

DET KGL. NORSKE VIDENSKABERS SELSKAB
MUSEET

MISCELLANEA

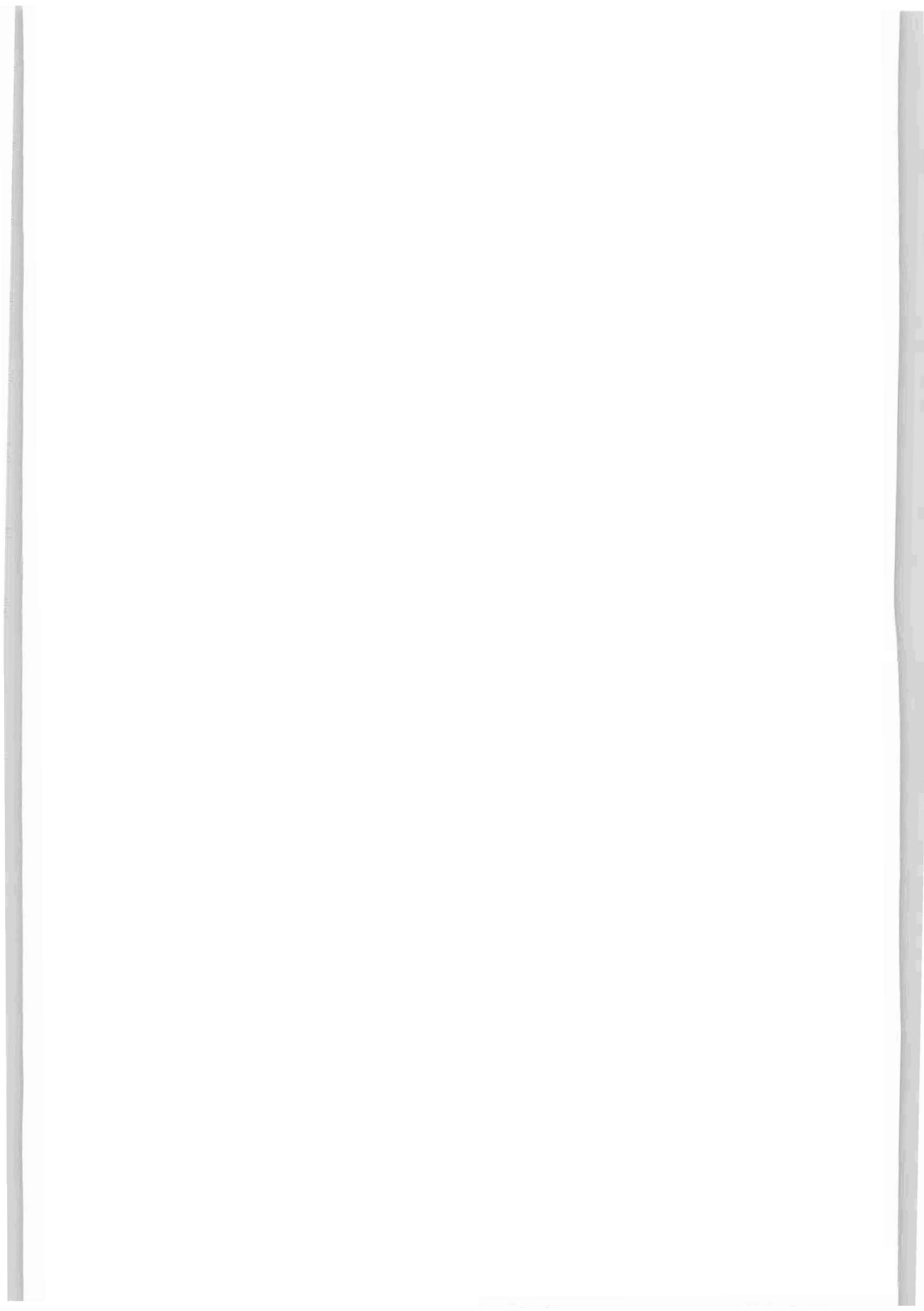
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Eirik Lande

GROWTH, SPAWNING, AND MORTALITY
OF THE MUSSEL (*Mytilus edulis* L.)
IN PRESTVAAGEN, TRONDHEIMSFJORDEN

TRONDHEIM 1973



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GROWTH, SPAWNING, AND MORTALITY OF THE MUSSEL
(*Mytilus edulis* L.) IN PRESTVAAGEN, TRONDHEIMSFJORDEN

by

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ABSTRACT

Lande, Eirik. 1973. Growth, spawning, and mortality of the mussel (*Mytilus edulis* L.) in Prestvaagen, Trondheimsfjorden. *K. norske Vidensk. Selsk. Mus. Miscellanea* 11: 1-26.

Investigations on growth, spawning, and mortality of *Mytilus edulis* were carried out from June 1966 to November 1967 in Prestvaagen, Trondheimsfjorden. Mussels ranging from 5-74 mm, were submerged in wirescreened cages 1.7 m below the surface where they were exposed to current.

Length and volume measurements show that the growth rate is highest in the summer (May/June - August/September) whilst in winter little or no growth occurs. The variations in growth rate are supposed to be caused by variations in the temperature. The growth rate is found to be about three times higher at 18°C than at 10°C and about two times higher at 10°C than at 5°C. Further, the growth rate decreases with increasing length of the mussels.

The von Bertalanffy growth curve for the mussels in the cages in Prestvaagen shows that they need 3 years to reach 70% (47.5 mm) of their maximum mean length (65 mm).

Two spawning periods (in June and August/September) were recorded by examining the condition of the mussels and settlement of larvae.

The lowest rate of mortality was recorded among mussels between 30-50 mm in length. The highest rate of mortality was recorded in the summer.

Transplantation of the mussels led to changes in the shell proportions and the mussels were relatively longer at the end of the experimental period compared to mussels of the same volume just before transplantation.

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INTRODUCTION

Growth of the mussel *Mytilus edulis* L. has been studied under natural and laboratory conditions by several investigators.

In Norway investigations have been carried out in Oslofjorden (Böhle 1965, Böhle & Wiborg 1967) and along the south and west coast (Bjerkan 1910, Löversen 1957).

In Trondheimsfjorden, where mussels are distributed more or less everywhere in the littoral zone, no growth investigations have been made earlier. From 16 June 1966 to 1 November 1967 an investigation was carried out in Prestvaagen in the inner part of Trondheimsfjorden (Fig. 1). Mussels are abundant in the intertidal zone in Prestvaagen, and previously the locality was regularly visited by fishermen collecting mussels for bait.

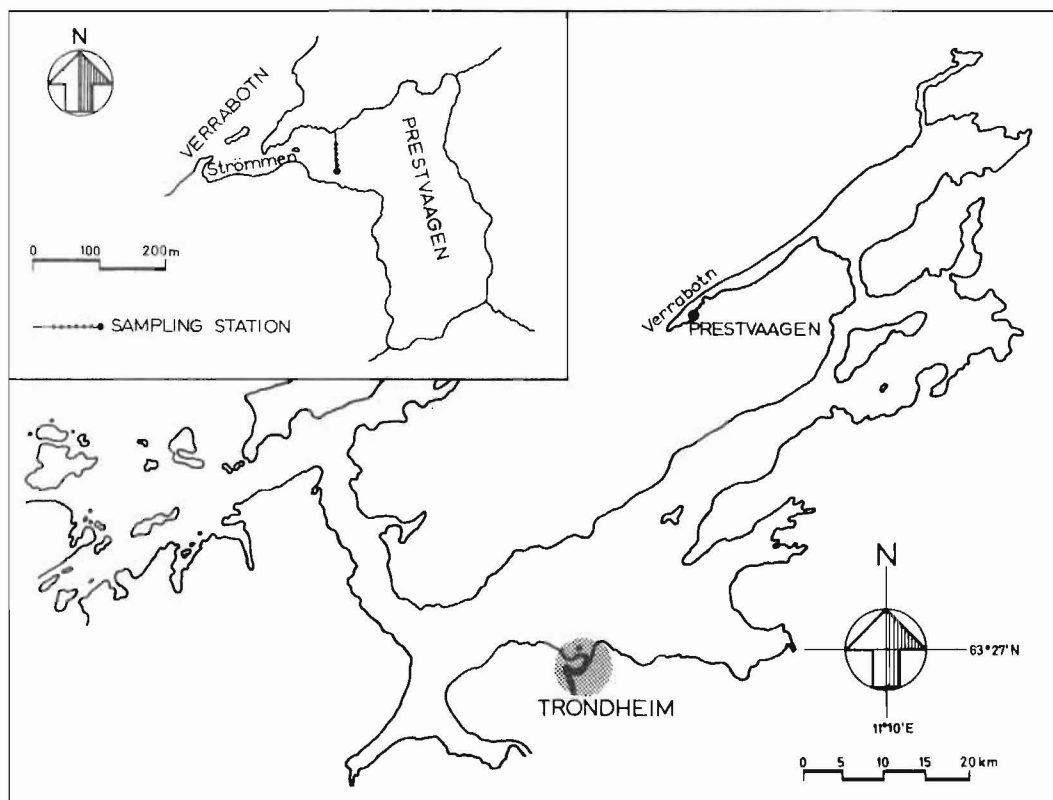


Fig. 1. Map of Trondheimsfjorden with Prestvaagen, the locality where the experiments were carried out.

