

JEM 322

## ASPECTS OF THE POPULATION ECOLOGY OF *LUCINOMA* *BOREALIS* (L.) (BIVALVIA) IN RAUNEFJORDEN, WESTERN NORWAY

BJÖRN TUNBERG

Kristineberg Marine Biological Station, S-450 34 Fiskebäckskil, Sweden

**Abstract:** 2194 *Lucinoma borealis* (L.) were obtained from 99 quantitative (0.2 m<sup>2</sup>) samples of substratum (stratified random sampling) collected between November 1975 and October 1976 in the archipelago of Eggholmane ≈ 20 km south of Bergen. The depth range of the 20900 m<sup>2</sup> area was 0.3–13.3 m, and the bottom sediment (fine to very coarse sand) was rich in calcium carbonate. The highest density was found in the deep (≈ 8–13 m) sub-areas, with fine sediment (median grain-size diameter ≈ 0.3–0.5 mm). *L. borealis* was the most abundant bivalve species in the area studied (59.6%, by number). The average density was 22.2 (C.I. ± 5.4) ind. · 0.2 m<sup>-2</sup>, and the biomass was 690 (C.I. ± 116) mg AFDW · 0.2 m<sup>-2</sup>. The average size of animals found in shallow water (coarse sediment), with low abundance, was markedly larger than that of those from deeper water. Adults from shallow water consisted of 49.5% females, but in deep water the corresponding figure was only 38.6%.

According to the data, spawning in deep water occurred in June, August–September, and possibly also in January–February. The spawning period in shallow water was more diffuse and uncertain. The egg diameter of 123.75 (C.I. ± 1.59) μm, indicates a lecithotrophic development. Maturation occurred at a shell length of 10–13 mm, and the largest animal found was 34.3 mm long. The shell of *L. borealis* grows allometrically.

Key words: Bivalvia; population dynamics; reproduction; biometry; Western Norway

### INTRODUCTION

The Lucinacea is a well-defined group, which shows many characteristic features, including an elongate anterior adductor muscle and a highly specialized foot, which forms the anterior inhalant tube (Allen, 1958). This foot is capable of extending to a remarkable length (Allen, 1953), and is also used for burrowing (Stoll, 1938; Allen, 1958). The digestive tract is simple and the Lucinacea are able to feed on large, variably sized particles.

In Scandinavian waters the Lucinacea includes three families, namely the Lucinidae, the Thyasiridae, and the Diplodontidae. The Lucinidae differ from the Diplodontidae by their less perfectly developed gills (Dall, 1901). The Lucinidae also differ from the Diplodontidae and the Thyasiridae in possessing an exhalant siphon. This is developed from the inner muscular lobe of the mantle and does not contract into a pallial sinus, but turns inside out and lies in the suprabranchial cavity.

*Lucinoma borealis* was first described by Linnaeus in 1766 as *Venus borealis*. In the Atlantic it occurs from the Norwegian Sea to Morocco (Tebble, 1966). Ockelmann (1958) notes findings from the north of Lofoten in Norway, and from the Faroes. Sars

(1878) states that it is common in shallow water at Vadsø in the Barents Sea. According to Haas (1938) it has also been found in the North Sea, Kattegat, and the Mediterranean. The distribution in the Mediterranean is also confirmed by Allen (1958). The depth distribution and habitat preference according to some different authors are presented in Table I.

The present survey was performed as part of a study of the quantitative distribution of endopsammon in a shallow, sandy bottom in Raunefjorden, with emphasis on aspects of the population dynamics of some of the most important bivalve species. Among the 32 bivalve species found in this area, *Lucinoma borealis* was by far the most abundant being 59.6%, by number (Tunberg, 1981). Little has been published on the biology of *L. borealis*, and it is possible that the name includes more than one species (K.W. Ockelmann, pers. comm.).

The number of specimens of *L. borealis* (L.) obtained from 99 quantitative samples in the area studied was large enough for studies on the population ecology of this species, with emphasis mainly on quantitative distribution, size composition, biomass, sex-distribution, reproduction, and biometry.

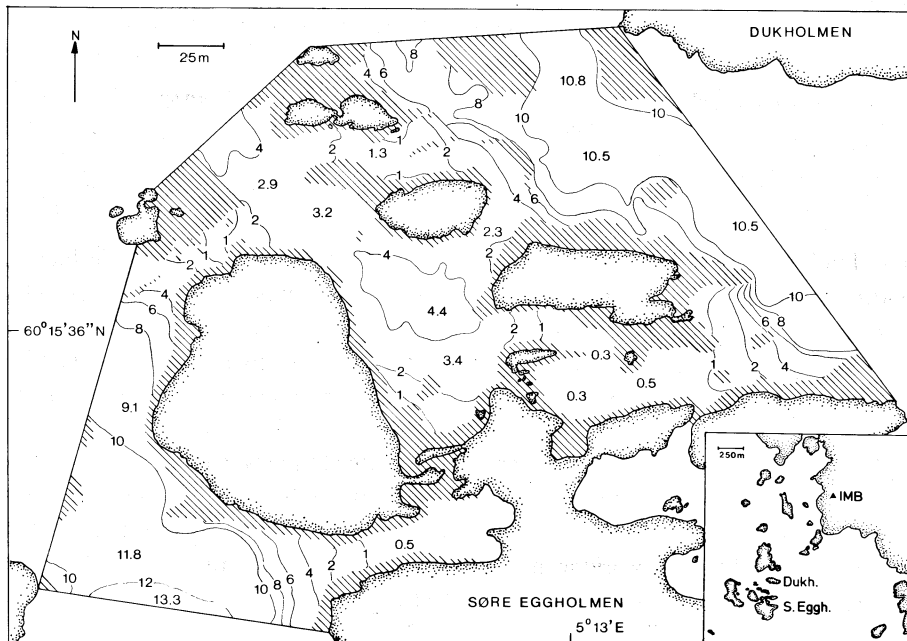


Fig. 1. The area studied: hatched parts indicate rock or pebble bottom; contours are shown for 1, 2, 4, 6, 10, and 12 m depth; all depths have been corrected to LWS; IMB, Department of Marine Biology; from Tunberg (1981).

## MATERIAL AND METHODS

The material and methods used have been presented in Tunberg (1981), and are only briefly summarized here.

