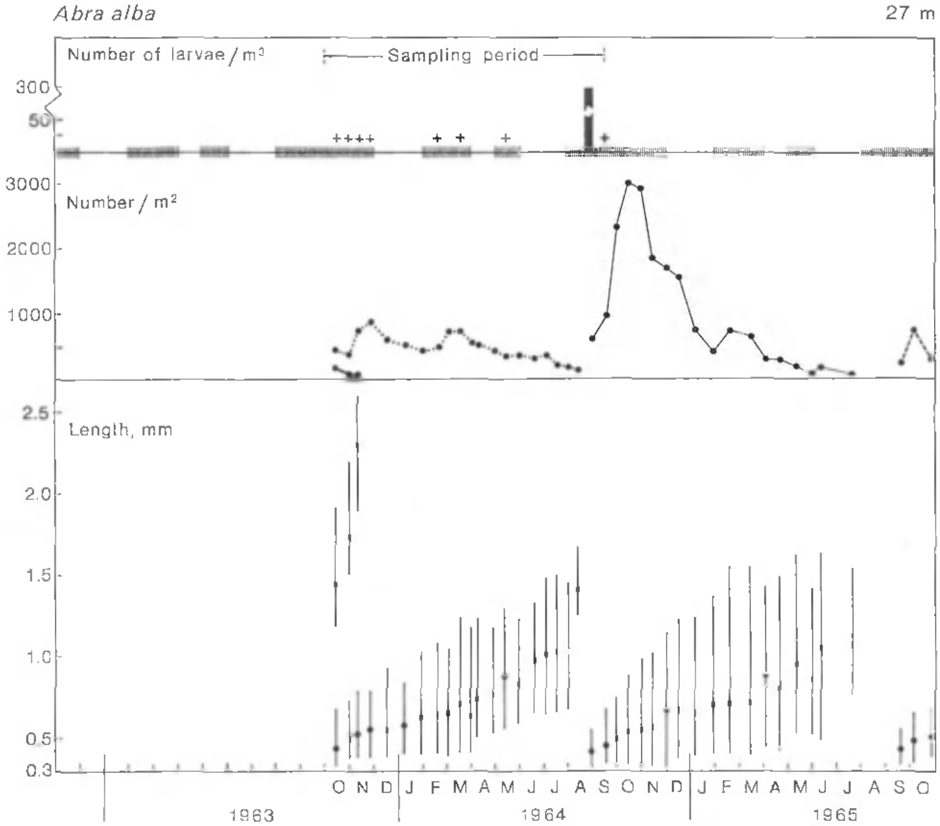

FIG. 14. *Abra alba*, 27 m. For explanation of symbols see Fig. 3.

Abra nitida (Figs 15 & 16)

As mentioned for *A. alba* the larvae of the genus could not be separated when Jørgensen and Schram made their respective investigations. Fosshagen found *A. nitida* larvae in October-November 1963, with a maximum of 26/m³ on 31st October, and in small numbers on three dates during May-August.

There was no spatfall of this species at 18 m.

At 27 m a spatfall appeared in January 1964 and again in October. The numbers per m² were rather different for the two groups. For the group which began to settle in January the number increased to about 1000/m² during the first 3½ months followed by a decline, but after that came a rise to 1200 per m² at the end of May coinciding with the plankton finds of that period. After that the decline continued and in middle November the spat became too few to be used in any calculations.

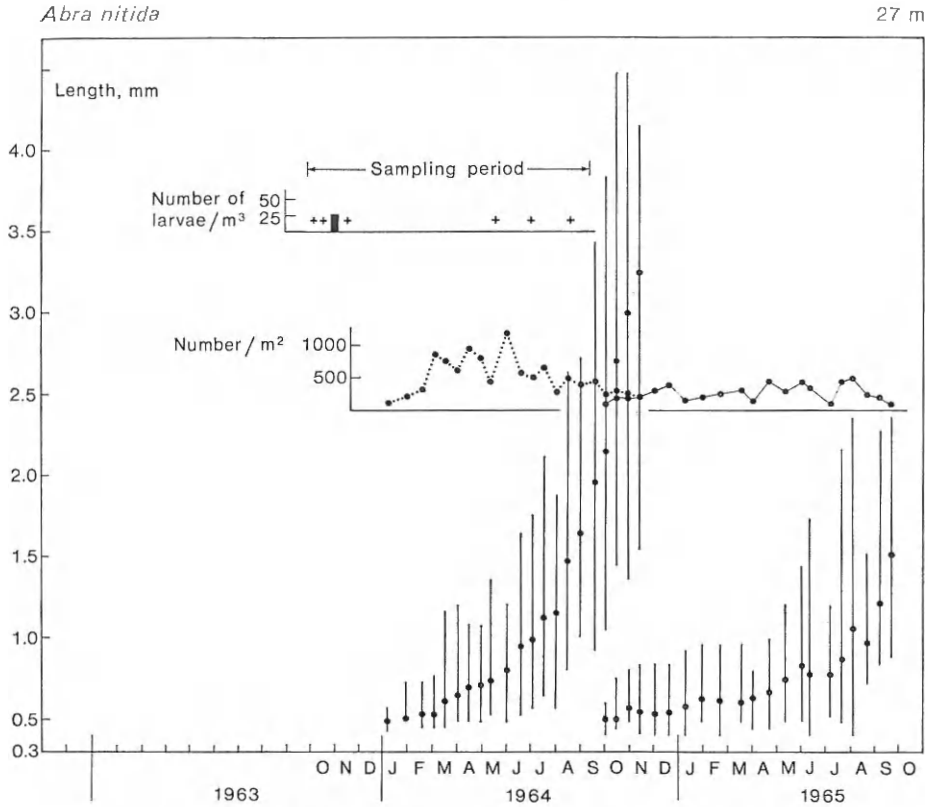

FIG. 15. *Abra nitida*, 27 m. For explanation of symbols see Fig. 3.