THE EXPERIMENTAL AREA

Prestvaagen is situated in the innermost part of Trondheimsfjorden (Fig. 1) sheltered from wind and waves, surrounded by coniferous wood and marchland. Three small creeks supply freshwater in the spring and summer. A small, narrow channel, Strømmen, leads from Verrabotn into Prestvaagen. In Strømmen and the adjacent areas the tide makes a strong current which mixes the water masses completely.

Tidal recordings were made by tide poles, one in Prestvaagen and one in Verrabotn. The ebb period in Prestvaagen is markedly longer than the flood period (Fig. 2), a little more than nine and three hours respectively, and the highwater level is reached about 20 min later in Prestvaagen than outside, due to the narrowness of the channel. The tidal current inside the channel runs fastest in the flood period. By means of an Ekman current meter a maximum velocity of 70 cm/sec was recorded at the experimental site 1.7 m below the surface about 50 m inside Strømmen. The

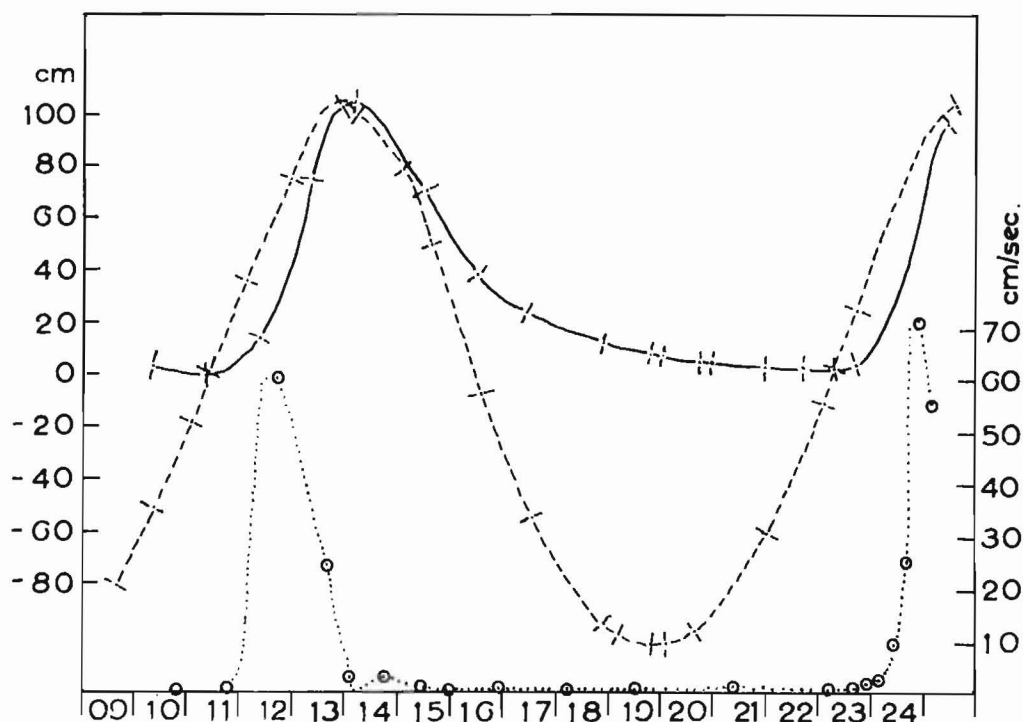


Fig. 2. Tide recordings from Prestvaagen and Verrabotn, and the velocity of the current at 1.7 m level about 50 m inside Strømmen at spring tide (19 May 1968).

———— : Tide recordings from Prestvaagen.

----- : Tide recordings from Verrabotn outside Prestvaagen.

..... : Current velocity.

maximum tidal range was 104 cm.

The maximum depth in Prestvaagen is about 12 m and the bottom sediment is mud with stones. In Strømmen the bottom consists of stones and shell gravel.

Extensive mussel banks are present in Prestvaagen and Strømmen. In Strømmen up to 1580 specimens per sq. m of *M. edulis* > 10 mm in length have been recorded. The maximum length recorded on mussels from the intertidal zone in Prestvaagen was 91 mm.

Hydrographic measurements were carried out in the surface because little or no difference was recorded by comparing data from the surface with data from 1.7 m depth. This was due to mixing of the water masses passing through Strømmen. Fig. 3 shows the variations in temperature and salinity in the investigated period. The temperature ranges from 1°C (February 1967) to 20°C (June 1966) and the salinity from 8.01 ‰ (May/June 1967) to 25.4 ‰ (October 1967). The low salinity recorded in May/June 1967 was due to melting of ice and snow in the mountains.

In winter Verrabotn and Prestvaagen are covered with ice. Only Strømmen and the areas immediately adjacent are icefree.

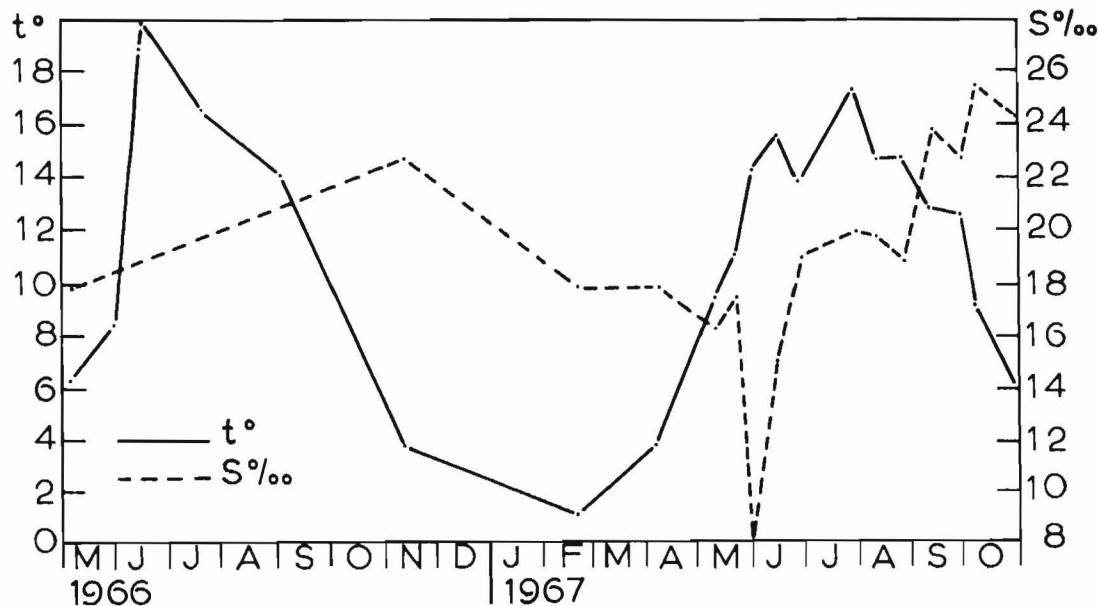


Fig. 3. Variation in temperature and salinity at the sea surface from May 1966 to November 1967.

MATERIAL AND METHODS

The mussels were collected in Prestvaagen in a small area, where the ecological conditions were relatively homogeneous. The length of the mussels (= maximum anterior - posterior axis) ranged from 5 to 74 mm. The material was divided into 7 size groups as shown below, each containing 150 specimens.

Size group 1:	5 - 14 mm
" "	2: 15 - 24 mm
" "	3: 25 - 34 mm
" "	4: 35 - 44 mm
" "	5: 45 - 54 mm
" "	6: 55 - 64 mm
" "	7: 65 - 74 mm

Each size group was kept separately in covered wirescreened cages (Fig. 4). The cages, containing two cells (50 x 30 x 30 cm) covered with nylon net (mesh size 2 mm), were fastened to an anchoring system (Fig. 5) at a level of 1.7 m below the surface, about 50 m inside Strømmen (Fig. 1).