The survey was made in a shallow (0.3–13.3 m), sandy bottom at Eggholmane,  $60^{\circ}15'36''\text{N}$ :  $5^{\circ}13'\text{E}$  (Department of Marine Biology, Ref. Numbers E191-75 and E298-76). The area studied covered  $38\,800\text{ m}^2$ , but was somewhat reduced because of bottom conditions (Fig. 1); it was divided into nine sub-areas, A–I (Fig. 2). The sizes of these areas are presented in Table II. Sixteen sediment cores were collected

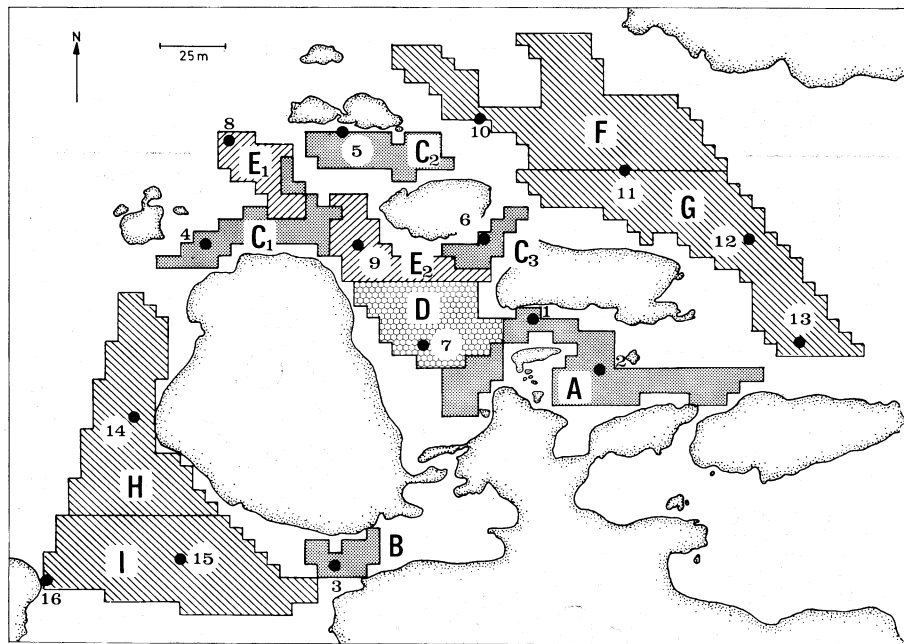


Fig. 2. The nine sub-areas, A–I, within the area studied: ●, 16 sediment sampling sites for grain-size and  $\text{CaCO}_3$  analyses; from Tunberg (1981).

TABLE I

Depth distribution and habitat preference of *Lucinoma borealis* according to different authors.

Depth	Habitat	Reference
Near LW – $\approx 165\text{ m}$	Sand	Forbes & Hanley (1853)
LWS – $150\text{ m}$	Muddy gravel and sand	Jeffreys (1863)
20–50 m (Kattegat)	–	Jensen & Spärck (1934)
0–100 m	–	Haas (1938)
ELWS – $\approx 165\text{ m}$	Sandy mud	Allen (1958)
Low intertidal – $\approx 100\text{ m}$	Sandy mud or gravel	Tebble (1966)

throughout the area for grain size and calcium carbonate analysis, and  $\approx 600$  soundings were made for mapping of the bottom topography. Quantitative bottom samples of  $0.2 \text{ m}^2$ , 16 cm deep, were collected from each sub-area 11 times at regular intervals between November 1975 and October 1976. The 99 samples were collected with a suction sampler described in Tunberg (1983). The locations of the substratum sampling points are shown in Fig. 3. The temperature was measured  $\approx 10 \text{ cm}$  above the bottom surface of each sampling location. Length, height, and width of the animals were measured by means of vernier callipers, with an accuracy of  $\pm 0.1 \text{ mm}$  (Fig. 4). Animals  $< 10 \text{ mm}$  were measured under a stereomicroscope. The material was preserved in 4% formalin before further treatment. Small samples of the gonads were taken and analysed microscopically for sex-determination. Dry weight (DW) and ash-free dry weight (AFDW) of the soft parts were calculated according to Crisp (1971). The accuracy of these measurements was  $\pm 0.1 \text{ mg}$ .

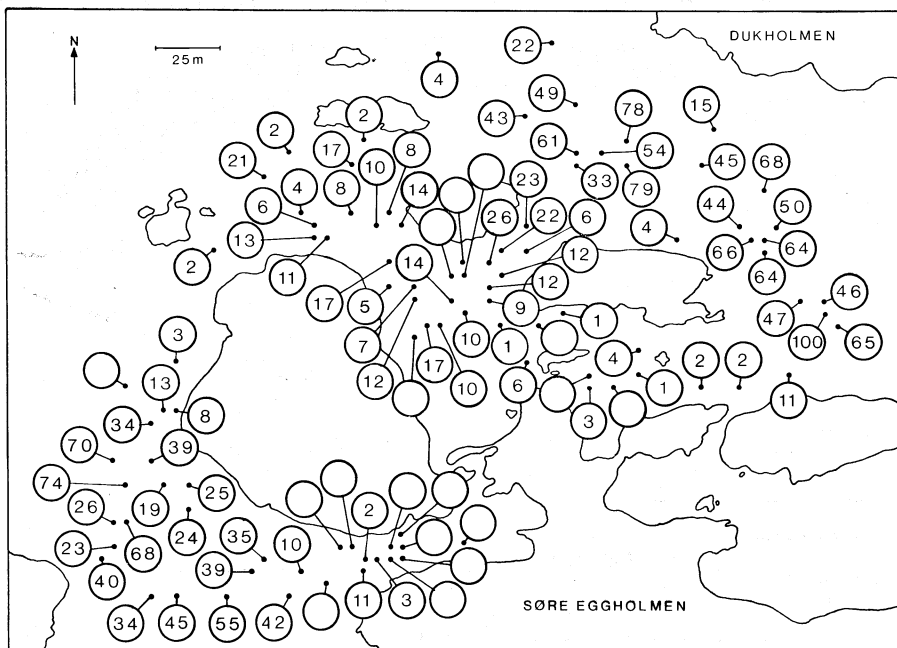


Fig. 3. Number of specimens of *Lucinoma borealis* found in each of the 99 quantitative ( $0.2 \text{ m}^2$ ) samples.

Four curves – linear, exponential, logarithmic, and power – were calculated for all sets of data for the biometrical relations in order to find the best fit (the highest coefficient of determination). The programme used applied the least-squares method, either to the original data (straight line, logarithmic curve) or to the transformed data (exponential curve, power curve). Confidence intervals of the mean were calculated on

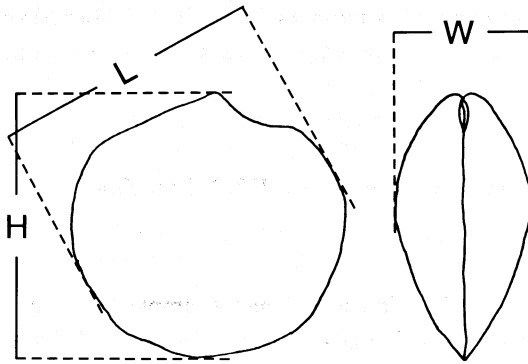


Fig. 4. Diagram showing length (L), height (H), and width (W) measurements made on the shells of *Lucinoma borealis*.

the 95% level, and the significance of the results of the covariance analyses was tested on the 0.05 level.

## RESULTS

### SEDIMENT, TEMPERATURE, AND SALINITY

The results of the analyses of grain-size distribution and  $\text{CaCO}_3$  content of the sediment have been described in detail in Tunberg (1981). The sediment of sub-areas A, B, C, and to a great extent also D and E, consisted of coarse and clean shell sand, while F to I consisted of finer and darker sand. The sediment of sub-areas F and G was finer than that of sub-areas H and I, with H coarser than I.