The other group which was first found in October was never very numerous, but had a rather constant density of a few hundred specimens per m² for 12 months.

The length at metamorphosis is 0.22-0.31 mm; at first appearance in the samples it was 0.4-0.6 mm (mean 0.5). The length-frequency distribution is seen in Fig. 16.

The growth patterns for the two groups were rather different. The group from January grew much faster than the other one. Although there were new spat present until about July and a distinct increase in number in May, the length-frequency distribution remained "normal" throughout the period (Fig. 16). So the numerical increase can only partly be due to a new spatfall. Accidental oscillations in numbers due to patchiness could be one reason. In the period from early January to the middle of November, i.e. 10 months, *Abra nitida* grew from 0.5 mm to 1.5-4.2 mm (mean 3.25). This is quite the fastest spat growth observed among bivalves in the Øresund.

The group which first appeared on 1 October had a much slower growth.

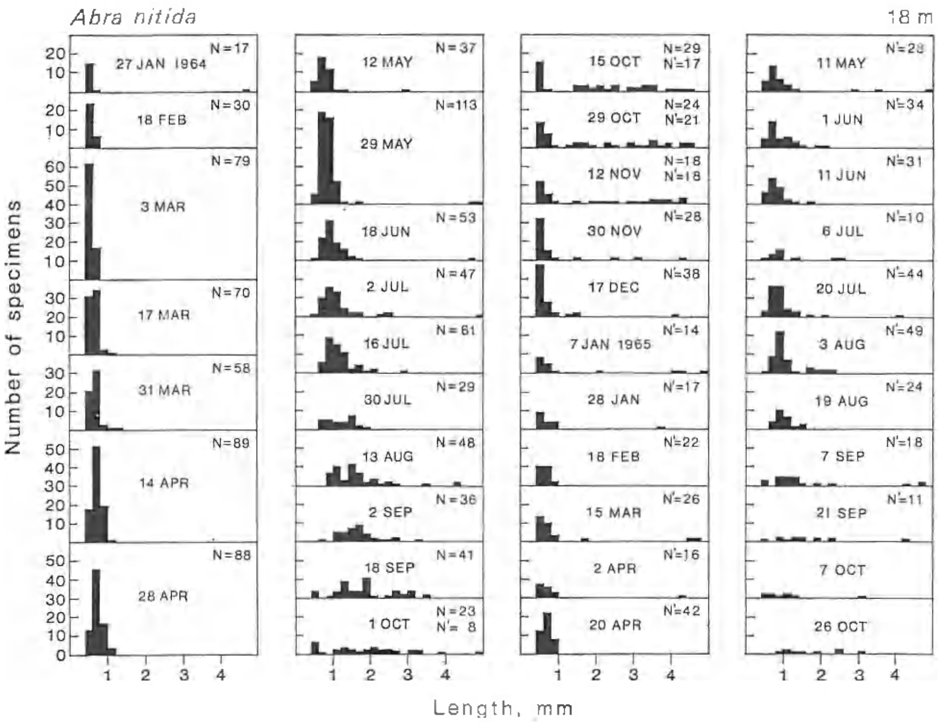

FIG. 16. Length-frequency distribution of *Abra nitida* specimens taken at the 27 m locality. The diagram for each date includes all *A. nitida* from the five samples (945 cm²).

In one year it grew from 0.5 mm to 0.9-2.4 mm (mean 1.5). There were new spat present until July, but not in numbers interfering with the length-frequency distribution pattern (Fig. 16).

The maximum length is 17 mm.

Spisula subtruncata (Fig. 17)

Jørgensen found the larvae in December-July with a maximum occurrence in April. Schram found them throughout the year with a maximum in May. Fosshagen found larvae in October-November, in February and in April-July, with a maximum of 20/m³ in the middle of July 1964. So the larvae have been taken at all times of the year.

The spatfalls at 27 m were scattered and with few specimens; but in July 1965 a number of about 700/m² occurred for a very short period.

At 18 m the spat was more numerous, but also scattered in time as could be expected from the plankton data. In July 1964 1500/m² was recorded, and in the same month of 1965 there was as many as 8500/m². In both cases the spat disappeared within two months.