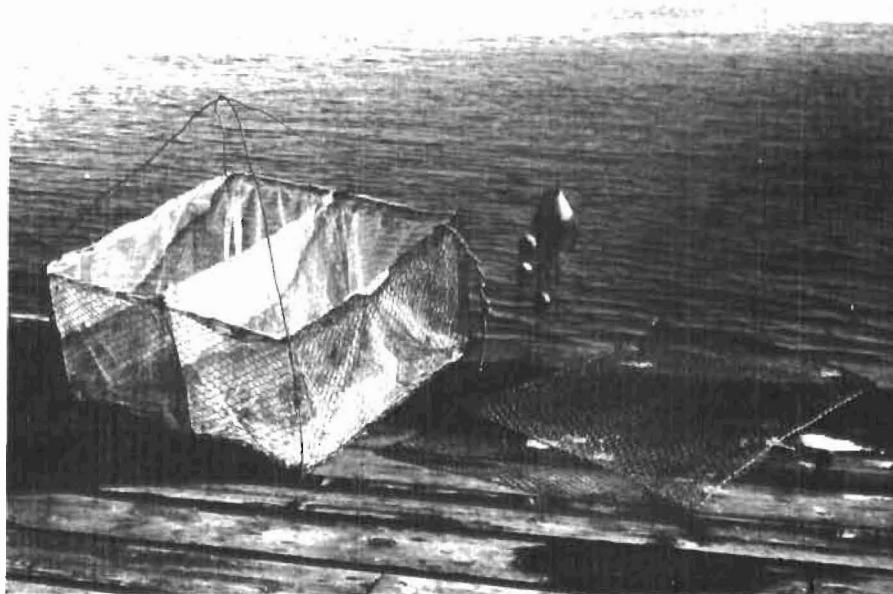


Fig. 4. Wirescreened cage where the mussels were kept during the experiment.

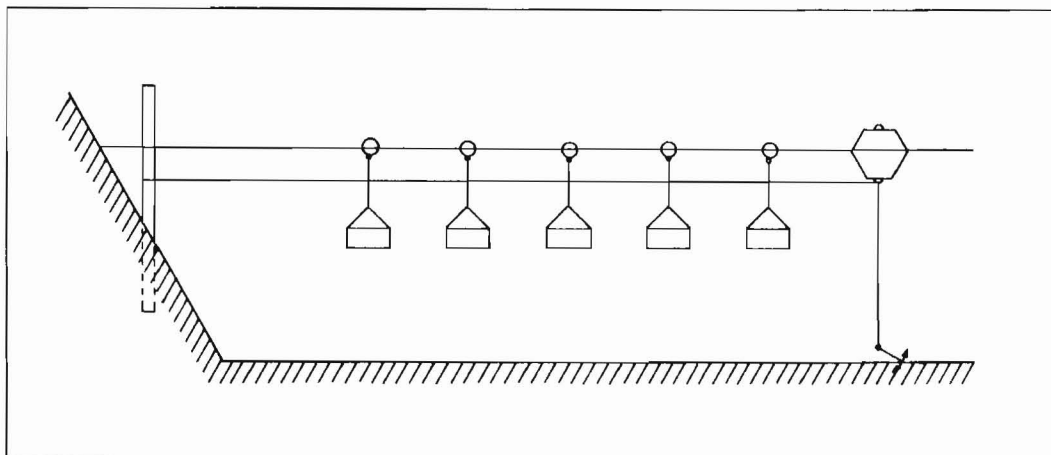


Fig. 5. The anchoring system to which the cages containing mussels were fastened.

Length and volume measurements of the mussels were carried out at approximately monthly intervals, except in the winter, due to formation of ice. The length measurements were carried out by means of a sliding gauge. From 10 repeated length measurements of the same 145 individuals the standard deviation was calculated to be ± 0.07 mm. Mean length, volume, and growth of each size group were calculated.

The volume of the different size groups was recorded in graduated cylinders where sea water functioned as displacement medium. The mean increase in volume for each mussel in the group was calculated. By repeating this operation 10 times with mussels from size group 6 after the investigation was finished, the standard deviation was calculated to be ± 0.10 ml.

In order to determine the spawning time, the condition of the mussels was studied. The index of condition was assessed by measuring the volume of the shell cavity and the weight of the meat contained therein, while both were wet, dividing the meat weight by the shell cavity volume.

$$\text{Index of condition: } \frac{\text{Meat weight}}{\text{Shell cavity volume}}$$

This method was similar to that described by Baird (1958), but he used the meat volume instead of the meat weight preferred here.

In February 1967, 1,100 mussels from Prestvaagen ranging from 35 to 45 mm were placed in cages and immersed 1.7 m below the surface

for condition studies. Measurements were carried out at monthly intervals, from May every fortnight, and about 60 specimens were examined each time. A standard routine was developed for the measurements, and the same routine was exactly repeated each time.

On 5 November 1967 the condition of 61 mussels from the *intertidal* zone in Prestvaagen was measured and compared with the condition of the mussels growing in the cages.

The settlement of larvae was investigated from June to November 1967.

Phytoplankton samples were collected from 4 September 1966 to 1 November 1967 (Table 1). The samples were taken in the surface at the experimental site by submerging 100 ml flasks with 2 ml of 10% neutralized formalin already added.

RESULTS

LENGTH AND VOLUME

The increment in mean length of the cage-mussels in Prestvaagen is highest in the summer, increasing from May/June and decreasing from August/September (Fig. 6).

The growth rate decreases with increasing length of the mussels (Fig. 7). Shells from size group 4 (35-44 mm) had a mean growth rate of 0.069 mm/day the first summer (16 June - 4 September 1966), then during the autumn, winter and spring the growth rate fell to 0.01 mm/day. The following summer (1 June - 23 September), however, it rose to only 0.029 mm/day, mainly due to the greater size attained.

Further, the reduction in growth rate by increasing size is demonstrated by comparing the growth of mussels from size groups 1 and 7 in the period from 16 June to 19 July 1966. By calculation an increase in mean length of 69.4% was found for small shells (group 1) and only 0.4% for the large ones (group 7). Correspondingly reduced growth rate has also been stated for *M. edulis* by Mossop (1922), Seed (1969), and by Wiborg (1946) for *Modiolus modiolus* (L.).