The water temperature during the survey period is presented in Fig. 5. The lowest and

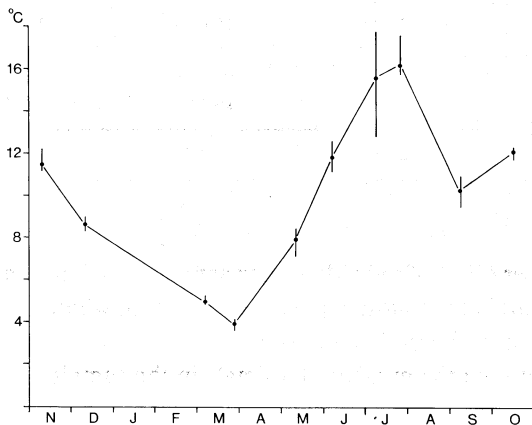


Fig. 5. Average water temperatures at Eggholmane on the sampling dates between November 1975 and October 1976: bars show the temperature range between the nine sub-areas.

highest temperatures were noted in sub-area A; 3.6 °C (25 March) and 17.7 °C (6 July), respectively. During the winter, the temperature was relatively homogeneous over the whole survey area, whereas during the summer the deepest sub-areas (F–I) were considerably colder than the more shallow ones. In July these deep areas had an average temperature of 13.6 °C, the others 17.7 °C.

The salinity remained fairly constant ( $\approx 33\%$ ) throughout the sampling period.

#### DISTRIBUTION

The number of animals found in each of the 99 samples of 0.2 m<sup>2</sup> is shown in Fig. 3, and the average number of individuals in each sub-area in Table II. Most specimens were found in the deep sub-areas (with fine sediment) G, F, I, and H (in decreasing order). In sub-area G the sediment consisted of fine to very coarse sand, with a median grain-size diameter of  $\approx 0.35$  mm in the surface layer (0–40 mm) (see Fig. 4 and Table 2 in Tunberg, 1981). In shallow water (A–E) the median grain-size diameter in the surface layer (0–40 mm), varied between  $\approx 0.70$  and 1.25 mm, and the corresponding values in the deep sub-areas (F–I) were between  $\approx 0.30$  and 0.50 mm.

TABLE II

Density and biomass (ash-free dry weight, AFDW, soft parts) of *Lucinoma borealis* in the nine sub-areas and totally: C.I., 95% confidence intervals.

Sub-area	Area (m <sup>2</sup> )	Ind. · 0.2 m <sup>-2</sup>	± C.I.	AFDW mg · 0.2 m <sup>-2</sup>	± C.I.
A	2075	2.8	2.2	228	177
B	400	1.5	2.2	42	66
C	2200	12.4	5.5	875	492
D	1525	8.7	3.6	517	240
E	1625	8.0	5.0	577	382
F	3550	43.9	15.6	1170	327
G	3525	56.2	15.7	1093	327
H	2750	28.1	16.7	884	364
I	3250	37.9	10.5	903	196
Total	20900	22.2	5.4	690	116

The greatest number (100) of individuals per sample of 0.2 m<sup>2</sup> was found in sample G7 (8.7 m water depth) in the southern part of sub-area G, where the median grain-size diameter was 0.38 mm in the 0–40 mm layer.

The correlation between the number of animals in the samples and the water depth at the sampling site (Table III) was positive and high, especially when all 99 samples were included in the analysis.

An analysis between number of animals per sample and the median grain-size

TABLE III

Correlation coefficients ( $R$ ) between number of individuals in the quantitative ( $0.2 \text{ m}^2$ ) samples and water depth where the samples were collected and average length of the shells: the analysis was also executed for shallow water (sub-areas A-E) and deep water (sub-areas F-I) separately;  $N$ , number of samples.

	Depth		Length	
	$N$	$R$	$N$	$R$
Shallow (A-E)	55	0.43	39	0.10
Deep (F-I)	44	0.23	42	-0.62
Totally	99	0.74	81	-0.62

diameter (in different sediment depths) showed a high negative correlation, however, (Table IV), which indicates that the finer the sediment the more animals found in the samples.

TABLE IV

Correlation coefficients between grain-size distribution (median value) in the 14 cores (all except 2 and 16 in Fig. 2) and the number of specimens in the quantitative sample taken closest to the respective core (A), and the average number of specimens in 2-11 substratum samples taken close around each core (B): the variation in the number was due to the difference in number of samples taken close to each core.

Depth (mm)	A	B
0- 40	-0.67	-0.66
40- 80	-0.59	-0.47
80-120	-0.39	-0.35
120-160	-0.61	-0.45

#### SIZE COMPOSITION

The shell length distribution of the animals in the quantitative samples taken in shallow water (A-E) is shown in Fig. 6, and that of deep water (G and I) in Fig. 7. It can be seen that there was a different size composition in these two areas. In shallow water individuals were generally bigger than those from deeper water. This is clearly shown in Fig. 8, where the average shell length of the specimens in each sample of  $0.2 \text{ m}^2$  is given. The average length of 373 specimens from the shallow sub-areas (A-E) was  $20.6 (\text{SD} \pm 3.6) \text{ mm}$ , and the corresponding length for 1834 specimens from the deep sub-areas (F-I) was  $15.9 (\text{SD} \pm 2.7) \text{ mm}$ .

The correlation analysis between number of individuals of the samples and the mean shell length of the animals in these samples (Table III) indicates that in deep water the more individuals per sample the smaller the average length. In shallow water there was however, no correlation. It was not possible to separate year classes by the method of

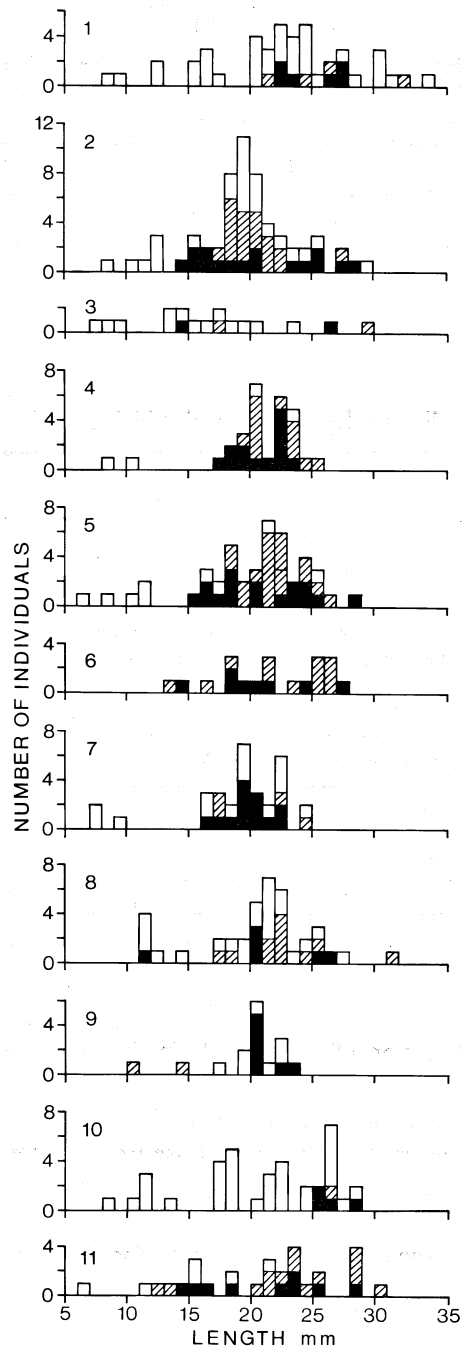


Fig. 6. Histograms of shell length plotted against numbers of specimens in each ( $5 \times 0.2 \text{ m}^2$ ) of the 11 collections made regularly between November 1975 and October 1976 in the five shallow sub-areas A-E: see Fig. 7 for explanation of shading.