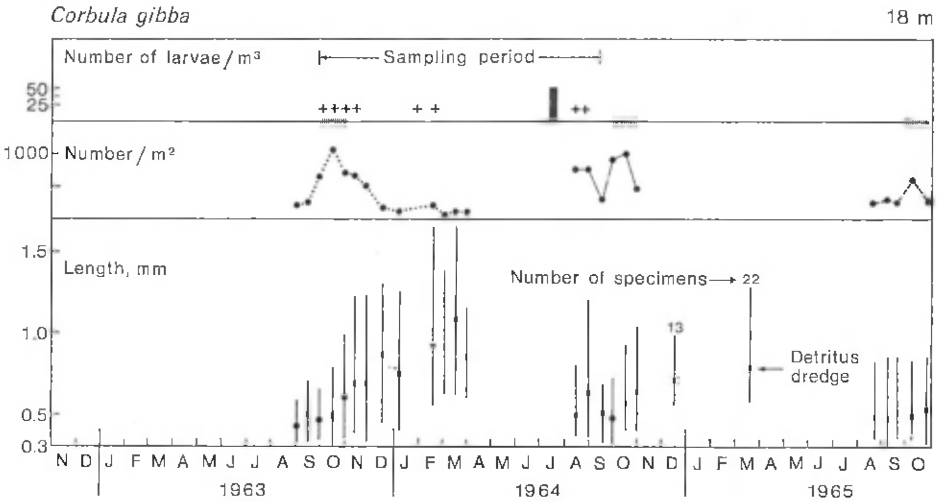

FIG. 19. *Corbula gibba*, 18 m. For explanation of symbols see Fig. 3.

C. gibba in October, on one sampling date only. Fosshagen found it in July-August, October-November and January-February with a maximum of 46/m³ in July.

At 27 m *Corbula* was few in number and had a scattered occurrence.

During all three years the first spat was found in the latter half of August at 18 m. In 1963 a few newly settled specimens occurred to the end of the year and in early January 1964. In 1964 and 1965 there were new spat until the end of October.

The number per m² reached about 1000 (October 1963, 1964) for a short period. The 1963 spat persisted for the longest period and was well-defined until March 1964. The length at metamorphosis is 0.25-0.33 mm; at first appearance in the samples it was 0.3-0.6 mm (mean 0.4), and after seven months it was 0.6-1.6 mm (mean 1.1).

The maximum length is 12 mm.

DISCUSSION

Choice of settling place

The problems concerning settling of planktonic bivalve larvae have been discussed for many years. A short review of this discussion was given by Thorson (1966). In the same paper Thorson stressed the importance of observations from nature of a possible choice of substratum by the larvae. Such observations have hitherto been scarce. Wood & Hargis (1971) also emphasized the necessity to present "unequivocal evidence from nature that bivalve larvae swim selectively". They showed, however, that oyster larvae (*Crassostrea virginica*) do this in the James River Estuary, Virginia.

The present investigation gave an opportunity to compare the numbers of settling specimens in two localities which, as far as we know, were visited by similar numbers of larvae.

The two localities are situated quite close to each other (appr. distance 1 km) and both are well below the discontinuity layer. Therefore, it must be the same water masses and the same larval swarms which pass the two localities on their way through the Øresund. If settling were random the two localities would receive approximately the same number of settling larvae.

Table 2 shows the number of spat per m^2 during the settling periods of the 11 bivalve species treated in this paper.

From these data it can be concluded that random settling is not the ruling principle. Four species, i.e. *Venus striatula, Tellina fabula, Spisula subtruncata* and *Corbula gibba* settled in higher numbers at the 18 m than at the 27 m locality, and three species, i.e. *Mysella bidentata, Abra alba* and *A. nitida* preferred the 27 m to the 18 m locality. Four species, i.e. *Montacuta ferruginosa, Arctica islandica, Macoma calcarea* and *Mya truncata* did not show preference for any of the localities. The material only permits conclusions as to which locality the larvae preferred. There might of course be other more attractive localities.

The fact that four species preferred one locality, three species the other and that four species were equally abundant in the two localities leads to the conclusion that the larvae can distinguish between different substrates and largely only settle in those where they can thrive as adults.

It would be natural then, to consider the eventual appropriateness of the choice of substrate for the survival of the different species. As mentioned before, the two substrates differ to some extent in the only qualities which were registered. The 18 m: sand 64-250 μ, silt content less than 1 %. The 27 m: sand 64-125 μ, about 5 % silt and clay. The hydrographic conditions are also different (Horikoshi, 1967). The 18 m station is situated below the normal position of the discontinuity layer, but oscillations in temperature and salinity can take place all the same.

Table 3 gives the distribution of the macrofauna specimens of the bivalves in question. It must be kept in mind that the macrofauna samples are much less representative than the meiofauna samples; only 10-12 samples were taken at each depth and all of them in November.

Of the four species whose larvae prefer the 18 m sandy locality, *Venus striatula* and *Tellina fabula* are well known sand dwellers and this also appears from Table 3. Adult specimens of *Spisula subtruncata* did not occur at any of the

TABLE 2. Numbers of newly settled bivalves per m² during the main settling period for each individual species at the two sampling stations.