The volume measurements show, as expected, the same seasonal

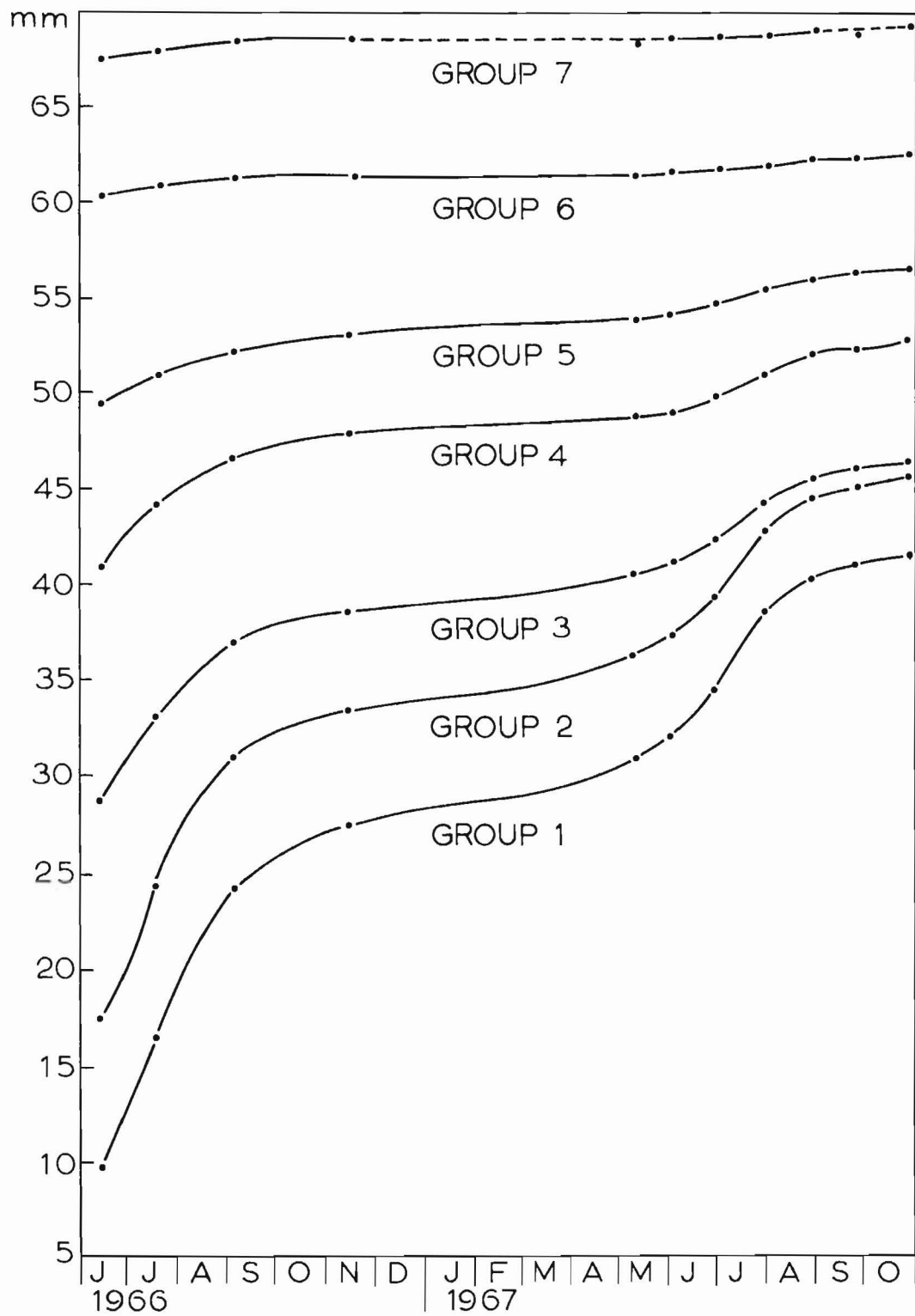


Fig. 6. Mean length of the different size groups from 16 June 1966 to 1 November 1967.

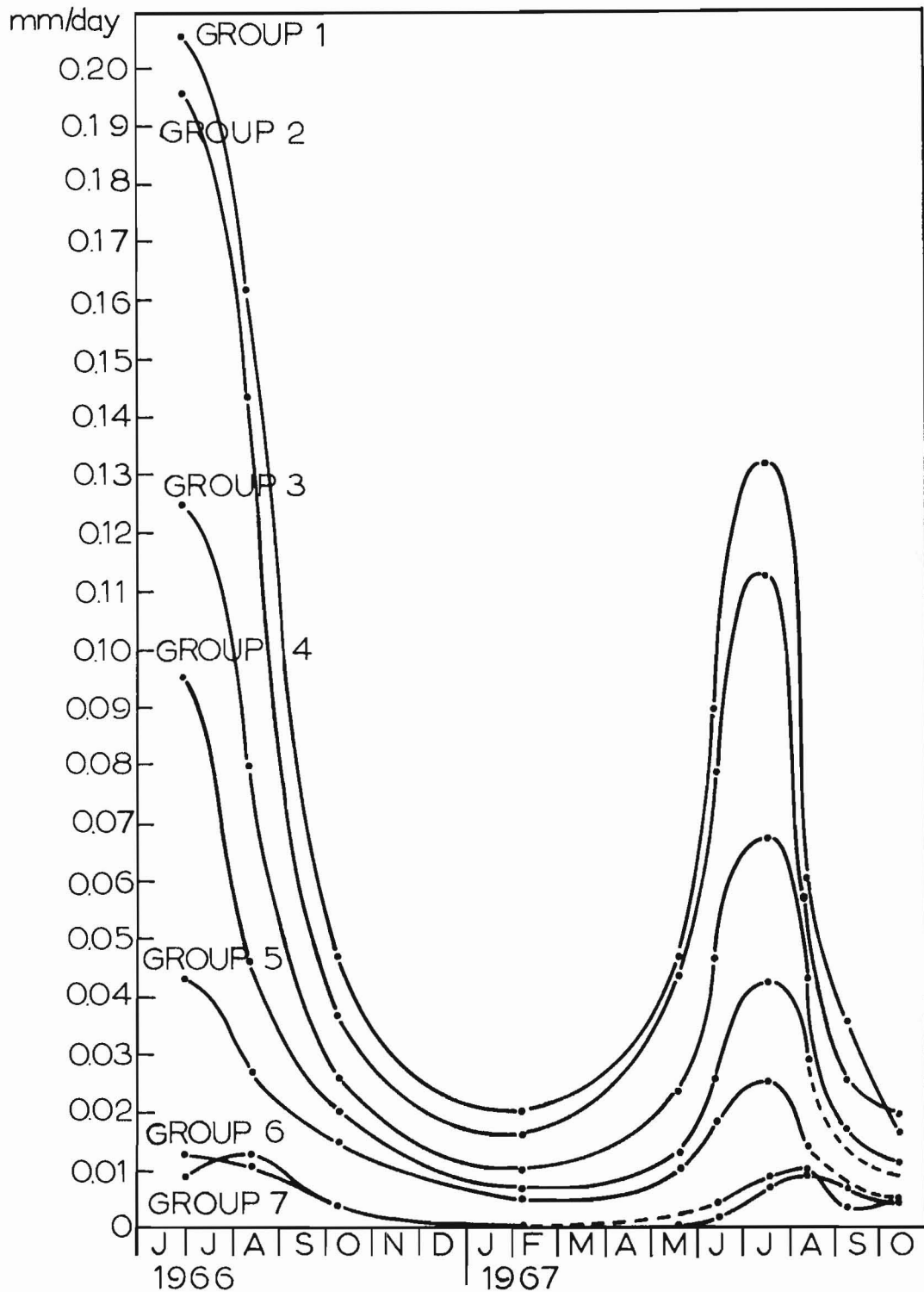


Fig. 7. Growth rates recorded for each size group.

variation in growth as the length measurements (Fig. 8). By calculation the volume increment of the mussels from size groups 1 and 6 from 16 June to 19 July 1966, a mean increase of 269.2% was found for the small mussels and only 1.7% for the large ones.

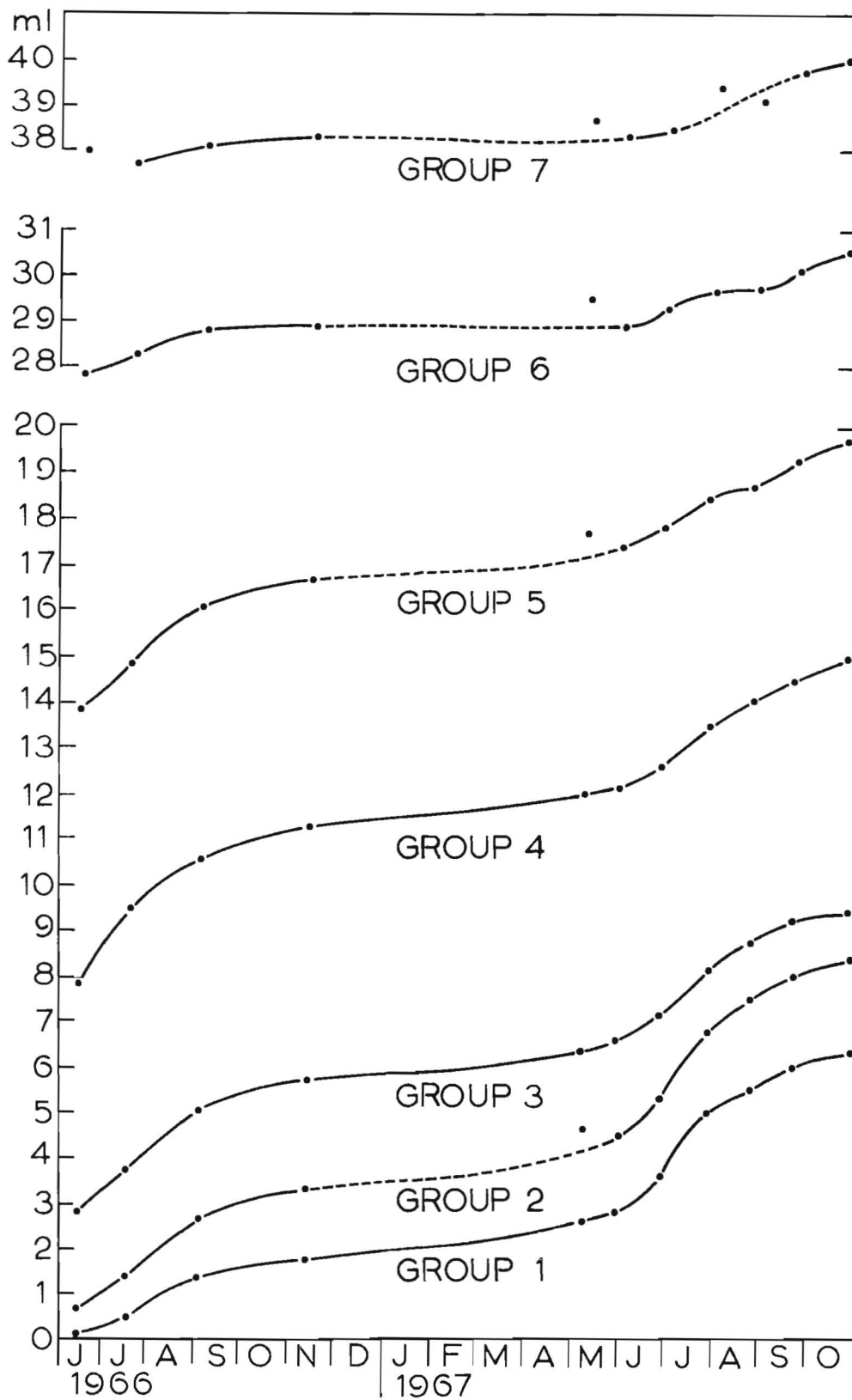


Fig. 8. Mean volume of the different size groups from 16 June 1966 to 1 November 1967.