Harding (1949) and Cassie (1954). The size distribution of sub-areas G and I particularly indicates that there was no noticeable shell growth during this 1-yr study period.

The biggest specimen that was found was 34.3 mm long (not identified to sex). The biggest female (32.4 mm) was found in sub-area C, and the biggest male (28.6 mm) in sub-area E.

#### BIOMASS

The biomass from each sub-area, and the whole sampling area, expressed as mg AFDW of the soft parts per 0.2 m<sup>2</sup> (Table II) was calculated from the relationship between length and AFDW in Table VI. The highest values were found in sub-areas F and G, followed by I and H, all in deep water with fine sediment. The abundance in sub-area C was rather low, but the biomass was high because of the size of the animals from this area (cf. also the other shallow sub-areas).

#### CONDITION

The condition of *L. borealis* during different parts of the year was expressed by the following equation,

$$\frac{\log DW}{L} \times 100,$$

where DW is dry weight of the soft parts in mg, and L is the shell length in mm. These relationships are presented in Fig. 9. Condition reached a maximum in March–April in both shallow (A–E) and deep (G) water. In shallow water minimum values were noted in late July and in August, but it was also low in November in sub-areas A–E, and in November–December in sub-area C. In deep water (sub-area G) the lowest value was noted in the beginning of June, but there were also pronounced drops in December, and in late July and September.

#### ORGANIC MATTER

The percentage of AFDW (organic matter) in relation to DW was calculated separately for shallow and deep water animals (Fig. 10). In shallow water the organic content of the soft parts was high from December to May, and also in late July. In deep water there was a continuous increase during the spring, followed by a pronounced drop in June–July, an increase in late July, and thereafter a drop again in September, followed by another increase in October.

As can be seen in Fig. 10, the fluctuations in the organic content of deep-water individuals were more distinct than in those from shallow water.

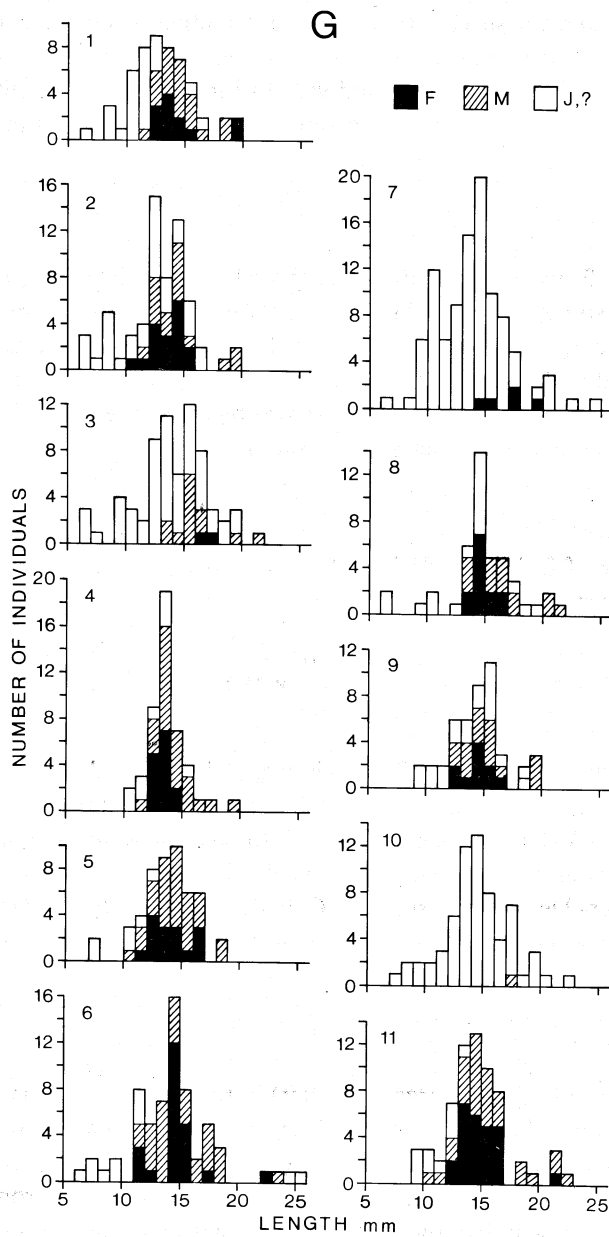


Fig. 7. Histograms of shell length plotted against numbers of specimens in each (0.2 m<sup>2</sup>) of the 11 collections made regularly in the deep sub-areas G (see above) and I (see opposite), between November 1975 and October 1976: F, females; M, males; J and ?, juveniles and individuals not identified to sex.

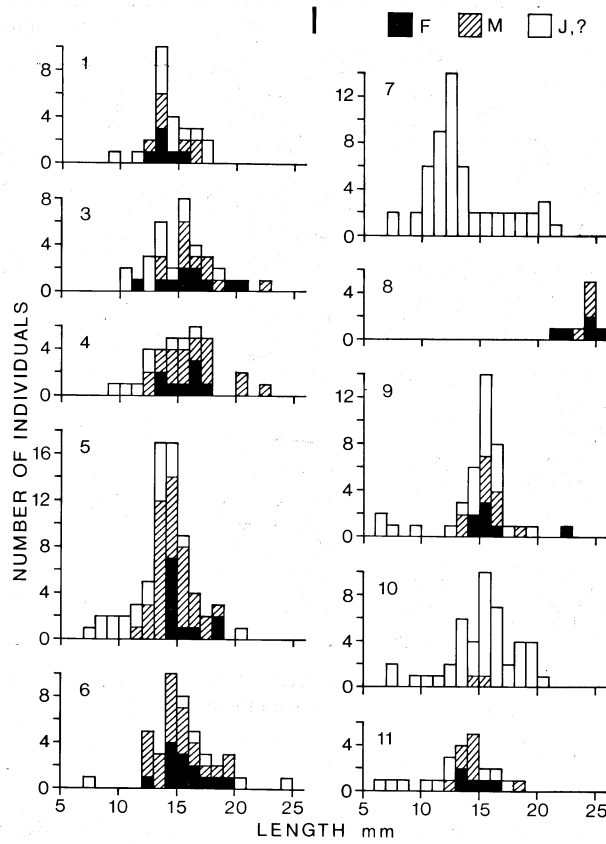


Fig. 7, continued.

## REPRODUCTION

When ripe the gonads of *L. borealis* are very swollen, nearly round in shape, and after spawning they are thin and almost transparent. In connection with the sex-determination, the degree of development of the gonads was graded from 0 (spent) to 5 (completely full of ripe eggs/sperm).