	1964	1.ix	18.ix	1.x	15.x	29.x	12.xi
Montacuta ferruginosa	18 m	300	300	300	800	1000	400
	27 m	100	600	200	600	300	200
	1965	3.viii	19.viii	7.ix	21.ix	7.x	
Mysella bidentata	18 m	700	800	1000	1200	300	
	27 m	2400	1500	1600	1600	1900	
	1964	3.iii	17.iii	31.iii	14.iv	28.iv	
Arctica islandica	18 m	300	700	1000	900	800	
	27 m	600	300	400	800	300	
	1964	16.vii	30.vii	13.viii	1.ix	18.ix	1.x
Venus striatula	18 m	70	300	600	200	200	100
	27 m	10	0	10	0	0	10
	1964	29.iii	18.vi	2.vii	16.vii	30.vii	
Macoma calcarea	18 m	300	700	1300	1100	900	
	27 m	70	400	1000	1500	700	
	1965	20.vii	3.viii	19.viii	7.ix	21.ix	
Tellina fabula	18 m	200	1000	1300	200	400	
	27 m	0	100	10	30	10	
	1964	13.viii	1.ix	18.ix	1.x	15.x	29.x
Abra alba	18 m	200	800	400	600	400	600
	27 m	90	600	1000	2300	3000	2900
	1964	1.x	15.x	29.x	12.xi	30.xi	17.xii
Abra nitida	18 m	0	0	0	0	0	0
	27 m	100	200	200	200	300	400
	1965	11.vi	6.vii	20.vii	3.viii		
Spisula subtruncata	18 m	500	8600	5500	6200		
	27 m	100	100	1000	400		
	1965	28.i	18.ii	15.iii	2.iv	20.iv	
Mya truncata	18 m	40	20	200	100	30	
	27 m	200	90	300	300	300	
	1964	13.viii	1.ix	18.ix	1.x	15.x	29.x
Corbula gibba	18 m	800	1200	300	900	1000	500
	27 m	0	40	100	200	100	30

TABLE 3. Number per m² of macrofauna specimens of 11 bivalve species. The samples (Smith-McIntyre grab, 0.1 m². Sieve with 1 mm meshes) were taken in November at or in the vicinity of the two sampling stations, 18 m and 27 m, used in the main investigation. 10-12 samples were taken at each depth. The figures for *Macoma calcarea* and *Mya truncata* are not accurate (cf. text).

Depth m	*Montacuta ferrug.*	*Mysella bident.*	*Arctica island.*	*Venus striat.*	*Macoma calc.*	*Tellina fabula*	*Abra alba*	*Abra nit.*	*Spisula subtr.*	*Mya trunc.*	*Corbula gibba*
16	0	3	8	33	2	74	3	0	0	1	7
17	0	3	7	29	0	100	3	0	0	2	8
18	0	0	2	30	0	54	2	1	0	1	4
19	0	7	4	22	1	15	3	0	0	2	4
20	0	14	5	22	1	1	2	7	0	3	5
21	15	188	9	8	1	0	1	1	0	4	2
22	26	505	10	1	1	1	0	3	0	2	2
27	4	94	1	0	0	0	2	16	0	3	3

localities, but is common in slightly shallower water on a more clean sandy bottom close to the 18 m locality. So the larvae can be said to prefer the bottom which comes closest to the appropriate one. *Corbula gibba* is in Danish waters known to live both on sandy and soft bottoms, as also indicated in Table 3. So in three out of four species the choice of the larvae seems to be appropriate.

The larvae which prefer the 27 m locality belong to three species. Of these *Mysella bidentata* clearly belongs to the 27 m and not to the 18 m locality as it appears from Table 3. (It nevertheless survives in the 18 m bottom for at least a year).

Abra alba and *A.nitida* are soft-bottom species. For *A.alba* no indication appears from Table 3, but for *A.nitida* the figures indicate that it is more common at 27 m. This shows that all three species probably make an appropriate choice of settling place.

The larvae of the remaining four species i.e. *Montacuta ferruginosa, Arctica islandica, Macoma calcarea* and *Mya truncata* do not clearly prefer any of the two localities and that concurs fairly well with the distribution of adult specimens as seen from Table 3.

As a conclusion it can be said that the results confirm the belief that bivalve larvae are somehow able to choose between different substrates when settling in nature.

Growth rate

The literature on bivalve growth is abundant, but exact data on growth in the period immediately after settling are lacking in most papers. There are several reasons for this. Two of the three methods for studying bivalve growth are impracticable in the early stages, i.e. 1) identification of annual rings, and 2) marking of individual specimens kept in their natural surroundings. The third method: Study of the length-frequency distribution of a population is practicable, but its reliability depends very much on the sampling method used.

The main drawback of the ring-counting method is that the countings for obvious reasons are done on older specimens, whose umbonal region often is eroded. In many cases the length of the first visible ring is measured, and it is stated that the bivalve reached this length before the first winter, but unless there is corroborative evidence as to the early growth, such statements are of a dubious value.

The method of marking or tagging individual specimens, keeping them in their natural surroundings in "cages" and checking the growth at suitable intervals is, of course, the most reliable, but impracticable with shells of a size less than one millimeter. It is difficult even to keep unmarked tiny lamellibranchs in some sort of cage under natural conditions. But there is a situation which gives essentially the same advantage. If a substrate is completely unpopulated by a certain species and then receives a dense spatfall, a parallel to the marking experiment is established, provided that the young do not migrate after settling. The substrate can be artificial, i.e. plates of some suitable material may be placed in the area before the settling (Boëtius, 1962; Böhle, 1971), or a natural clean substrate is available when for instance a severe ice-winter has extinguished a species from an area and there is a good spatfall next season (*Cardium edule* L., Kristensen, 1957).

