Reproduction of Mytilus edulis L. (Bivalvia) in a brackish water area, the Gulf of Finland

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The reproductive cycle of the common mussel, Mytilus edulis, was followed for one year from July 1978 to June 1979 from histological preparations of the mantle. Spawning occurred mainly in July, but individuals in spawning condition were found throughout the year. The most inactive time was from August to October, after which genital canals penetrated the mantle. The first ripe gametes emerged in February. The sex ratio was 1:1. Only two specimens out of 1832 individuals studied were hermaphrodites. No differences in the spawning periods were noted between age classes.

Mussels of different age and size are found in different locations. Small, less than 3 mm long, individuals settle in filamentous algae outside the mussel field. About 95 % of animals attached to algae were under 3 mm long, while only 0.2 % of those settled in the mussel field were of this size.

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1. Introduction

As a euryhaline species the common mussel Mytilus edulis L. is distributed in the brackish water of the Baltic Sea. In contrast to marine mussels, those found in brackish water are small. A salinity of about $4.5\,^0/_{00}$ limits the distribution of Mytilus (Segerstråle 1942). In the Tvärminne area such salinity limits are found in the Pohjanpitäjänlahti bay (Koli 1961). This bay has a vertical salinity gradient formed by rivers discharging into the head, of which fresh water remains in the surface layers (Niemi 1977).

The breeding cycle of Mytilus edulis from this area was studied for one year from histological preparations of the mantle. No previous information was found concerning the reproduction of Mytilus in the northern Baltic based on a whole year's studies. In the Gulf of Finland, the spawning of Mytilus has been studied from larvae in plankton by Lassig (1965), and in the southwestern Finnish archipelago from histological preparations collected during one summer by Heinonen (1960). Examinations have been made under true marine conditions by Battle (1932), Chipperfield (1953), Moore & Reish (1969), Seed (1968, 1975), Kennedy (1977), and others. After a pelagic phase the Mytilus larvae settle in

filamentous algae. When they have reached a certain size they detach themselves and move during an active phase to the final location (Bayne 1964). Adult mussels are found e.g. on stones, in Fucus or in mussel fields, where mussels are attached to the bottom and to each other so thickly that other animals or plants are seldom found there. The size and age structure of a mussel field and mussels on surrounding algae were studied.

2. Material and methods

Samples were taken monthly from July 1978 to June 1979 to determine the developmental stage of the gonads. Mussels were collected from a mussel field near Tvärminne Zoological Station (salinity 6—7 0 / $_{00}$, depth 5—7 m). In May 1979, samples were also taken from two other stations. The most inshore station is the last mussel field near Pohjanpitäjänlahti, before the salinity falls sufficiently to form limits of the distribution of *Mytilus* (Källvik, depth 5 m). At this station the salinity is 5—6 0 / $_{00}$ at the bottom and 1—4 0 / $_{00}$ on the surface (Halme 1944). The third sampling station is located in the outer archipelago near the open sea (Långskär, depth 2 m).

Samples were prepared immediately, or kept overnight in an aerated continuous flow aquarium. Two age and size classes were studied: maximum length 1.0-1.5

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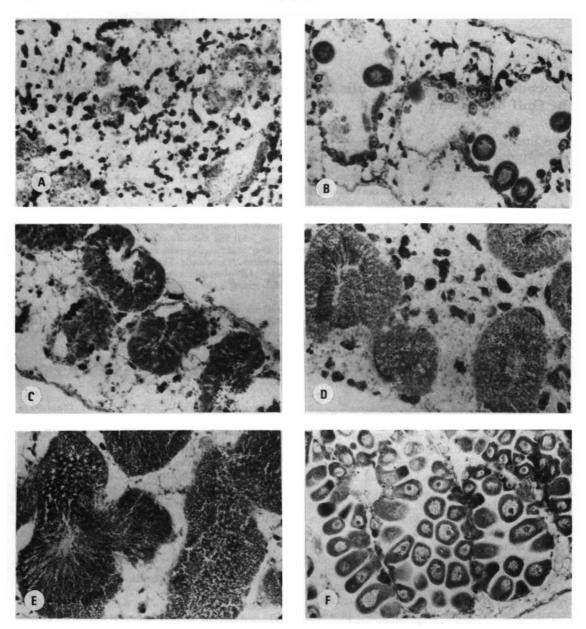