The results for shallow water (A–E and C) and deep water (G and I) are presented in Fig. 11. The situation in the two deep sub-areas was similar; sharp drops in the beginning of June and in September, with a strong increase in July. There were also relatively low values at the turn of the months January–February, especially in sub-area G. After this drop there was a recovery again up to late May. The situation in shallow water was more diffuse. When all sub-areas (A–E) were put together, the only sharp drop was noted in September, and the highest values were recorded for March, April, and May. There were also weak drops in July and in late January, but these were not nearly as pronounced as the ones in deep water. The sharp drops in June and September in deep water may, however, also be detected in sub-area C, but here the drops occurred

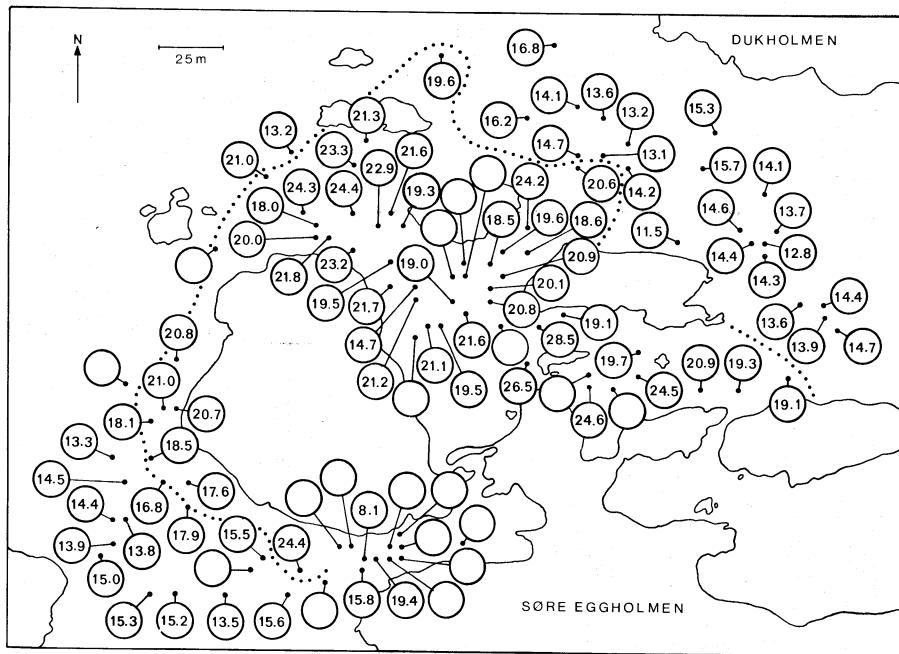


Fig. 8. Average shell length of all animals collected in each of the 99 samples of 0.2 m<sup>2</sup>: the dotted line shows the approximate border between the two size groups.

in July and September. The recovery between these two drops was also low and diffuse in sub-area C.

The sex-distribution of the different collections and different size classes is shown in the histograms of Figs. 6 and 7. The percentage of females in all samples from each sub-area (except F and H), shallow and deep water, and totally are presented in Fig. 12. In shallow water (A–E) there were 49.5% (101) females, in deep water (G and I) only 38.6%, and totally there were 41.7% (303) females of the 1399 adults ( $\geq 13$  mm) examined. In 672 of these it was, however, not possible to determine to sex (spent). The percentage of females of different size classes was also examined (Fig. 13). The smallest female found in sub-areas A–E was 11.8 mm long, and the smallest male was 10.9 mm. The corresponding values of the deep sub-areas G and I were 10.6 and 10.7 mm, respectively. In addition, 49 living individuals, collected in July 1981 in sub-area G, were also examined; the smallest female was 13.3 mm and the smallest male was 12.0 mm. The data indicate that maturation generally occurs at a shell length between 10 and 13 mm.

The egg diameter was also examined in two ripe animals collected in July 1975 in sub-area G. The mean diameter of five measurements on each of 166 randomly selected eggs was calculated; the mean diameter was  $123.75$  (C.I.  $\pm 1.59$ )  $\mu\text{m}$ .

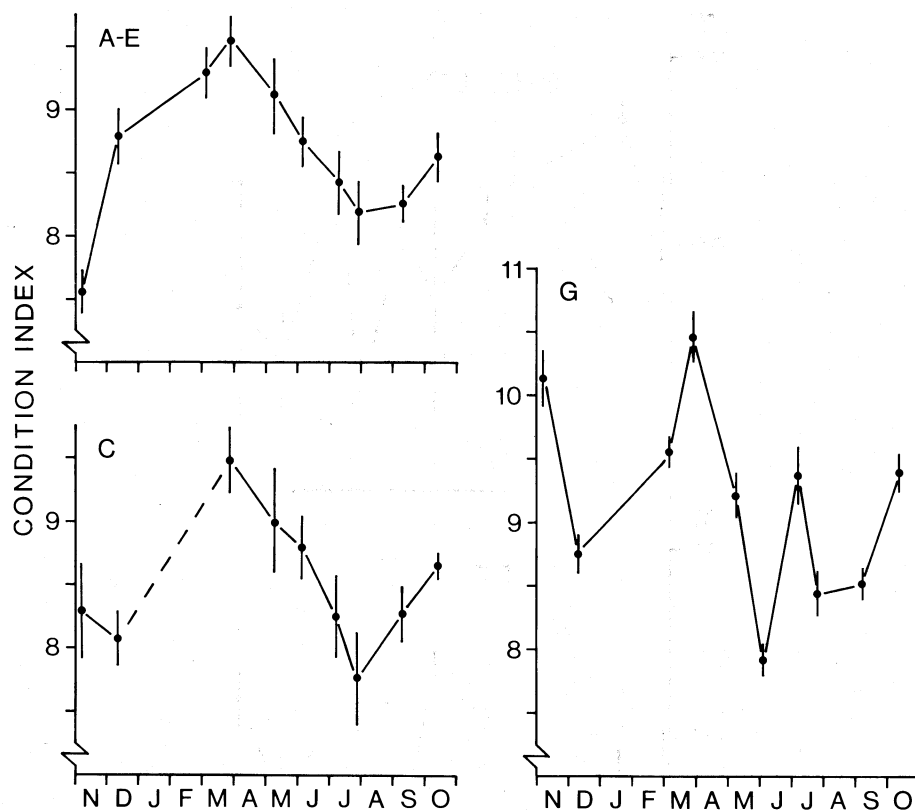


Fig. 9. Condition index, with 95% confidence intervals, expressed as  $[\log \text{DW (mg)/shell length (mm)}] \times 100$ , calculated for all the shallow sub-areas (A-E) together, sub-area C alone, and the deep sub-area G, during the study year 1975-1976: only animals  $\geq 13$  mm were examined.

#### BIOMETRY

The relationship between length and the two dimensions height and width were calculated for shallow and deep water separately (Table V). The differences between the power curves and the straight lines were rather small, and both are, therefore, presented in Table V. The analyses of covariance showed that there were no significant differences between shallow and deep water. The relationships between length-DW, length-AFDW, and DW-AFDW, expressed by means of power curves, are given in Table VI.