Kristensen (1957) had to face the disadvantage – pointed out by himself (p. 8) – that it was not possible to use a sieve with meshes small enough to catch the newly settled specimens.

For most of the bivalve species studied by me it was possible to ascertain when the main spatfall of the year began and to distinguish the new specimens from older ones. This means that the same advantage was obtained as in the "tabula rasa" cases mentioned. Accordingly the length-frequency distribution should be a reliable method to study growth right after settling.

My results on growth of bivalves during their first year after settlement (Table 4) disagree with most previous data. The growth in the Øresund seems to be much slower than generally supposed, even in other temperate areas. Data from the literature on early bivalve growth are listed in Table 5 for species identical to or related to the Øresund species. All data are from European temperate waters.

TABLE 4. Length at metamorphosis (Ockelmann, pers.comm.), mean length at first appearance in the samples, and estimated mean length after some months in the bottom.

Species	Length at metamorphosis, mm	Mean length at first appearance, mm	Number of months after first appearance	Mean length, mm
Montacuta ferruginosa	0.35-0.41	0.5	11	1.4
Mysella bidentata	0.40-0.55	0.4	12	1.5
Arctica islandica	0.23-0.30	0.4	5-7	0.9-1.5
Venus striatula	0.23-0.33	0.4	2	1.3
Macoma calcarea	0.29-0.37	0.4	5	0.75
Tellina fabula	0.29-0.40	0.4	12	1.5
Abra alba	0.30-0.40	0.4	12	1.5
Abra nitida	0.22-0.31	0.5	11	1.5-3.3
Spisula subtruncata ...	0.29-0.45	0.4	5	1.3
Mya truncata	0.27-0.36	0.4	6	0.8
Corbula gibba	0.25-0.33	0.4	7	1.1

TABLE 5. Data from the literature on growth of young bivalves.

Author	Species	Area	Mesh-size, mm	Age after spatfall, months	Length, mm
Ansell, 1961a	*Venus striatula*	Millport	?	14-17	9
Ansell, 1961b	*Venus striatula*	Millport	1	1-4	1-3
Quayle, 1952	*Venerupis pullastra*	Isl. Cumbrae	?	4-7	0.7-8.2
Stephen, 1931	*Macoma baltica*	Clyde	2	12	5
Stephen, 1932	*Tellina fabula*	Clyde	2(1)	about 6	4-5
Trevallion & Ansell, 1967	*Tellina tenuis*	Loch Ewe	?	24+	5
Stephen, 1932	*Abra alba*	Clyde	2(1)	12	8-11
Green, 1957	*Scrobicularia plana*	South Wales	6	at 1. winter	5
Davis, 1923	*Spisula subtruncata*	North Sea	1.5	12	12-15
Ford, 1925	*Spisula elliptica*	Plymouth	?	1	3.4
Smidt, 1951	*Mya arenaria*	Danish waddensea	1.9(1)	3	6
Jones, 1956	*Corbula gibba*	Isl. of Man	2	12	8

The apparently slower growth rate found in the Øresund may, of course, be due to unfavourable abiotic and/or biotic factors. But it may also only be apparent. It seems as if many authors have failed to find the 0-group and even one or more of the following groups due to an insufficient sampling-sieving technique. The chosen technique is in many cases connected with an apparent lack of knowledge of the size of newly settled bivalve spat. The 11 species treated by me are all about 0.4 mm long at spatfall, but in the literature bivalves up to 3 mm long are termed "spat". If an investigation is started in the belief that "spat" have the size of 1 mm or more it is natural to save time by using a not too fine sieve.

A good example is given by F. M. Davis (1923). He collected *Spisula subtruncata* on the Dogger Bank and the smallest mesh size in the sieves was 1.5 mm. He concludes on p. 23: "Since the smallest individuals yet found fall between 1 and 2 mm in length, 1.5 mm has been taken as the mean size at spatfall". This was quite a common sort of conclusion 50 years ago, but unfortunately a substantial part of *Spisula*'s reputation as a fast-growing species has rested on this foundation ever since.

However, observations made by Dr. Ockelmann (pers. comm.) have shown that *Spisula*, settling in early summer at a lower depth in the vicinity of the 18 m locality, may become 5-8 mm long before the first winter.

Several authors mention the date when the first spat are found in their samples, and various meanings are attached to this. The fact, that the date when the spat appear almost solely depends on the size of meshes used in the sieving gear, is almost never mentioned. I have only found the importance of mesh-size in connection with spatfall stressed in very few papers (e.g. Baggerman, 1953; Segerstråle, 1960). A correct interpretation would be: On this date the spat reached a size where they were retained by the sieve used (mesh-size).