CONDITION AND SPAWNING

The condition of the mussels (Fig. 9) shows a first decline from 1 to 15 June 1967. This is possibly due to spawning (Baird 1958, 1966), and the assumption is further confirmed by the observation of numerous settled spat six to eight weeks afterwards (30 July 1967). The spat were 3-4 mm long when observed.

A second decline in condition was recorded from 30 July to 23 September 1967. This drop is apparently also caused by spawning, as it was followed by settlement of larvae. This larvae was observed 2 November 1967, 13 weeks after the fall started and 5 weeks after it stopped. The mean length of the settled mussels was then 5.35 mm (51 specimens measured), while the mussels from the first settlement had attained a length of 20.75 mm (51 specimens measured).

A third decline in condition, which started around 8 October, was probably caused by factors other than spawning, and no settlement was observed afterwards.

The condition measurement made on 5 November shows that the natural growing population in the littoral zone were in a much lower condition than the mussels kept in the cages (Fig. 9).

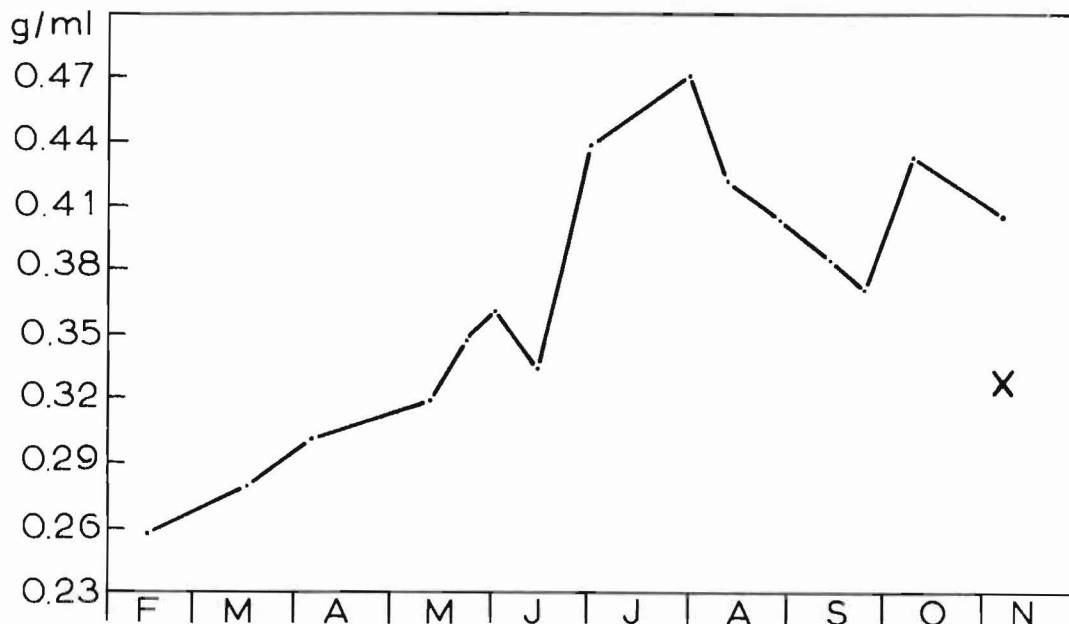


Fig. 9. The condition of mussels (length: 35-45 mm) from 14 February to 5 November 1967. X indicates the condition of natural growing mussels in the intertidal zone.

MORTALITY

The mortality of the mussels in the intertidal zone in Prestvaagen was highest in the winter, caused by the low temperature to which they were exposed at low tide. Mussels covered by seaweed survived to a greater extent. Otherwise, *Asterias rubens* L., present in large numbers, is believed to cause considerable mortality.

In the cages the mussels were never exposed to low air temperatures, but sometimes live *Asterias rubens* (always < 1.5 cm in outer radius) were observed. The mortality caused by them was difficult to estimate, but is believed small.

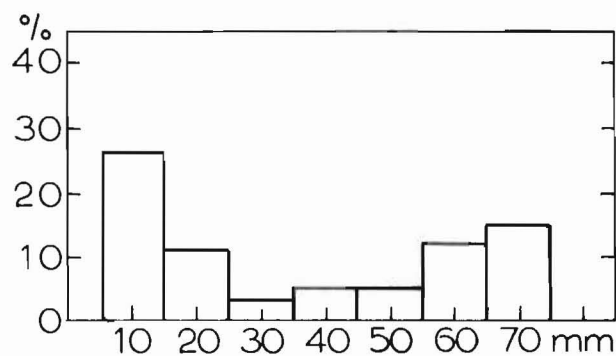


Fig. 10. Death rate (%) in the different size groups from 16 June 1966 to 1 November 1967.

From the observations of the mortality it is evident that the smallest and largest mussels show the highest death rate in the investigated period, 26% and 15% respectively (Fig. 10). The lowest mortality, only 3%, was recorded in size group 3. This indicates that mussels between 30 and 50 mm have the best survival rate.

The mortality per day of all groups combined throughout the experimental period is found to be highest in the summer (Fig. 11).

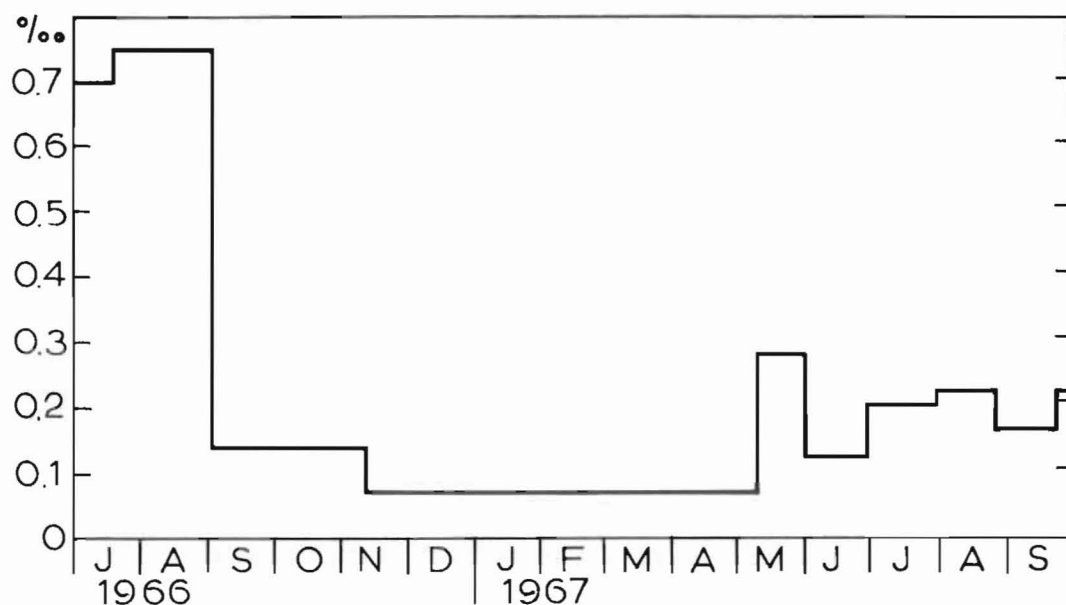


Fig. 11. Death rate in ‰ from 16 June 1966 to 1 November 1967.