#### DISCUSSION

As mentioned in Tunberg (1982) *L. borealis* is a characteristic species of this survey area. Of the 75 species of macrofauna found here, *L. borealis* comprised 41.4% of the

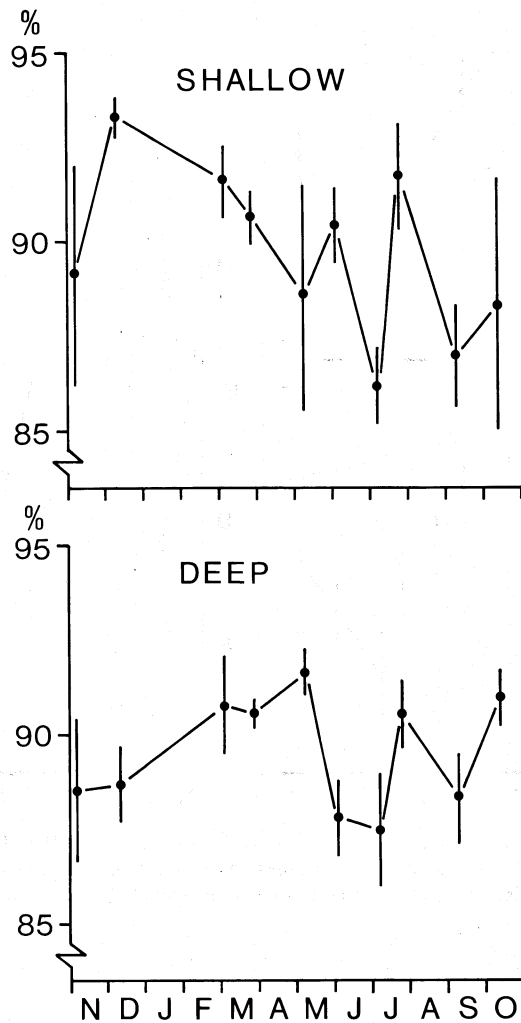


Fig. 10. Percentage of organic matter in the soft parts, with 95% confidence intervals, in shallow water (sub-areas A-E) and in deep water (sub-area G) during the year studied, 1975-1976.

individuals. To my knowledge it has not been recorded in such high densities before, although it has been recorded in numerous studies of the macrofauna (e.g. Gage, 1972; Lie, 1978). Since *L. borealis* is a deep burrower, there is reason to suspect that the grabs used (like the Van Veen grab) do not sample deep enough to get all the *L. borealis* in the area sampled.

The distributional pattern of *L. borealis* within the survey area indicates that it prefers the finer sediments of the deep ( $\approx 8-13$  m) sub-areas F-I. This is further suggested by the correlation analysis of Table IV. The importance of sediment structure for the

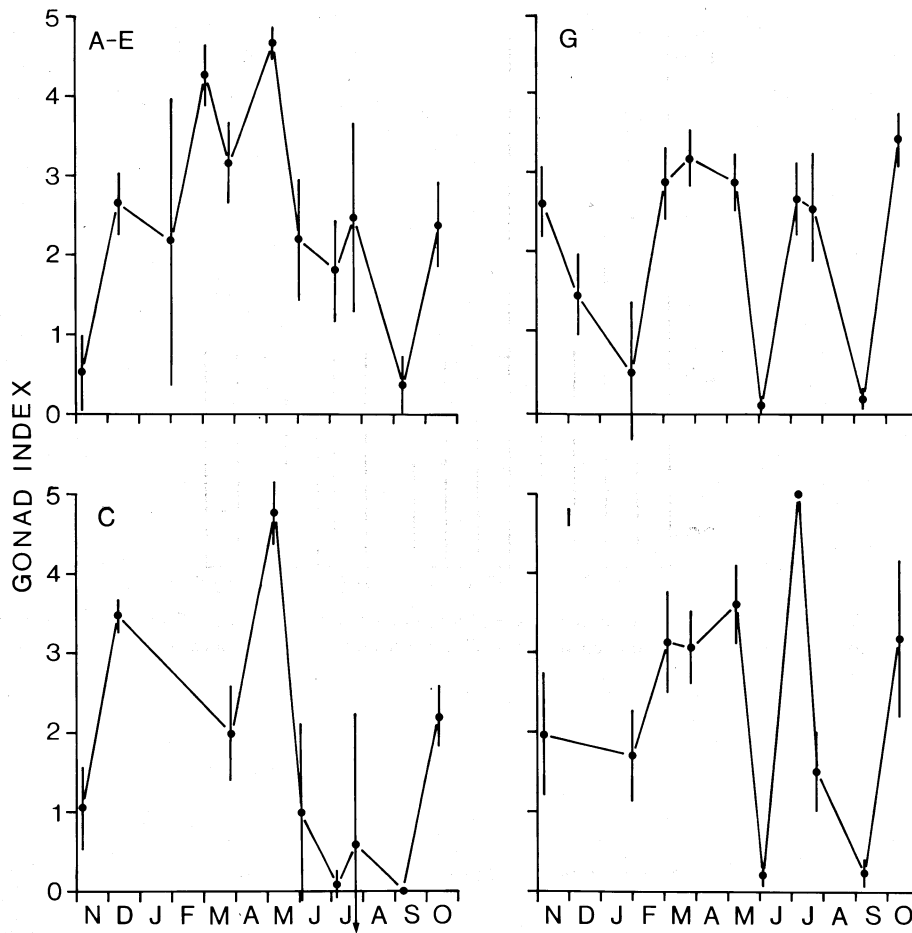


Fig. 11. Gonad index, graded from 0 (spent†) to 5 (ripe), with 95% confidence intervals for all adults ( $\geq 13$  mm) in the shallow sub-areas A-E together, sub-area C alone, and the two deep sub-areas G and I, during 1975-1976.

TABLE V

The relationship between length of the shell and height and width expressed by both power curves (P) ( $Y = aX^b$ ) and linear regressions (L) ( $Y = a + bX$ ): these relationships were also calculated for shallow water (sub-areas A-E) and deep water (sub-areas G-I) separately; N, number of data pairs.

	Height				Width				Curve
	N	a	b	R <sup>2</sup>	N	a	b	R <sup>2</sup>	
Shallow	131	0.866	1.023	0.993	130	0.242	1.233	0.947	P
		-0.186	0.938	0.991		-2.162	0.599	0.926	L
Deep	150	0.820	1.041	0.988	150	0.261	1.207	0.937	P
		-0.304	0.937	0.984		-1.083	0.532	0.901	L
Totally	500	0.847	1.028	0.992	500	0.288	1.173	0.940	P
		-0.250	0.933	0.991		-1.712	0.578	0.947	L

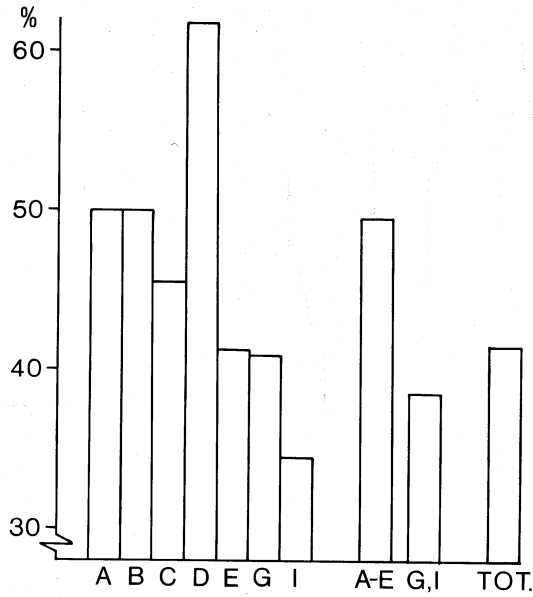


Fig. 12. The percentage of females in animals  $\geq 13$  mm in each sub-area (except F and H), the shallow sub-areas A-E together, the two deep sub-areas G and I together, and all collected specimens (TOT.).