Fig. 1. Classification of the developmental stages of the gonad. Sections are stained with Masson-Gomori (× 200). A. Female — developmental stage 1. B. Female — developmental stage 2. C. Male — developmental stage 2. D. Male — developmental stage 3. E. Male — developmental stage 5.

cm (2 — 4 years old) and 2.0 — 2.5 cm (5 — 7 years old). Age was determined from growth rings on the valves. The whole mantle from one valve was removed from small individuals and the middle third from large mussels. About 120 mussels were prepared each time. The tissue was fixed in Bouin's fluid and embedded in paraffin. About seven pieces were embedded together. Sections 10 μ m thick were stained with Masson-Gomori. To define the age

of attaining maturity, 70.5 - 1.0 cm long individuals of each age class (1, 2 and 3 years old) were prepared. The developmental stage was expressed by a gonad index, which was calculated according to Chipperfield (1953): the number of mussels at each stage was multiplied by the numerical score of the stage, products were added and the result divided by the number of individuals in the sample. Developing individuals were described by numerical

scores 1-5 and spawning by values 4-1. A resting or immature gonad was defined with value 0, and so the gonad index varied from zero, when no sexual activity was noted, to five, when all the individuals were mature. The classification of Seed (1969) was used (Figs. 1 and 2).

A sample of 1000 individuals was taken from the mussel field to examine the age and size distribution. Algae from the surroundings of the field were collected in order to find small individuals.

Classification of the gonad developmental stages

Stage 0. Immature or already spawned, resting gonads. No genital canals observed in the mantle: the sexes cannot be distinguished. Mantle is filled with fat or glycogen. It is transparent and thin, or thick and whitish depending on the state of nutrition.

Developmental stage 1. Ducts lined with germinal epithelium begin to appear in the middle of the connective tissue. Ripe gametes cannot be observed, but early stages of gametogenesis are present (Fig. 1A).

Developmental stage 2. The connective tissue makes room for the genital ducts. Ripe sperma and ova appear in the middle of the follicles, but the early stages — spermatogonids and spermatocytes and ovocytes fastened in the germinal epithelium — dominate (Fig. 1B and C).

Developmental stage 3. The follicles are about halffilled with gametes, the other half consisting of early stages of gametogenesis. The ducts have extended to fill about half of the mantle matrix (Fig. 1D).

Developmental stage 4. Follicles have invaded almost all of the mantle. Cells undergoing gametogenesis can still be found in the margins of the ducts, but ripe gametes dominate.

Developmental stage 5. The highest stage of sexual maturity is achieved. Follicles are full of ripe gametes. Some gametocytes are still in the margin of the ducts (gamètes de réserves, Lubet 1957). Tighly compacted ova have an angular configuration (Fig. 1E and F).

Spawning stage 4. The release of gametes into sea water has begun. Follicles are still full of gametes, but their numbers in the middle have decreased and the ova have a spherical shape.

Spawning stage 3. Follicles are half-full of gametes. This can be distinguished from the corresponding developmental stage by the scarity of developing cells. The number of fat and glycogen containing cells increases at the expense of the genital tissue.

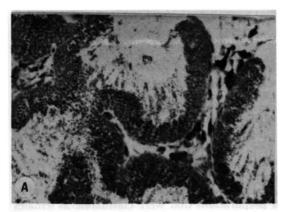
Spawning stage 2. Gametes fill less than half of the follicles. The ducts are still shrinking, whereas the connective tissue is expanding (Fig. 2A and B).

Spawning stage 1. The follicles have disappeared almost completely. Some sperma and ova are left. In the ducts phagocytes cytolyse residuals gametes — these parts stain yellowish.

3. Results

During the breeding period the genital tissue of *Mytilus edulis* spreads to almost all tissues, including the mantle, mesosoma, the outer surface of the digestive gland and the floor of the pericardium. Only the foot, gills, muscles and the dorsolateral walls of the pericardium are not occupied by the branched tubules of the gonads (White 1937). When spawning begins, genital canals penetrate the mantle matrix. Canals lined with ciliated epithelium terminate in follicles where gametes develop from germinal epithelium. After spawning the canals disappear.