DISCUSSION

GROWTH

By means of the growth curves of the different size groups (Fig. 6) and the settlement and growth of the spat, the area within which an expected growth curve had to pass, was drawn (Fig. 12, shaded area). According to the von Bertalanffy growth equation $L_t = L_{\infty} (1 - e^{-kt})$ (Beverton & Holth 1957) where L_t = length in millimetre at the age t in months, L_{∞} = maximum size towards which the length of the mussel is tending, and k = a measure of the rate at which length approaches L_{∞} , the best fitted curve (Fig. 12) is given by the equation $L_t = 65(1 - e^{-\frac{t}{27}})$.

The mussels growing in the cages in Prestvaagen needed almost three years to reach 70% of their maximum length (65 mm) (Fig. 12) and about four years and three months to reach 5 mm in length. Comparison with growth rates in other areas shows that in the Vigo area in North Spain mussels will reach 50 mm in seven months (Andreu 1957) while in Hudson bay they need nine years to reach this size (Lubinsky 1958). As a rule the mussels in the exploited beds of Western Europe reach a length of 50 mm in two to four years (Theisen 1968).

It is supposed that the relatively low growth rates recorded

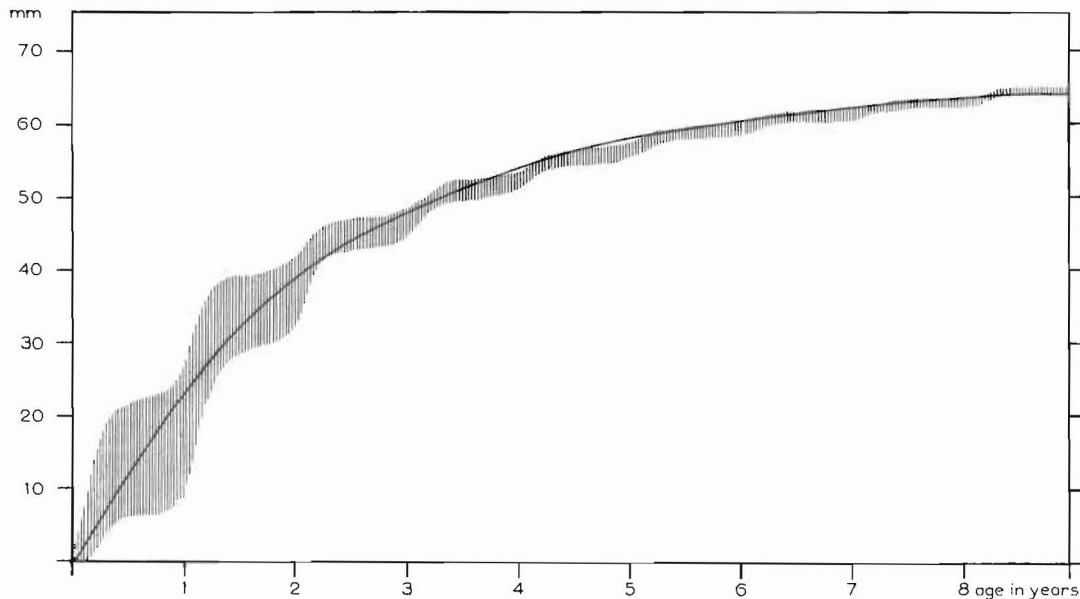


Fig. 12. Growth curve for the mussels in the cages in Prestvaagen.

in Prestvaagen, compared to values obtained in the musselbeds of Western Europe, mostly are due to the relatively low annual mean temperature in Prestvaagen. Correlation between growth of mussels and temperature has been demonstrated by several investigators (Richards 1935, Taylor 1959, 1960, Boëtius 1962, Ursin 1963, Boje 1965, Theisen 1968). High growth rates were found in the summer while little or no growth took place in the winter.

The high growth rate of *M. edulis* obtained in Prestvaagen in the summer also seems to be related to a rise in the sea water temperature (Figs. 3, 6). Further, the increase in growth rate mainly occurs when the seawater temperature exceeds 12°C. Coulthard (1929) recorded a similar rise between 10 and 13°C. (See also Boëtius (1962), p. 342 Fig. 2, where an acceleration in growth around 12°C can be observed). In the winter the growth of the mussels in Prestvaagen is negligible, particularly in the larger specimens.

From the growth data collected, the length increment in mm/day for different sizes of the mussels from Prestvaagen is calculated at 5°C, 10°C, and 18°C (Fig. 13). It is obvious that the growth increment per day is higher at the highest temperatures, and also higher for small than for larger mussels. It is necessary, however, to take other factors into consideration as well, for example the nutrition available, which changed greatly in Prestvaagen during the experiment.

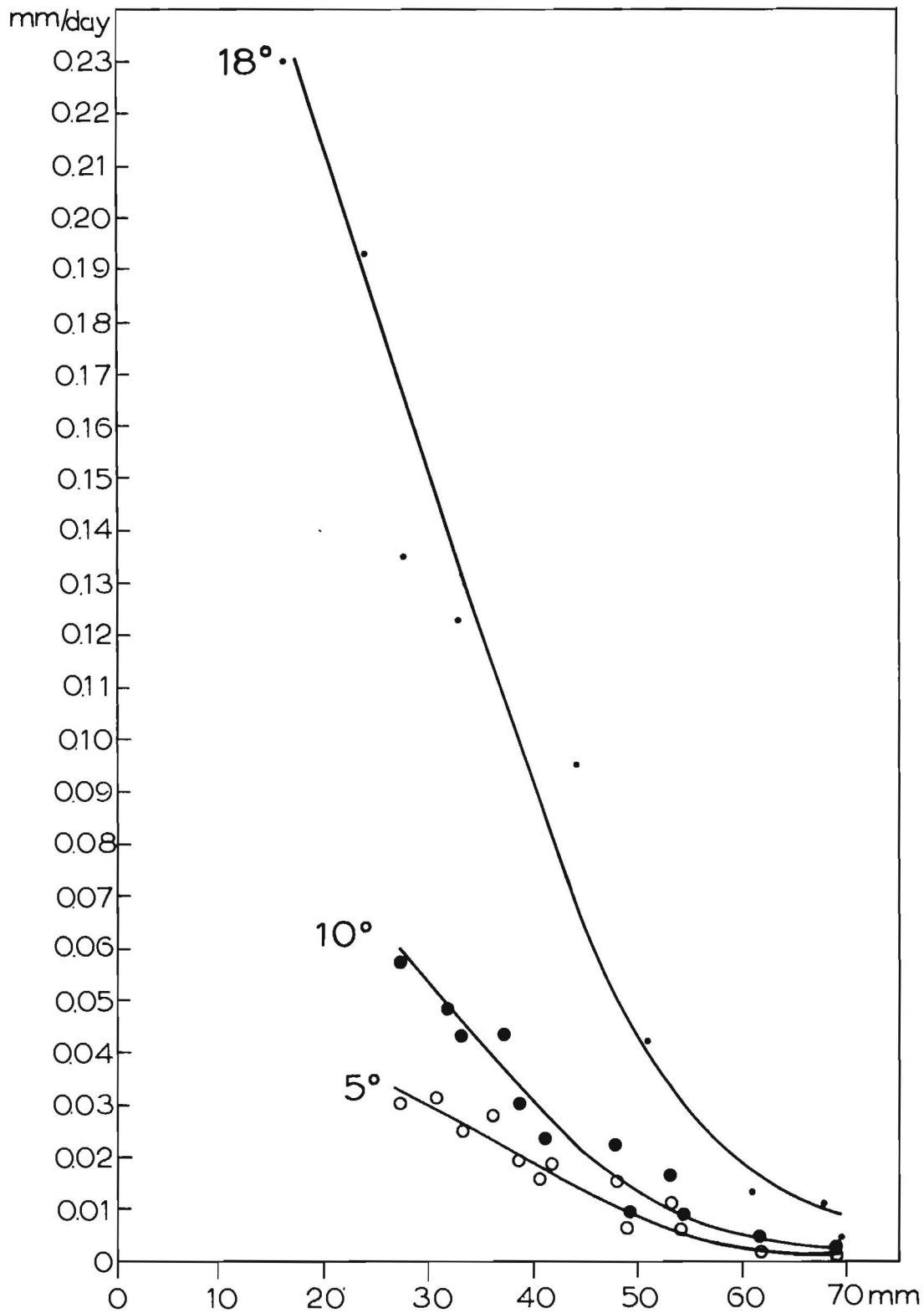


Fig. 13. Growth rates obtained at 5°, 10°, and 18°C for mussels of different size. The dates when 5°, 10°, and 18° were attained can be read from Fig. 3 and the length of the mussels at these actual dates were calculated from measurements. The values for length increment (mm/day) at the actual dates are taken from Fig. 7.