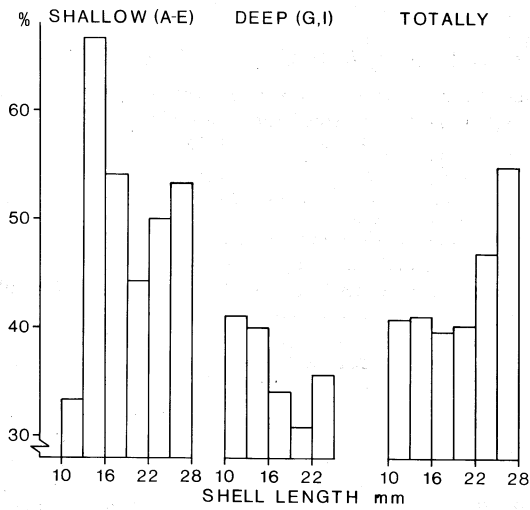


Fig. 13. The percentage of females in different size classes in shallow water (A-E), deep water (G, I), and totally.



TABLE VI

The relationships between length of the shell and dry weight soft-parts (DW) and ash-free dry weight soft parts (AFDW), and between DW-AFDW, expressed by means of power curves,  $Y = aX^b$ :  $N$ , number of data pairs.

	$N$	$a$	$b$	$R^2$
Length-DW	845	$3.66 \times 10^{-6}$	3.237	0.900
Length-AFDW	840	$3.50 \times 10^{-6}$	3.211	0.902
DW-AFDW	859	0.888	1.002	0.989

distribution of macrofauna has been shown by numerous authors (cf. Gray, 1974). This indication should be treated with caution, however (cf. Buchanan, 1963; Glemarec, 1973; Whitlatch, 1981).

A survey by Jackson (1973) on the ecology of molluscs of *Thalassia* communities in Jamaica implied that the distribution of the Lucinacea was not limited by physical characteristics of the sediment. In the present survey environmental stress was more accentuated in the shallow sub-areas than the deeper ones. Other factors like inter-specific competition, predation etc. may also be of major importance (cf. Jones, 1950).

In the area studied, where two groups of species with different distribution were found (Tunberg, 1981, 1982), *Lucinoma borealis* was associated with the following species (in decreasing order of correlation); *Ophiura albida*, *Pectinaria auricoma*, *Notomastus latericeus*, *Thyasira flexuosa*, *Dosinia lupinus*, *Astarte montagui*, *Astropecten irregularis*, *Corbula gibba*, and *Edwardsia tuberculata*.

According to Allen (1958) the Lucinacea have successfully adapted themselves to conditions in which food is at a minimum and where the oxygen content of the substratum is very low. In this area the comparably rich macrofauna, however, indicates that the food conditions were good, and the oxygen levels adequate.

Jackson (1972) found that (in Jamaica) the lucinids and other infaunal bivalves were larger in areas where they were most abundant. In the survey area at Eggholmane, however, there was a strong negative correlation between abundance and size of *Lucinoma borealis* (Table III). The distribution of the two size-groups of *L. borealis* agrees well with the distributional patterns of the two species groups of macrofauna found in this area (Tunberg, 1982). Whether or not this implies that the name *L. borealis* includes more than one species in this area is impossible to say with certainty from the information of this survey. The differences in reproductive patterns between shallow and deep water may be of great importance to these size differences. A migration towards shallow water with increasing age is not probable because of, among other things, the distance and topographical barriers between these areas.

The constant size composition during the whole survey year, especially distinct in the deep sub-areas, was exceptional. Because of the reproductional patterns it was impossible to distinguish separate year classes.

It is possible, but not very likely, that *L. borealis* grows extremely slowly and that this growth is not apparent during a 1-yr period. Another more probable reason is that the population in the deep sub-areas consisted of one strong year-class, and that the high densities prevented the establishment of new year-classes. Because of these high densities the intraspecific competition (food and space) was probably considerable, with reduced growth as one result. Curtis & Petersen (1977) also found great differences in the size composition of *Macoma baltica* in samples taken only a few metres apart in the Disko Bugt, Greenland. According to these authors settling behaviour and competition between year classes may explain the small scale heterogeneity.

Both the biomass and abundance figures indicate that *L. borealis* was a very important species within the area studied. Because of its sheltered position in the substratum, adults are not reached by many predators. A great amount of empty large shells bored by the gastropod *Lunatia intermedia* were, however, found especially in the deep sub-areas.

According to Thorson (1946) nothing is known about the reproduction of *Lucinoma borealis*. Lebour (1938) in her study on lamellibranch larvae from Plymouth, states that ripe eggs and sperm were found in March and April. Pelseneer (1926) writes that *Lucina lactea* attaches stalked egg capsules to the bottom. Whether or not *Lucinoma borealis* does the same was not investigated in this study.

The condition index may often be used as an indication of spawning (Ansell & Loosmore, 1963; Moore & Lopez, 1970). According to the joint data, spawning occurred several times during the year. In the deep sub-areas (G and I) there was a good correlation between condition index and gonad index. This indicates that spawning occurred in June, August–September, and possibly also in January–February. The organic content (Fig. 10) was, however, lower in the beginning of June than was expected. In the shallow sub-areas the situation was less clear (with wide confidence intervals), probably an effect of the less stable situation here. Spawning obviously occurred irregularly during the whole sampling period, but peaked in late summer and early fall (July–September).

The size of the ripe eggs (124  $\mu\text{m}$ ) also indicates a lecithotrophic development. Rees (1950) described the shelled larvae found in the plankton.

Provided that the theory of two species is excluded, the different sex-composition in shallow and deep water is hard to explain from the data obtained in this survey. According to Fig. 13, there is no indication of a migration of females from deep to shallow water with increasing length. Even though the females reach a maximum length somewhat larger than the males, this does not explain the differences between deep and shallow water. In this connection it is also important to remember that many animals were not identified to sex at all, which makes the data more uncertain. Unfortunately it is not possible to draw any certain conclusions about the differences in sex-composition; further thorough studies have to be done on this problem.