If the bottom of the Øresund had been sampled in the classical way with the purpose of studying the growth of e.g. *Mysella bidentata* the results would have differed from those now obtained. It was known (Jørgensen, 1946) that the larvae are present in the plankton from July to November with maximum numbers in September. The duration of the planktonic life is unknown, but bivalves are generally believed to have a short pelagic life – less than five weeks (Thorson, 1961). Thus the main spatfall would be expected to take place around October. Bottom samples taken monthly with a grab and washed through a set of sieves with a smallest mesh-size of 1 mm would have contained specimens of about 1.5 mm's length in November (see Figs 5 & 6). Until November the majority of young specimens would have passed the sieve and the few ones found in October would have been supposed to originate from the plankton finds in the period before the maximum.

The conclusion would be that *Mysella* had grown to a length of 1.5 mm in about a month, whereas the present investigation shows that it has spent about

14 months after settling before it obtains a length of 1.5 mm. Thus in the classical investigation the I-group would have been referred to the 0-group.

Stephen's two papers (1928, 1929) on the biology of *Tellina tenuis* from the Firth of Clyde have been much quoted during the past 40 years. They give valuable information on the growth of *Tellina*, although the data on time of spatfall and early growth are somewhat vague. Stephen normally used a sieve with circular holes, 2 mm in diameter, but "examinations for young broods were carried out with a sieve having holes 1 mm in diameter" (Stephen, 1928, p. 684).

Stephen examined the state of the reproductive organs of the bivalve at various times of the year and found mature ova in July. He also found some specimens in August which appeared more or less spent, but actual spawning was not observed. From the state of the reproductive organs he concluded that no young were to be found on the bottom before June. To test this conclusion, sieving of the samples was done with a 1 mm sieve in this period. We know now that the brood is only about 0.4 mm long at spatfall, so there is no security in this method. If, however, we consider the evidence of the gonads conclusive, we can fix the time of the main spawning to the latter half of July at the earliest, and if we assume the planktonic stage to last at least a fortnight the main spatfall will occur from early August onwards. On 13 August, Stephen found the first *Tellina*'s of the season in the 1 mm sieve and termed them "the spat". Their actual lengths are not given, but as they passed the 2 mm sieve and were retained by the 1 mm sieve we can assume their length to have been between 1.2 and 2.7 mm. So we can safely say that they were not the spat of August. Of course, there may have been *Tellina* in neighbouring areas whose ova were ripe before July and whose larvae were carried to Stephen's localities. However, in view of the results from the Øresund I will venture the assertion that Stephen's animals from August were one year old.

This assertion agrees with recent findings by McIntyre (1970) who sampled several populations of *Tellina tenuis* on the west coast of Scotland. The length analysis of the population at Aultbea in May 1968 shows a distinct peak at 2 mm (fig. 7). This group had probably settled during the previous summer and thus had spent about 10 months in the bottom. (In the Øresund the other *Tellina* species, *T. fabula* reaches a length of 2 mm about 14 months after spatfall.) In Stephen's graphs (1929) the September samples show peaks at 3-4 mm's length, and Stephen assumed that these animals were the spat of the year. If we assume the growth rate to be about the same in the whole area of western Scotland it is also reasonable to assume that the animals which are 2 mm long in May (McIntyre) escaped Stephen's 2 mm sieve, but were caught by him in September when they were 3-4 mm long and one year old. If, on the other hand, we compare the length with the length of *T. fabula* in the Øresund, which of course is somewhat risky, the indication is that Stephen's September animals were two years old.

Trevallion & Ansell (1967) worked with *Tellina tenuis* in the same area as McIntyre and they have a peak in their length-frequency histogram from April-May at 5 mm's length. They state – following personal communication from McIntyre – that this peak represents the 2+ group. This also implies that Stephen's September animals must have been two years old instead of one month.

Stephen (1932) also investigated *T. fabula*, but this paper is less detailed. The presence of a mode at 4 mm on the length-frequency curve for July is said to indicate breeding in the early summer.

This somewhat lengthy discussion of growth rate is given to stress that it can lead to erroneous results to use older statements on bivalve age/size-relations for further calculations on age at first spawning, production in an area, comparisons between fast-growing and slow-growing species etc.

The results on growth rate from the Øresund agree rather well with the growth rate of *Macoma baltica* in Finnish waters (Segerstråle, 1960). Unfortunately, *M. baltica* is in Danish waters restricted to shallow areas and it was not found in the Øresund samples. However, all the species from the Øresund had roughly the same length one year after spatfall so a comparison with Segerstråle's results seems justified. The closest relative to *Macoma baltica*, viz. *M. calcarea*, could only be followed for a short period in the Øresund. Another member of the family Tellinidae, *Tellina fabula*, could be followed during almost two years and was, therefore, chosen for the comparison.

Tellina reached a length of about 1.5 mm after one year's life in the bottom and about 4 mm after two years (Fig. 12). Segerstråle (1960, fig. 22) figure the growth rate of *M. baltica* at three stations with different hydrographic conditions in the Tvärminne area. In Fig. 20 the above *Tellina* data are plotted into Segerstråle's growth curves and they show a good agreement between *Tellina*'s growth in the Øresund and *Macoma*'s at Segerstråle's Station I.

At Station I the depth is 3 m and the salinity averages 6‰, thus differing very much from the salinity found at 18 m in the Øresund (Fig. 21).