Simple epithelium covers both sides of the mantle (Fig. 3A): it is ciliated on the visceral side. The early stages of gametogenesis occur in the margins of the ducts and the ripe gametes are found near the ciliated surfaces (Fig. 3D). The canals are lined with ciliated epithelium (Fig. 3B). The female follicles comprise folds where the ovocytes fasten (Fig. 3C). The ova are at first attached to the epithelium. They loosen after



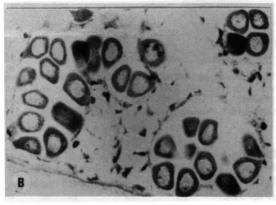


Fig. 2. Classification of the developmental stages of the gonad. A. Male — spawning stage 2. B. Female — spawning stage 2.

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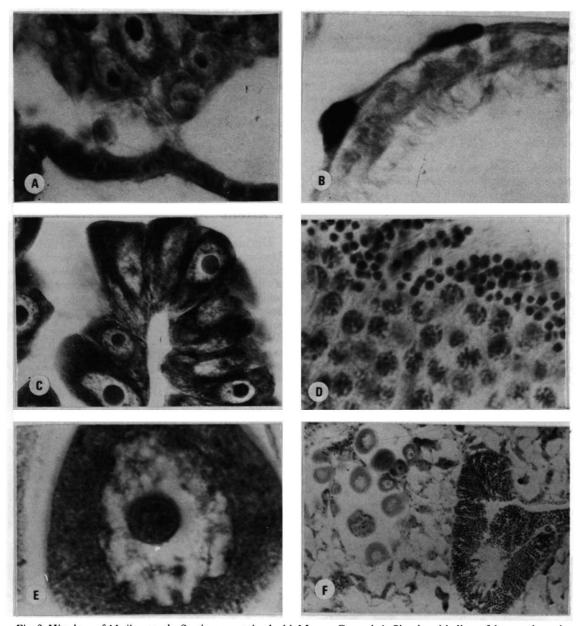


Fig. 3. Histology of Mytilus mantle. Sections are stained with Masson-Gomori. A. Simple epithelium of the mantle on the shell side (\times 1500). B. Ciliated epithelium of genital canal (\times 1500). C. Ovocytes fastened to a fold in a female follicle (\times 2000). D. Cross-section of a male follicle with gametocytes and ripe sperma (\times 2000). E. An ova with large nucleus, lamp-brush chromosomes and nucleolus (\times 2000). F. Hermaphrodite (\times 200).

forming a stalk and are angular until spawning begins. The nucleus is large and contains lamp-brush chromosomes and a well-defined nucleolus (Fig. 3E).

Only two of the 1832 investigated individuals were hermaphrodites (Fig. 3F). The sex ratio was

1:1 when calculated from the whole year's samples. The sexes cannot be distinguished in already spawned or inactive gonads. The number of preparations that were classifiable as females was larger at the beginning of the year until July, when it decreased, and reached a minimum in

October, when there were four times more males than females. During winter the numbers of females and males became even.

Eighteen per cent of 1-year-old and 6 % of 2 or 3-year-old mussels $0.5-1.0\,\mathrm{cm}$ long were not sexually mature. There were no differences in gonad indexes between large and small individuals.

The spawning peak was in July, though individuals in spawning condition were found throughout the year. The most inactive period was from August to October, after which the ripening of gametocytes began. Gametogenesis progressed slowly: the first ripe gametes appeared in the follicles in February. Before this the canals were invaded by the early stages of gametogenesis. Immature cells remained in the gonads (gamètes de réserves, Lubet 1957) even after spawning. The distributions of different stages and gonad indexes are given in Tables 1 and 2.

Gonad indexes with respect to the sea water temperature and the thickness of ice are illustrated in Fig. 4. The percentages of spawning, developing and spent individuals vary during the

Table 1. Distribution of different stages.