The main source of nutrition for *M. edulis* and *M. californianus* Conrad, which seems to possess identical food requirements (Harger 1970), consists of phytoplankton and detritus of phytoplanktonic origin (Coe 1945, Coe & Fox 1942, 1944, Fox 1936, Fox & Coe 1943, Jörgensen 1966). When temperatures higher than 10°C were attained in 1967, from May and onwards (Fig. 3), the standing stock of phytoplankton in Prestvaagen was below 350,000 cells/l (Table 1). This is a small amount compared with the densities recorded during the spring diatom bloom of March in earlier years (ca. 2 mill. cells/l, Sakshaug 1972), when temperature is usually below 5°C (Wendelbo 1970). In spite of the presumably high density of phytoplankton in March, which should give an excellent supply of nutrition, the growth increment per day is low (Fig. 7). This indicates that the mussels are unable to utilize the phytoplankton resources when the temperature is low.

Table 1. Dinoflagellates and diatoms (cells/litre) in Prestvaagen and the dominating species in each sample

Dato	Dinoflagellates	Diatoms	Dominating species
<u>1966</u>			
4.9	6,420	2,360	Peridinium trochoideum
13.11	1,000	122,540	Skeletonema costatum
<u>1967</u>			
11.5	2,580	27,620	Chaetoceros laciniosus
1.6	27,580	8,640	Gymnodiniaceae indet.
15.6	14,040	311,060	Skeletonema costatum
30.7	200	159,520	Nitzschia "delicatissima"
12.8	36,500	58,520	Nitzschia "closterium"
27.8	4,200	5,500	Nitzschia "closterium"
12.9	3,260	8,000	Nitzschia "closterium" and Licmophora
23.9	14,560	1,500	Nitzschia "closterium", Licmophora, and Cyclotella caspia
1.11	320	960	Ceratium lineatum

Segestråle (1944) and Remane (1958) state that the growth of mussels decreases when the salinity is reduced. During the experimental period in Prestvaagen the lowest salinity was recorded in May/June 1967, in the middle of a fortnight when the freshwater supply from the rivers were three to five times higher than normal (observations supplied by Norges Vassdrags- og Elektrisitetsvesen), and it is supposed that the low salinity is representative for this period. The temperature in the sea (Fig. 3), however, was high, and so was the growth rates (Figs. 3, 7). Therefore, it seems probable that variations in salinity are of minor importance to the growth compared with the influence of temperature.

The conclusion may be that the growth of mussels in Prestvaagen mainly depends upon the temperature, and accelerated growth will take place (within certain limits) with increasing temperature if sufficient nutrition is available. Nutrients never seem to be a limiting factor in Prestvaagen, and other factors may be of minor importance.

SPAWNING AND SETTLEMENT

The condition index indicated that the mussels in the cages in Prestvaagen spawn in two separate periods, in the first part of June and from the beginning of August to the last half of September (Fig. 9).

Spärck (1920) assumes that small mussels attain about 4 mm in length within one month after settlement (23 May) in Limfjorden. If the free swimming larval life is considered to be about four weeks (Chipperfield 1953) and the spat attain about 4 mm in length within four weeks after settlement, the time from spawning and until the mussels have attained 4 mm in length, will be about eight weeks. This fits well with the first observed spawning period in Prestvaagen.

The spat from the second settlement were probably much more than one month old, partly because of their length when observed (5.35 mm), but also due to the slower growth rate recorded in the autumn (Fig. 7). The duration of the free swimming larval life is probably also longer in the autumn because of the low temperature. As a consequence of the spat observed on 2 November it can be concluded that the second fall in condition was also due to spawning. Such a long decline in condition

due to spawning has also been observed by Baird (1958) in mussels at Conway.

A fall in condition index does not always mean that spawning takes place. This is shown by Baird (1966), who observed fall in condition while gonad examination showed that mature ova and sperm were not present. On the other hand, spawning always led to a fall in condition (Baird 1958), and if settlement of larvae is observed **some time** after fall in condition, spawning has surely taken place.

There is, however, no evidence that the same individuals spawned twice. This view was further confirmed by observations made while measuring the condition. In every sample studied, some mussels in more or less bad condition were always observed, prior to and after the spawning period.

MORTALITY

Little information is available from the literature concerning the quantitative changes occurring in a population of *M. edulis*. The most important investigations related to this item are perhaps those by Seed (1969).

In Prestvaagen the highest rate of mortality was recorded among the smallest and the largest mussels (Fig. 10). This is, for the small mussels, possibly caused by unfavourable changes in the environmental conditions, which the small mussels may be expected to be less tolerant of than the largest mussels. The high rate of mortality among the large mussels is probably due to death from old age (Seed 1969).

The mortality per day of all groups combined, was highest in the summer (Fig. 11). This can also be observed in the investigations by Seed (1969, p. 335, Fig. 10).

The increase in mortality in Prestvaagen in the summer may partly be a consequence of disturbing the mussels, for instance by partly removing the byssus threads, because the measurements in the summer were carried out at monthly intervals, while in the winter no measurements were made. In addition, transplantation of natural growing mussels to cages may result in increased mortality at the beginning of the

experimental period. According to Jørgensen (1966), bivalves are very sensitive to disturbance of their normal environment and Harger (1970) recorded mortalities between 10 and 15% caused by removal from water for 12 and 24 hours for measuring, marking, etc.

Much energy is required for maturing of gonads and spawning. It is possible that the energy required is so high that it weakens the viability for some of the mussels. This happens for instance to the oyster (*Ostrea edulis* L.) (Gaarder & Bjerkkan 1934). Therefore, the high death rate obtained in the summer (Fig. 11) may partly also be a consequence of spawning.

Other causes of mortality e.g. predators and competition for food and space, seem to be of minor importance in the wirescreened cages.

CHANGES IN SHELL PROPORTIONS CAUSED BY TRANSPLANTATION

The transplantation of mussels from the littoral zone to cages led to marked changes in their growth and shape. Changes in shell proportions due to transplantation is also showed by Bjerkkan (1911). In the cages the mussels were never exposed to air. This gave them opportunities to feed during the whole tidal period and thus grow faster, as demonstrated by Baird & Drinnan (1957) and Baird (1966). The mussels were also more exposed to the current after the transplantation, which also should bring them a greater supply of nutrition.

Under favourable growth conditions Seed (1968) states that shells of *M. edulis* attain a slender shape. From Fig. 14 it can be seen that mussels, especially in the smaller groups, at the end of the experimental period are longer than mussels of the same volume just transplanted.