The temperature at Station I during the years 1930-1932 can be seen in Segerstråle's fig. 5 (this paper, Fig. 21). The monthly mean temperatures at the Lappegrund (Brattström, 1941) for 1923-1939 in 15 and 20 m's depth were plotted into the curves from Station I (Fig. 21). The difference between the temperature curves from the two areas is rather large. The annual oscillations are much greater in the Tvärminne area, and it was not possible to compare the temperature conditions in the two areas directly. Therefore, I have calculated the amount of day degrees for one year at Station I. It was quite a rough calculation, based on the curves in Fig. 21. The result was about 2300 day degrees per year. The amount of day degrees per year was 3000 in the Øresund as calculated from the monthly mean values at the Lappegrund, depth 20 m.

The length of *Tellina* at a certain age (i.e. days after beginning of spatfall) was related to the corresponding number of day degrees (Fig. 22). The data for

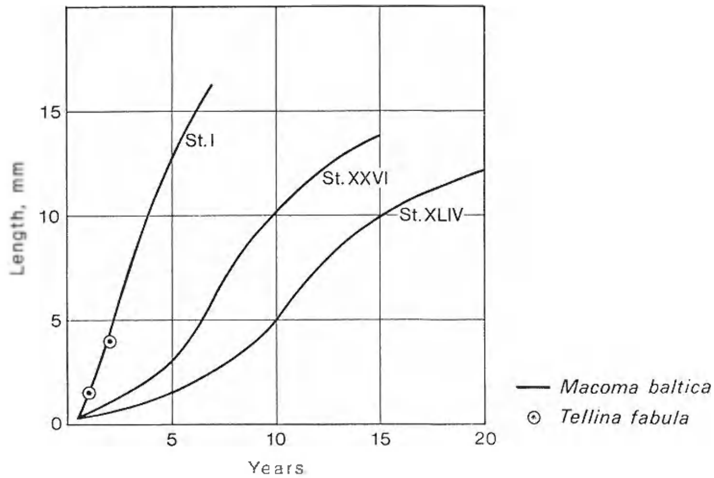

FIG. 20. Growth of *Macoma baltica* at three stations in the Tvärminne area. Redrawn from Segerstråle (1960, fig. 22). Two values for *Tellina fabula* from the Øresund are inserted.

Abra alba, which is also a fairly close relative of *Macoma*, can also be seen in Fig. 22. The two values for *Macoma:* one year old, 2300 day degrees, one mm long; and two years old, 4600 day degrees, 3.8 mm long, fit well with the *Tellina* and *Abra* values.

The growth rate, related to number of day degrees, was roughly the same for the two Tellinidae from the Øresund and the one from the Tvärminne area at Station I, although the salinity is much lower at Station I. The influence of other factors such as e.g. amount of food cannot be compared as these factors were not investigated.

Ansell (1961 b) found that *Venus striatula* in the Millport area reached a length of 1-3 mm before the first winter i.e. 1-4 months after spatfall. This result agrees well with my results from the Øresund: About two months after spatfall *Venus* had a mean length of 1.3 mm.

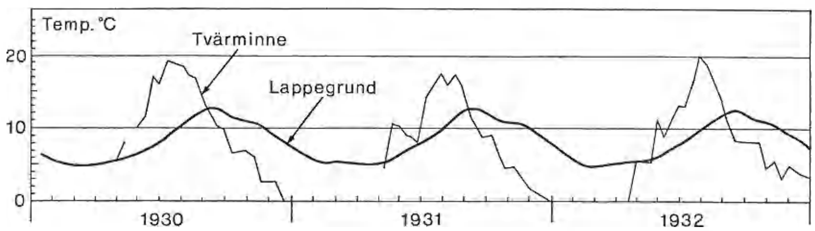

FIG. 21. Temperature conditions during 1930-1932 at the Tvärminne Station I, depth 3 m (from Segerstråle, 1960). Monthly mean temperature 1923-1939 at the Lappegrund lightship, depth 20 m (from Brattström, 1941).

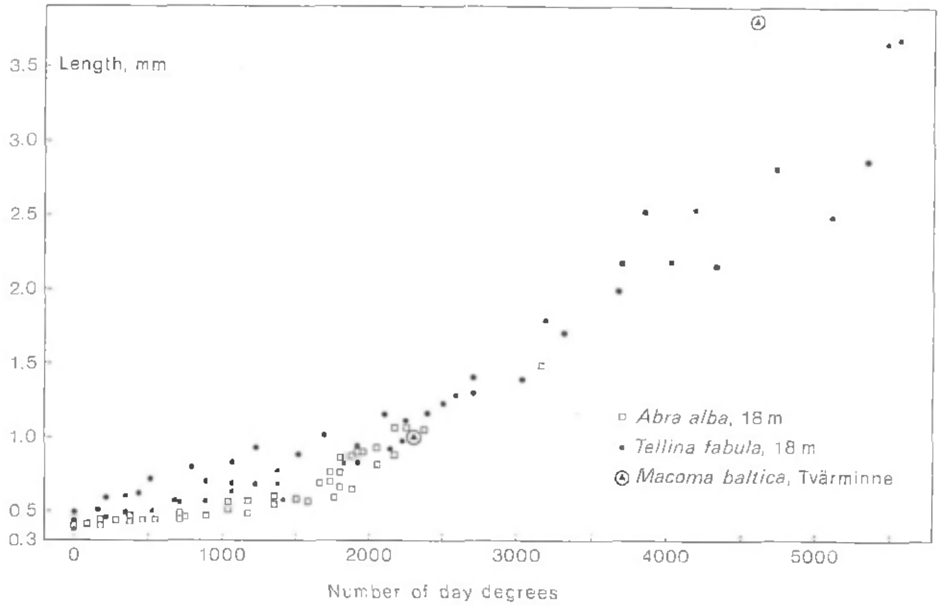

FIG. 22. Length of *Tellina fabula* and *Abra alba* related to number of day degrees after settlement. Two values for *Macoma baltica* from the Tvärminne Station I are inserted.