Sampling locality and date	N	Males		Females				
		developmental stages	spawning stages	developmental stages	spawning stages	spent 0		
		1 2 3 4 5	4 3 2 1	1 2 3 4 5	4 3 2 1			
Tvärminne								
18.I.79	111	13 10	118	52 12 — — —		5		
19.II.79	116	6 24 3 1 —	3 6	37 28 3 — —	3			
16.III.79	103	2 26 20		22 25 2 — —		2 6 2		
20.IV.79	126	2 31 19 4 —	2 1 1 —	3 44 14 3 —		2		
21.V.79	112	4 11 23 13 -		2 22 28 8 —		_		
10.VI.79	119	- $-$ 1 11 21	19 2 — —	— 4 12 22 10	9 3 2 2	1		
4.VII.78	118		15 35 5 5	1 2 1	14 23 6 3	6		
7. VIII. 78	117		— 6 21 15	4 2	- $-$ 7 20 42			
11.IX.78	109		— 6 21 14	3 2	- 1 11 10 41			
14.X.78	110		— 6 20 19	3 3	1 4	54		
18.XI.78	108	1	— 3 21 18	40 7 — — —	- 1	15		
18.XII.78	120	17 17 1 — —	— 1 10 13	36 15 1 — —		9		
Källvik								
22.V.79	128	— 9 16 29 3	1 1 1 —	— 7 18 31 9	1-	2		
Långskär								
24.V.79	120	— 1 15 22 1	6 1 — —	2 16 38 14 1	1 1	1		

Table 2. Distribution of gonad indexes.

Sampling locality and date	Sex		Size		\mathcal{N}		Salinity	Water	Thickness of ice	
	3	φ	Large	Small	Tot.	₫	·	(⁰ / ₀₀)	temp. (°C)	(cm)
Tvärminne										
18.I.79	1.50	1.19	1.30	1.20	1.25	42	64	6.58	-0.3	40
19.II.79	1.84	1.48	1.69	1.47	1.59	43	71	6.48	-0.3	65
16.III.79	2.38	1.59	1.89	1.83	1.86	48	49 ·	6.58	-0.3	77
20.IV.79	2.68	2.27	2.90	2.16	2.34	56	64	6.46	0.3	50
21.V.79	2.88	2.70	2.84	2.61	2.78	51	60	6.62	4.2	
10.VI.79	4.33	3.64	3.82	4.03	3.92	54	64	6.55	6.7	
4.VII.78	3.00	2.96	2.73	2.86	2.80	60	50	_	11.4	
7.VIII.78	1.79	1.27	1.14	0.83	1.00	42	33	5.90	18.0	
11.IX.78	1.80	1.56	1.27	0.82	1.06	41	27	5.70	14.2	
14.X.78	1.71	1.36	0.90	0.77	0.84	45	11	6.40	7.7	
18.XI.78	1.63	1.19	1.36	1.10	1.19	43	48	7.26	4.8	
18.XII.78	1.53	1.33	1.50	1.17	1.33	59	52	6.92	0.5	
Källvik										
22.V.79			3.75	3.18	3.48	60	66	4.63	7.8	
Långskär 24.V.79			3.25	3.14	3.19	46	73	6.62	8.8	

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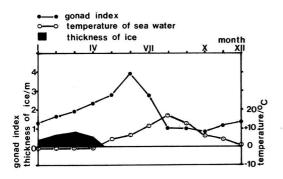


Fig. 4. Gonad indexes with respect to the sea water temperature and the thickness of ice.

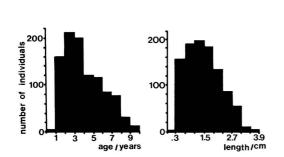


Fig. 6. The age and size distribution of a mussel field.

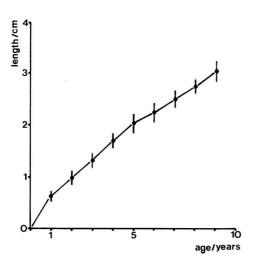


Fig. 7. Age in relation to length, in the mussel field.