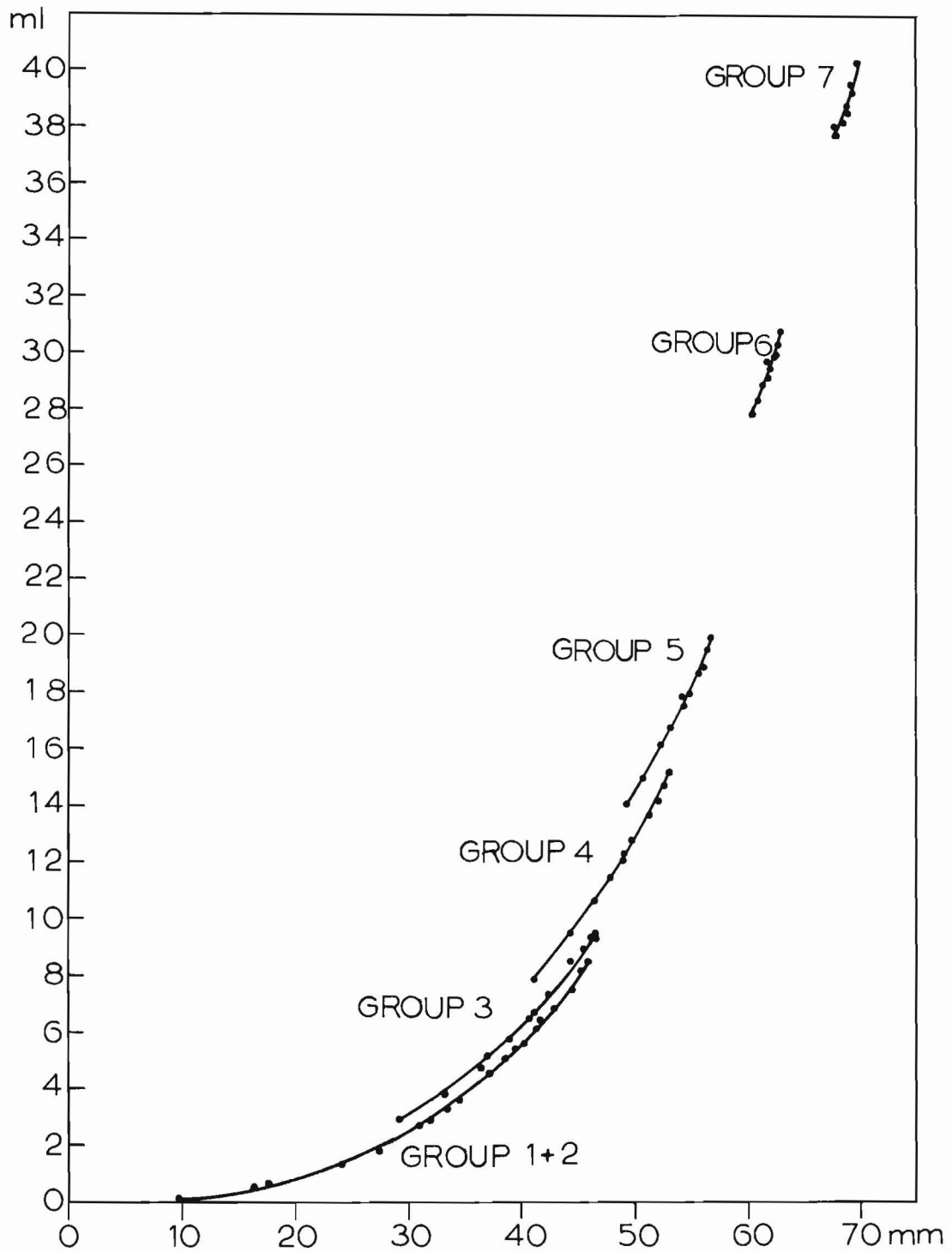


Fig. 14. Length and volume measurements obtained from each size group in the investigated period.

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REFERENCES

- Andreu, B. 1957. Sobre el cultivo del mejillon en Galicia. *Inst. Invest. Pesqueras, III. reunion sobre productividad y pesquerias*: 102-107.
- Baird, R.H. 1958. Measurement of condition in mussels and oysters. *J. Cons. perm. int. Explor. Mer* 23: 249-257.
- 1966. Factors affecting the growth and condition of mussels (*Mytilus edulis* L.). *Fishery Invest., Lond. Ser. II.* 25: 1-33.
- Baird, R.H. & R.E. Drinnan. 1957. The ratio of shell to meat in *Mytilus* as a function of tidal exposure to air. *J. Cons. perm. int. Explor. Mer* 22: 329-336.
- Beverton, R.J.H. & S.J. Holt. 1957. On the dynamics of exploited fish populations. *Fishery Invest., Lond. Ser. II.* 19: 1-533.
- Bjerkan, P. 1910. Om blaaskjæl og blaaskjælavl. *Norsk FiskTid.* 29: 383-385, 419-429.
- 1911. Omplantning af blaaskjæl. *Norsk FiskTid.* 11: 395-399.
- Boëtius, I. 1962. Temperature and growth in a population of *Mytilus edulis* (L.) from the Northern Harbour of Copenhagen (the Sound). *Meddr. Danm. Fisk.- og Havunders. N.S.* 3: 339-347.
- Boje, R. 1965. Die Bedeutung von Nahrungsfaktoren für das Wachstum von *Mytilus edulis* L. in der Kieler Förde und im Nord-Ostsee-Kanal. *Kieler Meeresforsch.* 21: 81-100.
- Böhle, B. 1965. Undersökelse av blåskjell (*Mytilus edulis* L.) i Oslo-fjorden. *Fiskets gang* 51: 388-394.
- Böhle, B. & K.F. Wiborg. 1967. Forsök med dyrking av blåskjell. *Fisken Hav.* (2): 6-10.
- Chipperfield, P.N.J. 1953. Observations on the breeding and settlement of *Mytilus edulis* (L.) in British waters. *J. mar. biol. Ass. U.K.* 32: 449-476.
- Coe, W.R. 1945. Nutrition and growth of the California bay-mussel (*Mytilus edulis diegensis*). *J. exp. Zool.* 99: 1-14.
- Coe, W.R. & D.L. Fox. 1942. Biology of the California sea-mussel (*Mytilus californianus*). I. Influence of temperature, food-supply, sex and age on the rate of growth. *J. exp. Zool.* 90: 1-30.

- Coe, W.R. & D.L. Fox. 1944. Biology of the California sea-mussel (*Mytilus californianus*). III. Environmental conditions and rate of growth. *Biol. Bull. mar. biol. Lab., Woods Hole* 87: 59-72.
- Coulthard, H.S. 1929. Growth of the sea mussel. *Contr. Can. Biol. Fish. N.S.* 4: 121-136.
- Fox, D.L. 1936. The habit and the food of the California sea-mussel. *Bull. Scripps Instn Oceanogr.* 4 (1): 1-64.
- Fox, D.L. & W.R. Coe. 1943. Biology of the California sea-mussel (*Mytilus californianus*). II. Nutrition, metabolism, growth and calcium deposition. *J. exp. Zool.* 93: 205-249.
- Gaarder, T. & P. Bjerkan. 1934. *Østers og østerskultur i Norge*. John Griegs boktrykkeri, Bergen. 96 pp.
- Harger, J.R.E. 1970. Comparison among growth characteristics of two species of sea mussel, *Mytilus edulis* and *Mytilus californianus*. *Veliger* 13: 44-56.
- Jørgensen, C.B. 1955. Quantitative aspects of filter feeding in invertebrates. *Biol. Rev.* 30: 391-454.
- 1966. *Biology of suspension feeding*. Pergamon press, Oxford. 357 pp.
- Lubinsky, I. 1958. Studies on *Mytilus edulis* L. of the "Calanus" expeditions to Hudson Bay and Ungava Bay. *Can. J. Zool.* 36: 869-881.
- Löversen, R. 1957. Forsök med dyrking av blåskjell. *Fisk-Dir. Småskr.* (4): 1-13.
- Mossop, B.K.E. 1922. The rate of growth of the sea mussel (*Mytilus edulis* L.) at St. Andrews, New Brunswick; Digby, Nova Scotia; and in Hudson Bay. *Trans. R. Can. Inst.* 14 (31): 3-22.
- Remane, A. 1958. Die Biologie des Brackwassers. *Die Binnengewässer* 22: 1-348.
- Richards, O.W. 1935. The growth of the mussel, *Mytilus edulis*, at Woods Hole, Massachusetts. II. *Anat. Rec.* 64 Suppl.: 68.
- Sakshaug, E. 1972. Phytoplankton investigations in Trondheimsfjord, 1963-1966. *K. norske Vidensk. Selsk. Skr.* 1972 (1): 1-56.
- Seed, R. 1968. Factors influencing the shell shape in the mussel *Mytilus edulis*. *J. mar. biol. Ass. U.K.* 48: 561-585.

- Seed, R. 1968. The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed rocky shores. II. Growth and mortality. *Oecologia* 3: 317-350.
- Seegerstråle, S.G. 1944. Ein Beitrag zur Kenntnis der östlichen Verbreitung der Miesmuschel (*Mytilus edulis* L.) an der Südküste Finnlands. *Memo. Soc. Fauna Flora. fenn.* 19: 5-7.
- Spärck, R. 1920. Nogle bemerkninger angående yngleforhold hos *Mytilus edulis* L. *Vidensk. Meddr dansk naturh. Foren.* 71: 161-164.
- Taylor, C.C. 1959. Temperature and growth - The Pacific razor clam. *J. Cons. perm. int. Explor. Mer* 25: 93-101.
- 1960. Temperature, growth, and mortality - the Pacific cockle. *J. Cons. perm. int. Explor. Mer* 26: 117-124.
- Theisen, B.F. 1968. Growth and mortality of culture mussels in the Danish Wadden Sea. *Meddr Danm. Fisk.- og Havunders. N.S.* 6: 47-78.
- Ursin, E. 1963. On the incorporation of temperature in the von Bertalanffy growth equation. *Meddr Danm. Fisk.- og Havunders. N.S.* 4: 1-16.
- Wendelbo, P.S. 1970. *Hydrografiske forhold i Trondheimsfjorden 1963-1966.* 98 pp. (Typewritten dissertation in geophysics deposited at the University of Oslo).
- Wiborg, K.F. 1946. Undersøkelser over oskjellet (*Modiola modiolus* (L.)). I. Alminnelig biologi, vekst og økonomisk betydning. *Rep. Norw. Fishery mar. Invest.* 8 (5): 1-85.