The biometric relations show that the shell of *L. borealis* grows allometrically, and that the allometry is somewhat different in different size-classes. This is, however, not

unusual. Ohba (1959) e.g. found great differences in the H/L, W/H, and W/L ratios for different size-classes of *Tapes japonica*. The covariance analyses indicating that there was no difference in shape of the shell of *Lucinoma borealis* between the shallow and deep sub-areas, contradict the assumption that it is a question of two different species in the area studied.

#### ACKNOWLEDGEMENTS

I wish to express my gratitude to Dr. T. Brattegard for valuable advice during the planning and field work and for critically reading the manuscript. I am also grateful to Professor J.-O. Strömberg who kindly provided me with facilities at Kristineberg Marine Biological Station for laboratory treatment of the material, and to Dr. K. W. Ockelmann, for valuable advice.

Part of this study was financed by a grant from the Nordic Council for Marine Biology.

#### REFERENCES

- ALLEN, J. A., 1953. Function of the foot in the Lucinacea (Eulamellibranchia). *Nature (London)*, Vol. 171, p. 1117 only.
- ALLEN, J. A., 1958. On the basic form and adaptations to habitat in the Lucinacea (Eulamellibranchia). *Phil. Trans. R. Soc. Ser. B.*, Vol. 241, pp. 421-484.
- ANSELL, A. D. & F. A. LOOSMORE, 1963. Preliminary observations on the relationship between growth, spawning and condition in experimental colonies of *Venus mercenaria* L. *J. Cons., Cons. Int. Explor. Mer.*, Vol. 28, pp. 285-294.
- BUCHANAN, J. B., 1963. The bottom fauna communities and their sediment relationships off the coast of Northumberland. *Oikos*, Vol. 14, pp. 154-175.
- CASSIE, R. M., 1954. Some uses of probability paper in the analysis of size frequency distributions. *Aust. J. Mar. Freshwater Res.*, Vol. 5, pp. 513-522.
- CRISP, D. J., 1971. Energy flow measurements. In *Methods for the study of marine benthos*, edited by N. A. Holme & A. D. McIntyre, IBP Handbook No. 16, Blackwell Scientific Publishers, Oxford, pp. 197-279.
- CURTIS, M. A. & G. H. PETERSEN, 1977. Size-class heterogeneity within the spatial distributions of subarctic marine benthic populations. *Astarte*, Vol. 10, pp. 103-105.
- DALL, W. H., 1901. Synopsis of the Lucinacea and of the American species. *Proc. U.S. Nat. Mus.*, Vol. 23, pp. 779-834.
- FORBES, E. & S. HANLEY, 1853. *A history of the British marine Mollusca, and their shells.*, Vol. 2. John van Voorst, London, 557 pp.
- GAGE, J., 1972. Community structure of the benthos in Scottish sea-lochs. I. Introduction to species diversity. *Mar. Biol.*, Vol. 14, pp. 281-297.
- GLEMAREC, M., 1973. The benthic communities of the European north Atlantic continental shelf. *Oceanogr. Mar. Biol. Annu. Rev.*, Vol. 11, pp. 263-289.
- GRAY, J. S., 1974. Animal-sediment relationships. *Oceanogr. Mar. Biol. Annu. Rev.*, Vol. 12, pp. 223-261.
- HAAS, F., 1938. *Bronn's Klassen und Ordnungen des Tierreichs, Mollusca* Vol. 3, Abt. 3 *Bivalvia*, Teil II, Lief. 2, pp. 209-466.
- HARDING, J. P., 1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. *J. Mar. Biol. Assoc. U.K.*, Vol. 28, pp. 141-153.
- JACKSON, J. B. C., 1972. The ecology of the molluscs of *Thalassia* communities, Jamaica, West Indies. II. Molluscan population variability along an environmental stress gradient. *Mar. Biol.*, Vol. 14, pp. 304-337.

- JACKSON, J.B.C., 1973. The ecology of molluscs of *Thalassia* communities, Jamaica, West Indies. I. Distribution, environmental physiology, and ecology of common shallow-water species. *Bull. Mar. Sci.*, Vol. 23, pp. 313-350.
- JEFFREYS, J.G., 1863. *British conchology, Vol. II, Marine shells*. John van Voorst, London, 466 pp.
- JENSEN, A. & R. SPÄRCK, 1934. Bløddyr II. Saltvandmuslinger. *Danm. Fauna*, Vol. 40, 208 pp.
- JONES, N.S., 1950. Marine bottom communities. *Biol. Rev.*, Vol. 25, pp. 283-313.
- LEBOUR, M.V., 1938. Notes on the breeding of some lamellibranchs from Plymouth and their larvae. *J. Mar. Biol. Assoc. U.K.*, Vol. 23, pp. 119-144.
- LIE, U., 1978. The quantitative distribution of benthic macrofauna in Fana fjorden, western Norway. *Sarsia*, Vol. 63, pp. 305-316.
- MOORE, H.B. & N.N. LOPEZ, 1970. A contribution to the ecology of the lamellibranch *Dosinia elegans*. *Bull. Mar. Sci.*, Vol. 20, pp. 980-986.
- OCKELMANN, K.W., 1958. Marine Lamellibranchiata. (In the zoology of east Greenland). *Medd. Grønland*, Vol. 122(4), 256 pp.
- OHBA, S., 1959. Ecological studies in the natural population of a clam, *Tapes japonica*, with special reference to seasonal variations in the size and structure of the population and to individual growth. *Biol. J. Okayama Univ.*, Vol. 5, pp. 13-42.
- PELSENEER, P., 1926. Notes d'embryologie malacologique. Ponte et développement de *Cypraea europaea*, *Triforis perversa* et *Lucina lactea*. *Bull. Biol. Fr. Belg.*, Vol. 60, pp. 88-112.
- REES, C.B., 1950. The identification and classification of lamellibranch larvae. *Hull. Bull. Mar. Ecol.*, Vol. 3, pp. 73-104.
- SARS, G.O., 1878. *Bidrag til kundskaben om Norges arktiske fauna. I. Mollusca Regionis Arcticae Norvegiae*. A.W. Brøgger, Christiania, 466 pp.
- STOLL, E., 1938. Sur le mode de locomotion de quelques mollusques marins. *Trav. Stn. Biol. Roscoff*, Vol. 16, pp. 5-29.
- TEBBLE, N., 1966. *British bivalve seashells*. British Museum (Natural History), London, 212 pp.
- THORSON, G., 1946. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the Sound (Øresund). *Meddr. Kommn. Havunders.*, Vol. 4(1), 523 pp.
- TUNBERG, B., 1981. Two bivalve communities in a shallow and sandy bottom in Raunefjorden, western Norway. *Sarsia*, Vol. 66, pp. 257-266.
- TUNBERG, B., 1982. Quantitative distribution of the macrofauna in a shallow, sandy bottom in Raunefjorden, western Norway. *Sarsia*, Vol. 67, pp. 201-210.
- TUNBERG, B., 1983. A simple, diver-operated suction sampler for quantitative sampling in shallow, sandy bottoms. *Ophelia*, Vol. 22, pp. 185-188.
- WHITLATCH, R.B., 1981. Animal-sediment relationships in intertidal marine benthic habitats: some determinants of deposit-feeding species diversity. *J. Exp. Mar. Biol. Ecol.*, Vol. 53, pp. 31-45.