Mortality

It appears from Figs 3, 5-15 and 17-19 that the number of settling bivalve specimens had very little influence upon the success of the season's spatfall.

If we consider three of the most successful spatfalls (successful in the sense that the settled specimens survived a year or more in considerable numbers), i.e. *Tellina fabula* (Fig. 12), *Abra alba* (Fig. 14) and *A. nitida* (Fig. 15) the number of settling specimens was in all three cases moderate.

The 1962 spatfall of *Tellina* was particularly successful as its members could be followed during 17 months. The spatfall itself was not registered as the sampling started three months later. But the number of specimens at the start of sampling (250-500/m^2) does not indicate a particularly heavy spatfall (Fig. 12). In contrast to this the 1965 spatfall was the biggest registered (1250/m^2) but its members vanished within three months.

Another example appears from Fig. 14 (*Abra alba,* 27 m). The number per m^2 of newly settled specimens when sampling began (15/10-63) was below 500. Exactly 12 months later the number of newly settled specimens was 1750/m^2. At the end of the years (1963 and 1964 respectively) both populations had the same size, i.e. 500/m^2. Furthermore, the date when the populations became too few in numbers to be registered was about the same: 1964: 13th August, 1965: 20th July. The more than three times higher numbers of young bivalves in the autumn of 1964 had no effect, either on the number during the following spring or on the length of the period in which it was possible to follow the fate of the year-class.

The general survival pattern for most of the bivalves in question seems to be that the number of specimens decreases rapidly to some hundred per m^2, regardless of the size of the main spatfall. No conclusions about success and survival of a year-class can, therefore, be drawn from the size of the spatfall. A consequence of this is that it will also be hazardous to draw such conclusions from numbers of larvae in the plankton.

There are several possible causes for the rapid initial disappearance of most of the spat, among which must be mentioned 1) migration, 2) burrowing below sampling depth, and 3) predation.

During the first months after settling the loss was very severe regardless of whether the larvae had settled in an appropriate bottom or not. The loss due to a bad choice of settling place came later.

The bottom samples represented at least the upper 2 cm of the substratum. When the big decrease in number of spat took place, i.e. within the first months after settling, the bivalves had only reached a length of about 1 mm. It is therefore very unlikely that they should have buried in the substratum to a depth of more than 2 cm. For *Venus mercenaria,* Turner & George (1955) have observed that no juvenile animal less than 750 μ long will bury itself completely. There might be exceptions like *Montacuta ferruginosa* which is able to associate itself with *Echinocardium,* when the bivalve is only 0.33 mm long (Gage, 1966c). This association might involve that some *Montacuta* were to be found deeper in the substratum.

As mentioned earlier adult specimens of *Macoma calcarea* and *Mya truncata* have been found to be more common in the area than can be seen from grab-samples. This indicates that also juveniles may sit deeper in the substratum than the digging-depth of the mouse-trap.

Horizontal migration is another possible explanation of the disappearance of spat. *Mytilus* is known to settle first on algae and then on its final substratum (Bayne, 1964). *Mya truncata* is likewise supposed to settle first in one place and then in another (i.e. Thorson, 1936), but I have not seen a detailed description of this behaviour. As the length of the spat of *Mya* was 0.4 mm when it appeared in the bottom samples it must be a first settling. As adult specimens thrive in the area one might also ask why the spat should move elsewhere. Moreover the loss of spat of *Mya* during the first months after settling was very small. As far as I know, none of the other bivalves in question is known to settle twice.

Transport of cockle spat (*Cardium edule*) has been described by Baggerman (1953), but the results are not comparable to those of this investigation because the cockles in Holland live on tidal flats which become exposed at low tide.

The most likely cause of disappearance is predation. Several predators are known to feed on tiny bivalves. According to Christensen (1970) *Astropecten irregularis* can digest at least 200 newly settled *Spisula* per day. He estimated the population in the Hornbæk area (where the present investigation was carried out) to be one *Astropecten* per 10 m^2 and concludes that *Astropecten* may be responsible for the extermination of 1100 spat/m^2 during eight weeks of the main spatfall.

Thorson (1966) discussed predation and "accidental" predation by many other invertebrates found in the Øresund.

Fishes such as e.g. young dab, gobies and haddock can also be suspected of eating spat.

Although the knowledge of predators and quantitative data on predation on bivalve spat still must be considered as unsatisfactory, it is almost certain that predation is the dominant cause of mortality among juvenile bivalves.

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