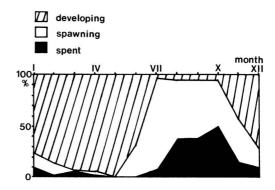


Fig. 5. The percentages of developing, spawning and spent individuals during the year.

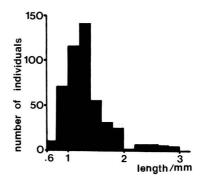


Fig. 8. Size distribution of the mussels in the filamentous algae.

year as shown in Fig. 5.

Small and large bivalves appear in different surroundings (Fig. 9A and B). Less than 3 mm long mussels are absent from the field: they are fastened to the algae outside it. The age and size distributions of the mussel field near Tvärminne Zoological Station are illustrated in Fig. 6 and mussel age in relation to length in Fig. 7.

The filamentous algae supporting the community of small individuals were composed mainly of the brown algae *Ectocarpus siliculosus* and *Pilayella litoralis*. The size distribution of the mussels in the algae is shown in Fig. 8.

About 95 % of mussels in the filamentous algae were less than 3 mm long in the beginning of July. In the mussel field only 0.2 % were of this size.

4. Discussion

The absence of small individuals from the mussel field might be a result of sampling: the

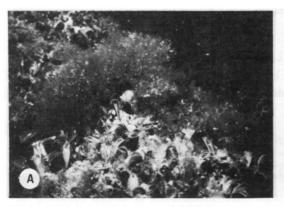




Fig. 9. A. Adult mussels in a mussel field. B. Less than 3 mm long mussels attached to filamentous algae. Photographs Markku Porkka.

diver collected only stones and mussels attached to them. The small bivalves are, furthermore, weakly fastened. It is, however, possible that small and large individuals choose different environments (primary and secondary settlement system, Bayne 1964). The larva develops in plankton for about three weeks and then sinks down to the filamentous algae and fastens onto them (Thorson 1946). Development to the plantigrade stage occurs in this milieu (Suchanek 1978). Thereafter the byssal attachment loosens and the mussel moves to the adult field. According to Bayne (1964) this happens when the mussel becomes 0.9-1.5 mm long, and according to Seed (1969) at 1-2 mm.

The reason for the primary and secondary settlement system might be competition between different generations for food and oxygen (Bayne 1964). Planktic larvae crossing the mussel field are taken with the filtered water into the mussel and are incorporated with pseudo-faeces. One adult *Mytilus* is estimated to filter 100,000 larvae in 24 hours (Bayne 1964).

The sex ratio was 1:1, but unequal sex ratios of Mytilus are often observed. Such results are obtained, if the whole sample is taken at the same time in a season, when some of the mussels have already spawned and the gonads are inactive. The sexes cannot then be distinguished. Males and females seem to reach the resting stage at different times. In August there was a preponderance of males over females in the ratio of four to one. Individuals representing the resting stage were clearly mostly females.

The hermaphrodites were at different spawning stages, ova being released first. The spawning peak was in July. According to Lassig (1965) bivalve larvae can be found in plankton in the

Gulf of Finland from the middle of June to the beginning of September. On the British coasts spawning occurs in April — June according to Bayne (1964), in April — May according to Chipperfield (1953), and mainly in March according to Seed (1969). No differences were noted between sampling stations or age (size) classes, and the period of spawning varies annually (Seed 1969).

Alterations in sea water or air temperatures clearly did not induce spawning. According to Battle (1932) the lunar cycle induces spawning through the tides. According to Bouxin (1956) it is induced by some sudden phenomen after ripening of the gametes; e.g. change in temperature or salinity, shaking, chemical stimulation, etc. According to Suchanek (1978) spawning is induced by mechanical movement such as severe storms at the end of the winter. Shaking induces spawning in the laboratory.

Almost every individual in the mussel field was mature. Maturity is attained in the first year of life (Seed 1969). Immature animals might be found outside the field of filamentous algae.

There are many schemes of classification of the gonad stages (Chipperfield 1953, Bayne 1964, Seed 1969, Kennedy 1977). The existence of the "gamètes de réserves" makes the classification more difficult, because it is difficult to distinguish recently spawned and developing individuals. Already spawned animals can "remature" by using the reserve gametes (Kennedy 1977).

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